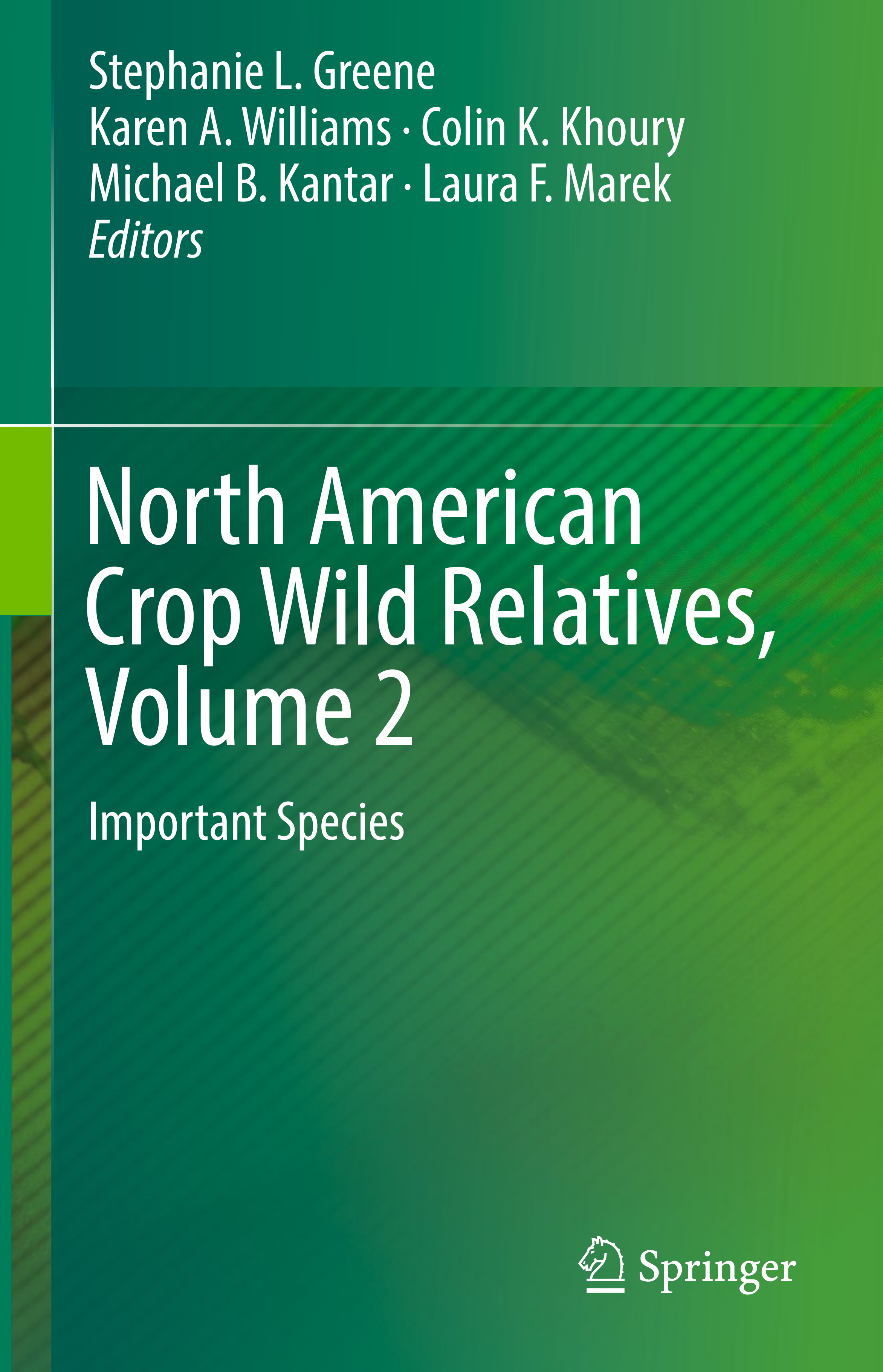

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North American Crop Wild Relatives, Volume 2

Important Species

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Editors
Stephanie L. Greene
USDA, Agricultural Research Service
Center for Agricultural Resources
Research, National Laboratory
for Genetic Resources Preservation
Fort Collins, CO, USA

Karen A. Williams
USDA, Agricultural Research Service
Beltsville Agricultural Research
Center, National Germplasm
Resources Laboratory
Beltsville, MD, USA

Colin K. Khoury
USDA, Agricultural Research Service
Center for Agricultural Resources
Research, National Laboratory
for Genetic Resources Preservation
Fort Collins, CO, USA

International Center for Tropical
Agriculture (CIAT)
Cali, Colombia

Michael B. Kantar
Tropical Plant and Soil Science
University of Hawaii at Manoa
Honolulu, HI, USA

Laura F. Marek
Department of Agronomy/North Central
Regional Plant Introduction Station
Iowa State University
Ames, IA, USA

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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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Fort Collins, CO, USA	Stephanie L. Greene
Beltsville, MD, USA	Karen A. Williams
Fort Collins, CO, USA	Colin K. Khoury
Honolulu, HI, USA	Michael B. Kantar
Ames, IA, USA	Laura F. Marek

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Reviewers

Brian S. Baldwin Mississippi State University, Mississippi, MS, USA

Lynn Bohs University of Utah, Salt Lake City, UT, USA

Clarice Coyne USDA Agricultural Research Service, Pullman, WA, USA

Daniel Debouck International Center for Tropical Agriculture, Cali, Colombia

Hannes Dempewolf Crop Trust, Bonn, Germany

Chad Finn USDA Agricultural Research Service, Corvallis, OR, USA

Candice Gardner USDA Agricultural Research Service, Ames, IA, USA

Thomas Kono University of Minnesota, St Paul, MN, USA

Richard Manshardt University of Hawaii at Manoa, Honolulu, HI, USA

Rick Miller Hammond, LA, USA

Tim D. Phillips University of Kentucky, Lexington, KY, USA

Chris Richards USDA Agricultural Research Service, Fort Collins, CO, USA

Kanin Routsen Tucson, AZ, USA

Gerald Seiler USDA Agricultural Research Service, Fargo, SD, USA

Ryan Warner Michigan State University, East Lansing, MI, USA

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

Carlos I. Cruz-Cárdenas, Moisés Cortés-Cruz, Candice A. Gardner, and Denise E. Costich

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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C. I. Cruz-Cárdenas (✉)
Laboratorio de Recursos Genéticos Agrícola-Forestal, Sección Semillas Ortodoxas,
Centro Nacional de Recursos Genéticos, Tepatitlán de Morelos, Jalisco, Mexico
e-mail: cruz.ivan@inifap.gob.mx

M. Cortés-Cruz
Laboratorio de ADN y Genómicas, Centro Nacional de Recursos Genéticos,
Tepatitlán de Morelos, Jalisco, Mexico
e-mail: cortes.moises@inifap.gob.mx

C. A. Gardner
USDA-ARS, North Central Regional Plant Introduction Station, Ames, IA, USA

Iowa State University, Ames, IA, USA
e-mail: candice.gardner@ars.usda.gov

D. E. Costich
Centro Internacional de Mejoramiento de Maíz y Trigo (CIMMYT),
El Batán, Texcoco, Mexico
e-mail: d.costich@cgiar.org

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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

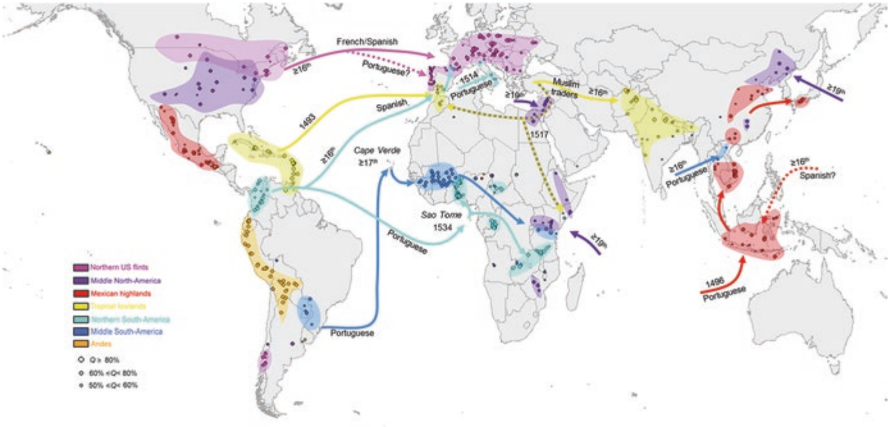

Fig. 1.1 Map of hypothetical major routes of global maize diffusion out of the Americas (Mir et al. 2013)

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.

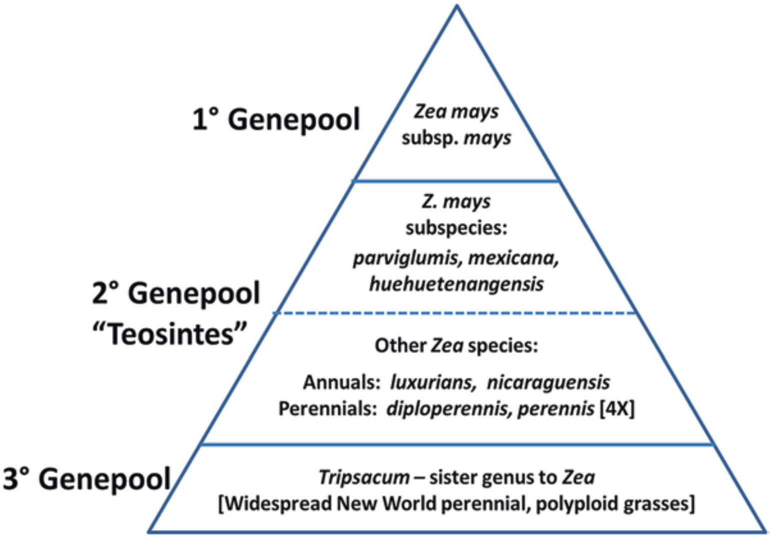

Fig. 1.3 Genepool classifications of maize and its wild relatives

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

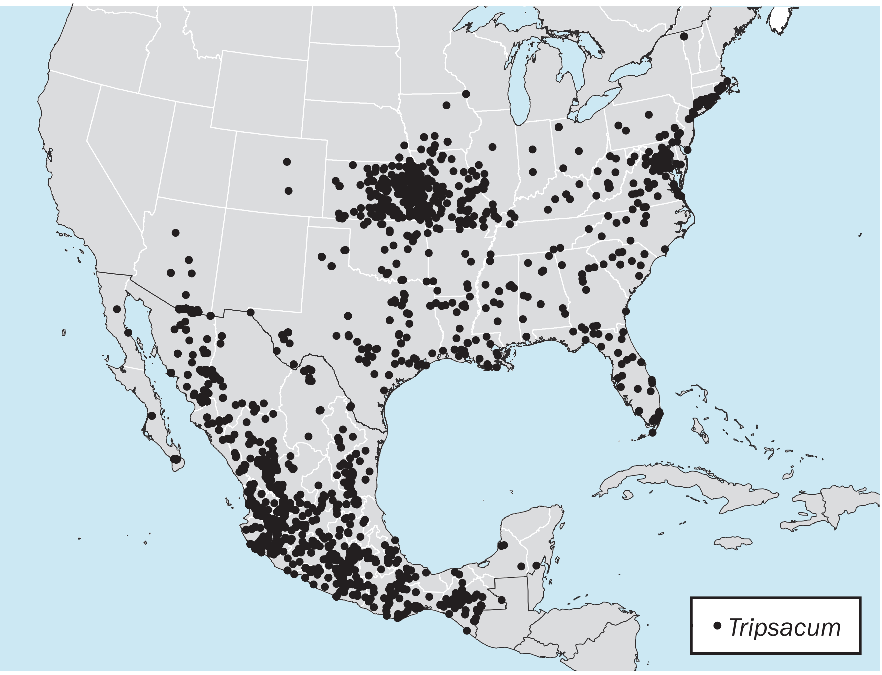

Fig. 1.4 Map of center of diversity and widespread distribution for *Tripsacum* L. in North America

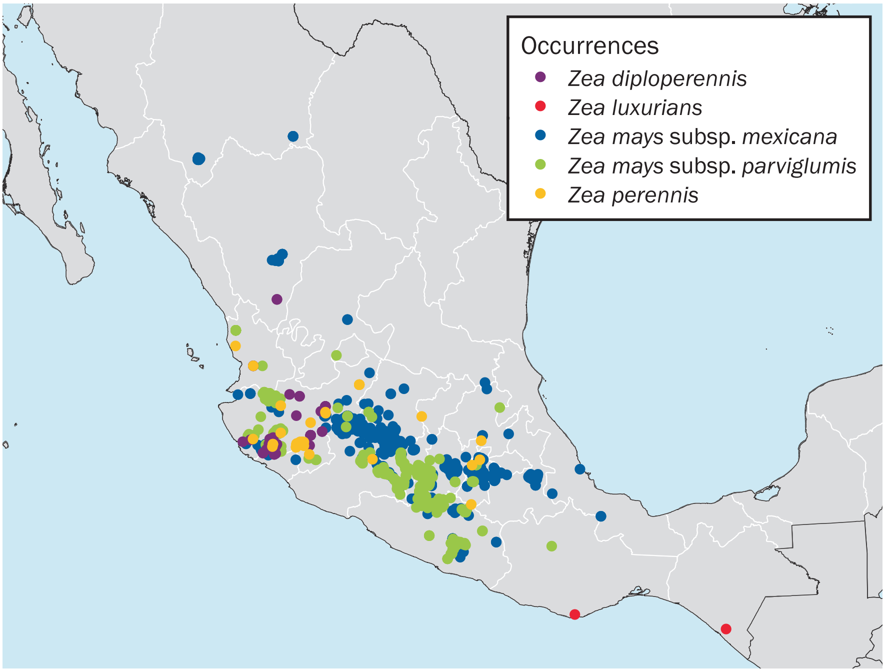

Fig. 1.5 *Zea* L. center of diversity and widespread distribution map in North America

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).

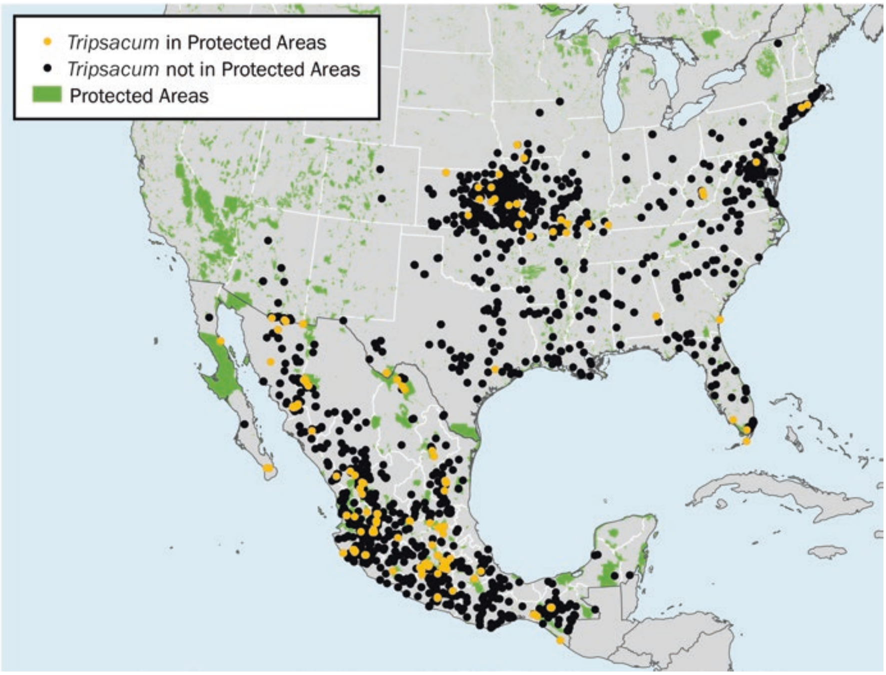

Fig. 1.6 *Tripsacum* L. distribution map for in situ conservation status in North America. All *Tripsacum* individuals located inside and outside protected natural areas are shown

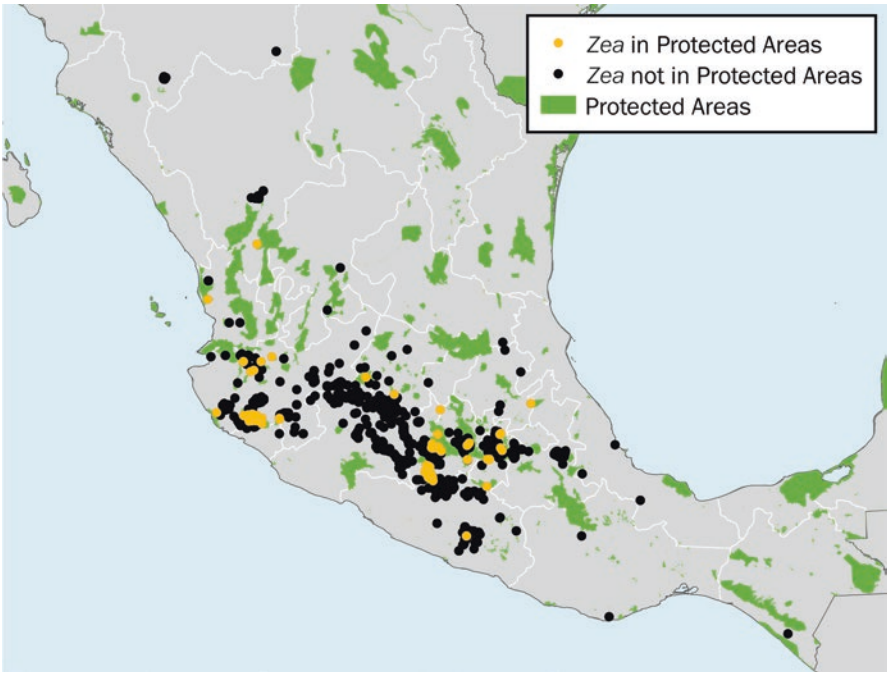

Fig. 1.7 *Zea* L. distribution map for in situ conservation status in North America. All *Zea* individuals located inside and outside protected natural areas are shown

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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Chapter 2
North American Wild Relatives of Grain Crops

David M. Brenner, Harold E. Bockelman, and Karen A. Williams

Abstract The wild-growing relatives of the grain crops are useful for long-term worldwide crop improvement research. There are neglected examples that should be accessioned as living seeds in gene banks. Some of the grain crops, amaranth, barnyard millet, proso millet, quinoa, and foxtail millet, have understudied unique and potentially useful crop wild relatives in North America. Other grain crops, barley, buckwheat, and oats, have fewer relatives in North America that are mostly weeds from other continents with more diverse crop wild relatives. The expanding abilities of genomic science are a reason to accession the wild species since there are improved ways to study evolution within genera and make use of wide gene pools. Rare wild species, especially quinoa relatives in North American, should be acquired by gene banks in cooperation with biologists that already study and conserve at-risk plant populations. Many of the grain crop wild relatives are weeds that have evolved herbicide resistance that could be used in breeding new herbicide-resistant cultivars, so well-documented examples should be accessioned and also vouchered in gene banks.

Keywords Gene pool · Germplasm · *Amaranthus* · *Avena* · *Chenopodium* · *Echinochloa* · *Hordeum* · *Panicum* · *Setaria*

D. M. Brenner (✉)
Department of Agronomy/North Central Regional Plant Introduction Station,
Ames, IA, USA
e-mail: dbrenner@iastate.edu

H. E. Bockelman
USDA, ARS National Small Grains Collection, Aberdeen, ID, USA
e-mail: harold.Bockelman@ars.usda.gov

K. A. Williams
USDA, Agricultural Research Service, Beltsville Agricultural Research Center,
National Germplasm Resources Laboratory, Beltsville, MD, USA
e-mail: karen.williams@ars.usda.gov

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2.1 Introduction

This chapter discusses a sample of the world's grain crops, concentrating on those that have close crop wild relatives (CWR) in North America. We hope that compiling this information will improve use and conservation of our North America plant genetic resources. The grain crops without close CWR in North America are mostly omitted from this chapter. There are excellent reviews of grain CWR published in the *Wild Crop Relatives* (Kole 2011) book series, so here we update and condense from a North American perspective. Floristic information about North America is compiled in the *Flora of North America* (FNA, Flora of North America Editorial Committee 1993), which also has good maps of distributions and for Mexico, in Villaseñor (2016). Summary information about threatened and endangered species status is available online at the NatureServe (2017) website. Also the GRIN (USDA, ARS 2017) website is valuable for updated and readily available CWR information.

2.2 Amaranth (*Amaranthus* L.)

2.2.1 Introduction

2.2.1.1 Origin of the Crop and Brief History of Use

Amaranth grain is harvested from broadleaf summer annual plants of New World origin. The crop was reviewed by Brenner et al. (2000), and the CWR were reviewed by Trucco and Tranel (2011). Amaranths in the form of ornamentals, vegetables, wild and weed plants, and grain types occur worldwide. The cultivated grain types have pale seeds, unlike their dark-seeded progenitors. Three grain species are grown: *Amaranthus caudatus* L., which originated in South America, and *Amaranthus cruentus* L. and *Amaranthus hypochondriacus* L., which originated in Mexico and Central America. Much of the amaranth grain processed in the United States originates in Himalayan India (personal communication Jonathan Walters, Nu-World Foods), although amaranth can be grown in many other parts of the world. The production methods in India are described by Bhatia (2005).

2.2.1.2 Cultivation

Amaranth, cultivated from the equator to the high latitudes of the temperate zone, is less limited by edaphic conditions than many crops and is also tolerant of drought and heat. Harvesting the small seeds is more easily accomplished in dry rather than humid conditions, making regions with dry harvest seasons favorable for grain production (Kauffman 1992). There is potential for new sophistication in amaranth plant breeding now that the genome is sequenced (Sunil et al. 2014), and improved laboratory plant handling techniques are available for making crosses (Stetter et al. 2016) and karyotyping (Tatum et al. 2005).

2.2.2 Crop Wild Relatives in North America

2.2.2.1 Gene Pools

Brenner et al. (2000) included 23 *Amaranthus* L. species in one combined primary (GP-1) and secondary (GP-2) gene pool for grain amaranths because the systematics and crossing compatibility information was too fragmented and contradictory for clear statements about crossing ability. We are parsing the gene pool differently here (Table 2.1) into GP-1, GP-2, and GP-3, after additional years of experience. The 23 *Amaranthus* species listed by Brenner et al. (2000) with some crossing ability are in subgenera *Acnida* and *Amaranthus* (Mosyakin and Robertson 2003) and are distinct from subgenus *Albersia*, in which the species are not known to cross with the grain amaranths. Most of these 23 species are native or naturalized in North America; only *Amaranthus celosioides* Kunth and *Amaranthus quitensis* Kunth are not native or naturalized but are included to completely represent the gene pools. The GP-1 CWR species are in the hybridus complex (Costea et al. 2001) and, using nomenclature adapted to conform to GRIN (USDA, ARS 2017), are the cultivated species *A. caudatus*, *A. cruentus*, *Amaranthus hybridus* L., and *A. hypochondriacus* and the wild species *Amaranthus powellii* S. Watson, *A. quitensis*, and *Amaranthus retroflexus* L. One rare and understudied species *Amaranthus wrightii* S. Watson may also be in GP-1 based on new DNA evidence (Stetter and Schmid 2017). The non-hybridus complex GP-2 allies have some history of crossing, many resulting in sterile F_1 hybrids. They include the remainder of the *Amaranthus* species listed by Brenner et al. (2000): *Amaranthus arenicola* I. M. Johnst., *Amaranthus australis* (A. Gray) J. D. Sauer, *Amaranthus brandegeei* Standl., *Amaranthus cannabinus* (L.) J. D. Sauer, *Amaranthus celosioides* Kunth, *Amaranthus dubius* Mart. ex Thell., *Amaranthus floridanus* (S. Watson) J. D. Sauer, *Amaranthus greggii* S. Watson, *Amaranthus palmeri* S. Watson, *Amaranthus scariosus* Benth., *Amaranthus spinosus* L., *Amaranthus torreyi* (A. Gray) Benth. ex S. Watson, *Amaranthus tuberculatus* (Moq.) J. D. Sauer, *Amaranthus viscidulus* Greene, and *Amaranthus watsonii* Standl. There are additional species in North America that may be in the GP-2 based on morphology but are understudied: *Amaranthus acanthobracteatus* Henrickson, *Amaranthus acanthochiton* J. D. Sauer, *Amaranthus chihuahuensis* S. Watson, *Amaranthus fimbriatus* (Torr.) Benth. ex S. Watson, *Amaranthus lepturus* S. F. Blake, *Amaranthus obcordatus* (A. Gray) Standl., *Amaranthus scleropoides* Uline & W. L. Bray, *Amaranthus tamaulipensis* Henrickson, and *Amaranthus ×tucsonensis* Henrickson. The morphology of *A. ×tuconensins* is especially similar to the species in the hybridus complex (Henrickson 1999), but in the interpretation of Stetter and Schmid (2017), they are not closely related. There are many reports of the GP-2 species crossing with GP-1 species (Brenner et al. 2000, 2013; Gaines et al. 2012), but Murray (1940a, b) presents especially thorough information about restoring fertility of sterile F1 plants with colchicine polyploidization. There is no report of species in the *Albersia* subgenus, which composes most of the genus with approximately 50 species, crossing with GP-1 or GP-2 species. These GP-3 species include some species, such as *A. tricolor*, that are cultivated as vegetables. Substantial systematics

Table 2.1 Germplasm accessions of *Amaranthus* species that are wild in North America

Species	Native	Naturalized	Accessions in the NPGS of any geographic origin[a]	Accessions in GENESYS of any geographic origin, excluding NPGS accessions[b]	Provisional gene pool of the grain amaranths	Distribution[c]
Amaranthus acanthobracteatus Henrickson	Yes		0	0	GP-2?	Northern Mexico
Amaranthus acanthochiton J. D. Sauer	Yes		2	0	GP-2?	Southwestern United States and northern Mexico
Amaranthus acutilobus Uline & W. L. Bray	Yes		2	5	GP-3	Southern Mexico
Amaranthus albus L.	Yes		7	27	GP-3	United States and Canada
Amaranthus arenicola I. M. Johnst.	Yes		7	0	GP-2	Central United States
Amaranthus australis (A. Gray) J. D. Sauer	Yes		2	1	GP-2	Caribbean basin wetlands
Amaranthus blitoides S. Watson	Yes		7	23	GP-3	Ubiquitous weed
Amaranthus blitum L.		Yes	10	62	GP-3	Domesticated and weedy forms, pantropical and European. The "emarginatus" type is not accessioned
Amaranthus brandegeei Standl.	Yes		0	0	GP-2	Mexico
Amaranthus brownii Christoph. & Caum	Yes		0	0	GP-3	Hawaii, very rare
Amaranthus californicus (Moq.) S. Watson	Yes		1	0	GP-3	Western United States and western Canada

(continued)

Table 2.1 (continued)

Species	Native	Naturalized	Accessions in the NPGS of any geographic origin[a]	Accessions in GENESYS of any geographic origin, excluding NPGS accessions[b]	Provisional gene pool of the grain amaranths	Distribution[c]
Amaranthus cannabinus (L.) J. D. Sauer	Yes		3	1	GP-2	Atlantic coastal wetlands
Amaranthus chihuahuensis S. Watson	Yes		0	0	GP-2?	Mexico
Amaranthus crassipes Schltdl.	Yes		2	1	GP-3	Southern United States and Mexico
Amaranthus deflexus L.		Yes	5	12	GP-3	Widely naturalized, especially coastal
Amaranthus dubius Mart. ex Thell.	Yes		43	106	GP-2	Southeastern United States and Mexico
Amaranthus fimbriatus (Torr.) Benth. ex S. Watson	Yes		24	2	GP-2?	Southwestern United States and Mexico
Amaranthus floridanus (S. Watson) J. D. Sauer	Yes		1	1	GP-2	Florida
Amaranthus graecizans L.		Yes	14	30	GP-3	Domesticated and weedy forms, pantropical and European
Amaranthus greggii S. Watson	Yes		3	1	GP-2	Caribbean shore from Louisiana into Mexico
Amaranthus hybridus L.	Yes		129	173	GP-1	Ubiquitous weed
Amaranthus lepturus S. F. Blake	Yes		0	0	GP-2?	Mexico

(continued)

Table 2.1 (continued)

Species	Native	Naturalized	Accessions in the NPGS of any geographic origin[a]	Accessions in GENESYS of any geographic origin, excluding NPGS accessions[b]	Provisional gene pool of the grain amaranths	Distribution[c]
Amaranthus neei D.B. Pratt et al.	Yes		0	0	GP-3?	Southern Mexico
Amaranthus obcordatus (A. Gray) Standl.	Yes		0	0	GP-2?	Southern United States and northern Mexico
Amaranthus palmeri S. Watson	Yes		15	2	GP-2	Central United States into Mexico
Amaranthus polygonoides L.	Yes		1	1	GP-3	Southeastern United States, Mexico, and Caribbean
Amaranthus powellii S. Watson	Yes		19	29	GP-1	Southwestern United States and Mexico
Amaranthus pumilus Raf.	Yes		7	1	GP-3	Atlantic shore from South Carolina to Delaware
Amaranthus retroflexus L.	Yes		24	122	GP-1	Ubiquitous weed
Amaranthus scariosus Benth.	Yes		0	0	GP-2?	Mexico
Amaranthus scleropoides Uline & W. L. Bray	Yes		0	0	GP-2?	Central United States into Mexico
Amaranthus spinosus L.		Yes	24	70	GP-2	Widespread weed, pantropical and southern United States
Amaranthus tamaulipensis Henrickson	Yes		1	0	GP-2?	Northern Mexico and Texas
Amaranthus torreyi (A. Gray) Benth. ex S. Watson	Yes		1	0	GP-2	Southern United States and northern Mexico

(continued)

Table 2.1 (continued)

Species	Native	Naturalized	Accessions in the NPGS of any geographic origin[a]	Accessions in GENESYS of any geographic origin, excluding NPGS accessions[b]	Provisional gene pool of the grain amaranths	Distribution[c]
Amaranthus tuberculatus (Moq.) J. D. Sauer	Yes		51	2	GP-2	United States and Canada
Amaranthus ×tucsonensis Henrickson	Yes		1	0	GP-2?	Southwestern United States and northern Mexico
Amaranthus viridis L.		Yes	18	91	GP-3	Southern and eastern United States, and Mexico
Amaranthus viscidulus Greene	Yes		0	0	GP-2	New Mexico
Amaranthus watsonii Standl.	Yes		1	1	GP-2	Southern United States and northern Mexico
Amaranthus wrightii S. Watson	Yes		2	0	GP-1?	Southwestern United States
Total			472	764		

[a](USDA, ARS 2017)
[b](Global Crop Diversity Trust 2017)
[c](Mosyakin and Robertson 2003)

research supports this arrangement of the gene pools (Lanoue et al. 1996; Chan and Sun 1997; Mosyakin and Robertson 2003; Wassom and Tranel 2005; Kolano et al. 2013; Kietlinski et al. 2014; Park et al. 2014; Bayón 2015; Clouse et al. 2016; Stetter and Schmid 2017).

2.2.2.2 Useful Crop Wild Relative Traits

The grain amaranth CWR are potential sources of useful herbicide tolerance, increased seed size, non-shattering seed, high-protein foliage, squalene seed oil, wider geographic adaptation, and improved harvest index. The INDEAR company in Argentina is preparing to release a new grain amaranth cultivar, INDEAR-9, that has resistance to ALS inhibitor herbicides provided by an *A. hybridus* allele (personal communication, Gerónimo Watson). The largest seeds in the genus are found in *A. cannabinus* and *Amaranthus pumilus* Raf., and increased seed size is an important goal for grain amaranth improvement (Brenner et al. 2000). If seed size is eventually increased, there may be a simultaneous increased need for non-shattering seed. The non-shattering seed trait was derived by crossing CWR *A. powellii* with both *A. cruentus* and *A. hypochondriacus* (Brenner 2002); the resulting enhanced lines are distributed by Iowa State University but have not been used commercially. Based on the 1,733 observations in the GRIN database on seed-shattering traits in all three gene pools (USDA, ARS 2017), including 145 accessions identified with some form of non-shattering seeds, there are substantial genetic resources available for breeders to modify shattering traits. Both the grain and the foliage of amaranths are excellent sources of dietary protein and other nutrients. The highest reported foliage protein level, 29%, is in a wild species (Andini et al. 2013). Amaranth seeds contain a commercially desirable oil, squalene (Popa et al. 2015). Assays of many wild *Amaranthus* species for squalene content have revealed that they are generally a rich source (Han-Ping and Corke 2003). There is a potential market for oilseed use of weedy amaranth seeds removed as contaminants from other seed lots or harvested from any weedy fields. Escobedo-López et al. (2014) determined that the distribution of *A. hybridis* within Mexico is wider than the amaranth grain crop's region of cultivation, and therefore, climatic adaptation from *A. hybridus* could be used to genetically expand the crop's adaptation. Weedy amaranths, which have a harvest index (25–40%) that is substantially higher than the domesticated species (10–15%), could be a source of yield-improving characteristics, especially increased branching (Hauptli and Jain 1978).

2.2.3 Wild Economic Species

Wild *Amaranthus* species are most important economically as harmful weeds, but there are minor uses. Two wild amaranth species, *A. palmeri* and *A. tuberculatus*, are among the five most troublesome agricultural weeds in North America (Van Wychen 2016). Their evolving herbicide resistance makes control difficult (Ward et al. 2013; Waselkov and Olsen 2014). The wild amaranths are useful as vegetables (Gibbons 1962) and food for wildlife (Martin et al. 1951). Another use is that of *A. australis* as the champion in tallest amaranth contests (Guinness World Records 2017). *Amaranthus australis* is a gigantic annual wetland species that is not weedy and could someday have agricultural use for biomass or nitrogen scavenging. Plants of this species grow up to nine meters tall as wild plants in Florida (Mosyakin and Robertson 2003).

The amaranth grain crop has the unusual problem of the pollen of weedy amaranths pollinating cultivars, which is a substantial challenge for maintaining genetically pure seed stocks. The problem of crossing with weeds could be moderated by plant breeding for increased crossing incompatibility (Brenner et al. 2013). Indeed, Pal et al. (1982) describe a potentially useful genetic incompatibility of this kind:

an *A. hypochondriacus* white-seeded grain type which crosses with weedy *A. hybridus* but only if *A. hypochondriacus* is the pollen parent. Existing grain cultivars should be evaluated for similar useful weed incompatibility.

2.2.4 Conservation Status of North American Wild Relatives

Most North American *Amaranthus* species are treated in the FNA (Mosyakin and Robertson 2003) and by Bayón (2015) or are included in a checklist of Mexican plants by Villaseñor (2016). *Amaranthus pumilus* is listed by the US Fish and Wildlife Service (USFWS 2017) as threatened, but germplasm is conserved in the NPGS. In contrast, *Amaranthus brownii* Christoph. & Caum, a Hawaiian endemic species listed as endangered by the USFWS (2017), lacks accessions in the NPGS (USDA, ARS 2017) and should be acquired. The remaining *Amaranthus* species of Mexico and the adjacent southwestern United States that are under-accessioned in gene banks should be accessioned and made available for breeding and studies of evolution. Two of these rare species now have maps of modeled potential distributions based on their documented occurrences (Figs. 2.1 and 2.2).

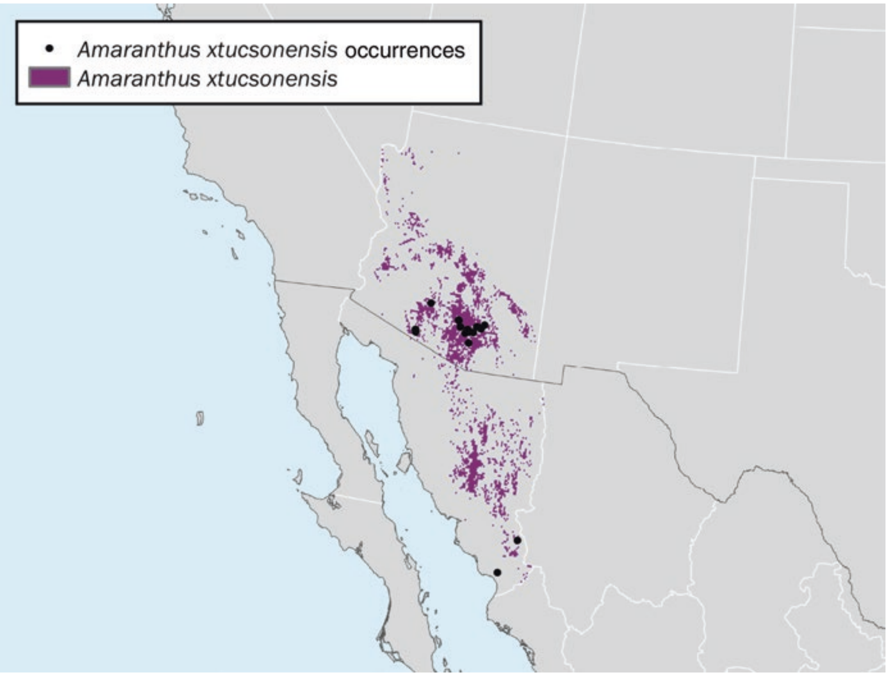

Fig. 2.1 Species distribution map of modeled potential distribution of *Amaranthus* ×*tucsonensis* Henrickson based on climatic and edaphic similarities with herbarium and gene bank reference localities. Full methods for generation of map and data providers are given in Appendix 1

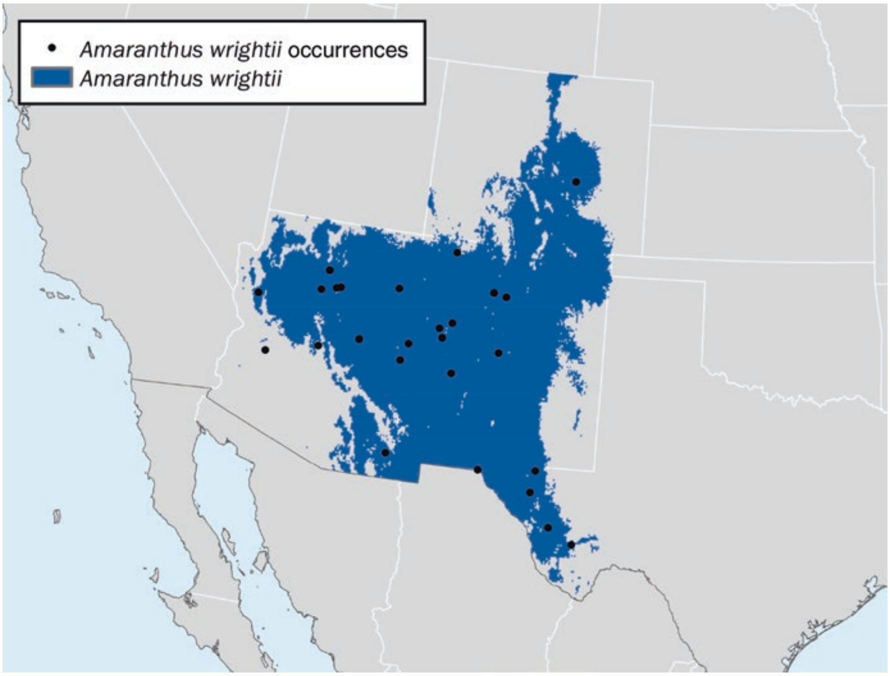

Fig. 2.2 Species distribution map of modeled potential distribution of *Amaranthus wrightii* S. Watson based on climatic and edaphic similarities with herbarium and gene bank reference localities. Full methods for generation of map and data providers are given in Appendix 1

2.3 Barley (*Hordeum vulgare* L. subsp. *vulgare*)

2.3.1 Introduction

Barley (*Hordeum vulgare* subsp. *vulgare*), an Old World crop (Fertile Crescent, Western Asia, secondarily Ethiopia), was one of the earliest crops to be domesticated and has been cultivated since the beginnings of civilization. It is grown over a broader environmental range than any other cereal. Barley is widely grown throughout North America and is utilized for feed, food, and malt/brewing. It is subject to damage from a range of bacterial, fungal, and viral diseases, as well as pests such as aphids, ants, and mealybugs.

2.3.2 Crop Wild Relatives in North America

In North America there are six native *Hordeum* species, all in the tertiary gene pool of *H. vulgare* (von Bothmer et al. 1991). Crossability of these species with *H. vulgare* is extremely difficult and generally yields no useful hybrids. Maps of the North American distributions of these *Hordeum* L. species are available in von Bothmer et al. (1991).

2.3.3 *Wild Economic Species*

Little barley (*H. pusillum* Nutt.) has been found at many Native American archeological sites in eastern United States and is believed to have been part of a prehistoric complex of cultivated plants (Smith and Yarnell 2009). While it was deliberately planted and seed was saved, it is not clear whether it was domesticated (Price 2009). Its cultivation was likely abandoned when the more productive complex of squash, beans, and maize arrived from Mexico. Other *Hordeum* species utilized by Native Americans were *H. brachyantherum* Nevski, *H. depressum* (Scribn. & J. G. Sm.) Rydb., and *H. jubatum* L., (Fowler 1986).

Squirrel tail grass (*H. jubatum*) is used in the horticultural trade for landscaping; the plants are admired for their silky silver and pink sheen. Salt tolerance and adaptation to dry gravely soil contribute to the success of *H. jubatum* as a showy road-edge weed (Hilty 2017).

2.3.4 *Conservation Status of North American Wild Relatives*

2.3.4.1 In Situ

According to NatureServe (2017), *H. pusillum* has been extirpated (state rank, SH) or is vulnerable to being eliminated (state rank, S3) in some locations in the United States and Canada. *Hordeum arizonicum* Covas and *H. intercedens* Nevski have both been assigned a conservation status rank of globally vulnerable (G3) by NatureServe.

2.3.4.2 Ex Situ

All of the native *Hordeum* species are represented in the germplasm collections of the Plant Gene Resources of Canada, while two of them are absent from the NPGS (Table 2.2).

2.4 Barnyard Millet (*Echinochloa* P. Beauv.)

2.4.1 *Introduction*

2.4.1.1 Origin of the Crop and Brief History of Use

The two main species of cultivated barnyard millets, Indian barnyard millet (*Echinochloa frumentacea* Link) and Japanese barnyard millet (*E. esculenta* (A. Braun) H. Scholz), were reviewed recently by Sood et al. (2015). *Echinochloa frumentacea* was domesticated from *E. colona* (L.) Link at an undetermined time.

Table 2.2 Germplasm accessions of barley crop wild relatives in North America

Species	Native	Naturalized	Accessions in the NPGS of any geographic origin[a]	Accessions in GENESYS of any geographic origin, excluding NPGS and PGRC accessions[b]	Accessions in the PGRC of any geographic origin[c]	Provisional gene pool of cultivated barley	Distribution[d]
Hordeum arizonicum Covas	Yes		1	12	7	GP-3	Southwestern United States and northern Mexico
Hordeum brachyantherum Nevski	Yes		25	104	95	GP-3	Kamchatka Peninsula and western North America
Hordeum depressum (Scribn. & J. G. Sm.) Rydb.	Yes		0	28	25	GP-3	Western United States
Hordeum intercedens Nevski	Yes		0	15	18	GP-3	Southwestern California and adjacent Mexico
Hordeum jubatum L.	Yes		38	73	120	GP-3	Siberia and most of North America
Hordeum marinum Huds.		Yes	23	263	89	GP-3	Eurasia and now a scattered invasive in the United States
Hordeum murinum L.		Yes	67	564	629	GP-3	Eurasia and now weedy in southwestern North America and Alaska
Hordeum pusillum Nutt.	Yes		13	23	26	GP-3	United States and northern Mexico
Total			167	1082	1009		

[a] (USDA, ARS 2017)
[b] (Global Crop Diversity Trust 2017)
[c] (AAFC 2017)
[d] (von Bothmer et al. 2007)

The domestication of *E. esculenta* from its wild progenitor, *E. crus-galli* (L.) P. Beauv., occurred approximately 4,000 years ago in Japan. The modern use of both species is primarily in Asia and Africa, where the crop is in decline. The seeds of other *Echinochloa* species have been gathered from either wild plants or plants in cultivation for use as human food.

2.4.1.2 Cultivation

Barnyard millets have the advantages of being adapted for unfavorable weather and especially low rainfall but also for tolerance to standing water, such as is found in rice paddies. In addition, they are nutritious. Recent improvements in machinery for grain processing and easier threshing, as well as higher-yielding varieties, may help reverse the decline in use by making the crop more attractive. One of the beneficial nutritional properties of millets is the low glycemic index that is beneficial to diabetic people (Saleh et al. 2013). In the United States, *Echinochloa* is used as forage and is planted to feed wildlife (Sheahan 2014).

2.4.2 Crop Wild Relatives in North America

2.4.2.1 Gene Pools

There are 19 wild *Echinochloa* species in North America (Table 2.3). Nine of these species are naturalized and eight are native (Michael 2003; Villaseñor 2016). Four species are included from the West Indies, but all four are naturalized from outside of the region (Mckenzie et al. 1993). *Echinochloa colona* (L.) Link and *E. crus-galli*, the widespread weeds from which the crop species were domesticated, are now common in North America (Michael 2003) and make up the GP-1 gene pool (Sood et al. 2015). *Echinochloa orizoides* (Ard.) Fritsch, which is naturalized in North America, makes up part of the genome of *E. crus-galli* and has some crossing fertility, placing it in the secondary gene pool. The North American native *E. crus-pavonis* (Kunth) Schult. has genomic affinities with *E. orizoides* and *E. crus-galli* (Aoki and Yamaguchi 2009) but unknown crossing ability, provisionally placing it in GP-2. The other North American native *Echinochloa* species, *E. holiciformis* (Kunth) Chase, *E. jaliscana* McVaugh, *E. muricata* (P. Beauv.) Fernald, *E. oplismenoides* (E. Fourn.) Hitchc., *E. paludigena* Wiegand, *E. polystachya* (Kunth) Hitchc., and *E. walteri* (Pursh) A. Heller (Michael 2003; Villaseñor 2016), are not closely related to the crop species and are provisionally placed in GP-3, although most are understudied. The remaining naturalized species, *E. glabrescens* Munro ex Hook. f., *E. haploclada* (Stapf) Stapf, *E. orzoides*, *E. oryzicola* (Vasinger) Vasinger, *E. picta* (J. Koenig) P.W. Michael, *E. pyramidalis* (Lam.) Hitchc. & Chase, and *E. stagnina* (Retz.) P. Beauv., are also provisionally placed in GP-3. Surprisingly, the native species *E. muricata* (P. Beauv.) Fernald closely resembles the crop progenitor

Table 2.3 Germplasm accessions of barnyard millets (*Echinochloa* P. Beauv.) and their crop wild relatives in North America

Species	Native	Naturalized	Accessions in the NPGS of any geographic origin (USDA-ARS 2016)[a]	Accessions in GENESYS of any geographic origin, excluding NPGS accessions (GENESYS 2016)[b]	Provisional gene pool	Distribution[c]
Echinochloa colona (L.) Link		Yes	41	617	GP-1	Southern United States and south, weedy
Echinochloa crus-galli (L.) P. Beauv.		Yes	75	223	GP-1	United States and south, weedy
Echinochloa crus-pavonis (Kunth) Schult.	Yes		1	3	GP-2	United States and south, weedy
Echinochloa esculenta (A. Braun) H. Scholz			4	9	GP-1	Crop, especially in Asia
Echinochloa frumentacea Link			159	79	GP-1	Crop, especially in Asia
Echinochloa glabrescens Munro ex Hook. f.		Yes	0	0	GP-3	West Indies, but native in Asia
Echinochloa haploclada (Stapf) Stapf		Yes	3	16	GP-3	West Indies, but native in Africa
Echinochloa holiciformis (Kunth) Chase	Yes		0	0	GP-3	Mexico
Echinochloa jaliscana McVaugh	Yes		0	0	GP-3	Mexico
Echinochloa muricata (P. Beauv.) Fernald	Yes		2	1	GP-3	Widespread in the United States and south, close resemblance to E. crus-galli
Echinochloa oplismenoides (E. Fourn.) Hitchc.	Yes		0	0	GP-3	Mostly in Mexico
Echinochloa oryzicola (Vasinger) Vasinger		Yes	1	0	GP-3	California rice field weed but native in Asia

Echinochloa oryzoides (Ard.) Fritsch		Yes	1	4	GP-2	Weed of rice fields worldwide
Echinochloa paludigena Wiegand	Yes		0	0	GP-3	Florida wetlands
Echinochloa picta (J. Koenig) P. W. Michael		Yes	1	0	GP-3	West Indies, but native in Asia
Echinochloa polystachya (Kunth) Hitchc.	Yes		0	1	GP-3	Gulf Coast wetlands
Echinochloa pyramidalis (Lam.) Hitchc. & Chase		Yes	4	38	GP-3	Mexico, but native in Africa
Echinochloa stagnina (Retz.) P. Beauv.		Yes	1	19	GP-3	Puerto Rico, but native in the tropical Old World
Echinochloa walteri (Pursh) A. Heller	Yes		1	0	GP-3	Atlantic coastal wetlands
Total			294	1004		

[a] USDA-ARS, National Plant Germplasm System 2017
[b] Global Crop Diversity Trust (2017)
[c] Mckenzie et al. 1993; Michael 2003

E. crus-galli, but is not closely related (Ruiz-Santaella et al. 2006). The GP-1 CWR and crop plants are allohexaploids, with a genome that has not been traced to an existing species (Aoki and Yamaguchi 2009). Accessioning a comprehensive set of *Echinochloa* species could help with finding the source of the second genome and provide more opportunity for crop improvement.

2.4.2.2 Useful Crop Wild Relative Traits

The CWR of barnyard millet can be used in crop improvement. *Echinochloa colona* is a possible source of resistance to grain smut (*Ustilago*) and improved dietary iron nutrition (Sood et al. 2015). Both *E. colona* and *E. crus-galii* could be used in breeding for improved dietary calcium (Mandelbaum et al. 1995). The resistance to numerous herbicides that has evolved in both GP-1 weed species (Heap 2017) suggests that herbicide-resistant cultivars could be developed by conventional crossing with the wild species.

2.4.3 Wild Economic Species

In North America the grain of *Echinochloa* has historically been gathered from the wild and used as food by native peoples (Doebley 1984; Moerman 2017). Wildlife, especially waterfowl, also feed on the grain (Martin et al. 1951; Silberhorn 1999). In Ames, Iowa, and many other places, E. *crus-galii* is one of the most flood-tolerant grasses known, making it useful as a volunteer self-seeding lawn grass in areas that have occasional standing water (Fig. 2.3). When the soil dries, it tolerates mowing as a turf grass.

2.4.4 Conservation Status of North American Wild Relatives

As of 2016, only 10 of the 17 wild *Echinochloa* species that are native or naturalized in North America are represented in the NPGS, while 9 of the 17 are known to be in other ex situ collections (Table 2.3). More should be accessioned. Plant collectors from Japan made at least one expedition to collect the North American wild *Echinochloa* (Tanesaka et al. 2008), presumably for use in plant breeding. However, it is probable that the *Echinochloa* breeders in Asia have inadequate access to North American species, which could be remedied by accessioning in the NPGS or other collections. The most vulnerable *Echinochloa* species in North America is *E. paludigena*, which has an occasional distribution in Florida and is not found elsewhere (Natureserve 2017). Its presence in protected areas (Wunderlin et al. 2017) gives it some security.

Fig. 2.3 Some of the grain crop wild relatives are tolerant of flooding. In a parking lot drainage area in Ames, Iowa, the common grasses are *Echinochloa crus-galli* (L.) P. Beauv., *Hordeum jubatum* L., *Setaria pumila* (Poir.) Roem. & Schult., with some *Panicum dichotomiflorum* Michx.; all are CWR covered in this chapter. These grasses established spontaneously where commercial lawn grasses fail because of occasional standing water. When the soil dries, they are mowed as a lawn

2.5 Buckwheat (*Fagopyrum* Mill.)

2.5.1 Crop Wild Relatives in North America

Buckwheat is an Old World crop that tolerates unproductive land and short agricultural seasons. In North America the two species of buckwheat (*Fagopyrum esculentum* Moench and *F. tataricum* (L.) Gaertn.) can escape from cultivation, but the escaped populations are ephemeral (Hinds and Freeman 2005). The CWR were reviewed by Chrungoo et al. (2011). Sanchez et al. (2011) included *Fagopyrum* in the tribe *Fagopyreae*, which is comprised of three genera native only in the Old World; therefore, there are no closely related CWR species of buckwheat in North America.

2.6 Oat (*Avena sativa* L.)

2.6.1 Introduction

Oat (*Avena sativa* L.) is an important small grain cereal crop originating in Europe and Asia. It is widely cultivated in North America for food and feed and also serves a role in soil conservation.

2.6.2 Crop Wild Relatives in North America

There are no native CWR of oat in North America, but there are several naturalized species (Table 2.4). *Avena fatua* L., a hexaploid species in the primary gene pool of oat, is one of the more noxious weeds of cultivation in temperate and north temperate areas (including the United States, Canada, and northern Mexico). The awns have a peculiar adaptation; they twist in response to changes in humidity, drilling the seeds into the soil (Stinson and Peterson 1979). *Avena fatua* grows among field crops, in waste places, along disturbed river banks, in orchards, and along shoulders of highways. It thrives in cultivated oat fields and among small grain cereals in general.

Hybrids between the hexaploid species, including *A. sativa* and *A. fatua*, normally are sufficiently fertile to produce an F2 population (Stevens and Brinkman 1982). However, meiotic irregularities in the form of univalent, inversions, and translocations have been reported (Thomas 1992).

Avena fatua has been utilized in cultivar development (Burrows 1970; Suneson 1967a, b) and has been extensively evaluated for use in oat improvement (Luby and Stuthman 1983; Reich and Brinkman 1984; Rines et al. 1980).

2.6.3 Wild Economic Species

After the introduction and escape of *A. fatua* in the New World, its seeds were gathered and used as a food by numerous Native American tribes (Moerman 2017).

2.6.4 Conservation Status of North American Wild Relatives

In situ conservation is not a concern in North America because there are no native CWR of oat. There are many germplasm accessions of the wild species (Table 2.4). *Avena fatua* has been collected in North America, especially from northern states in the midwestern to western US (North Dakota, South Dakota, Montana, Idaho, Montana, and Minnesota) and the southern parts of the Canadian Prairie provinces (Alberta, Saskatchewan, and Manitoba).

Table 2.4 Germplasm accessions of oat crop wild relatives in North America

Species	Native	Naturalized	Accessions in the NPGS of any geographic origin[a]	Accessions in GENESYS of any geographic origin, excluding NPGS and PGRC accessions[b]	Accessions in the PGRC of any geographic origin[c]	Provisional gene pool of cultivated oats	Distribution[d]
Avena barbata Pott ex Link		Yes	824	1063	2106	GP-2	Mediterranean and now western North America
Avena fatua L.		Yes	1323	1795	644	GP-1	Europe, Central Asia, and now Canada and the United States
Avena occidentalis Durieu		Yes	0	7	67	GP-1	Canary Islands, North Africa, Saudi Arabia, and now western North America
Avena sterilis L.		Yes	8293	10,972	11,524	GP-1	Mediterranean to Afghanistan and now California
Total			10,440	13,837	14,341		

[a] (USDA, ARS 2017)
[b] (Global Crop Diversity Trust 2017)
[c] (AAFC 2017)
[d] (Baum 2007)

2.7 Proso and Related Millets (*Panicum* L.)

2.7.1 Introduction

2.7.1.1 Origin of the Crop and Brief History of Use

There are three domesticated *Panicum* L. millet species. Proso millet (*Panicum miliaceum* L.), the most important species, is grown in the US High Plains. It is commercially available as bird seed but is also the millet generally marketed for human consumption in the United States as "millet." Proso is a traditional crop in China and across Eurasia, especially in Eastern Europe and India (Wang et al. 2016). Little millet or sama (*Panicum sumatrense* Roth), indigenous to the Indian subcontinent (de Wet et al. 1983; Gowda et al. 2008), is grown in India, Myanmar, and Burma. Sauwi (*Panicum hirticaule* J. Presl) is a traditional pre-Columbian crop of the lower Colorado River, where indigenous peoples usually grew it on river mud flats until seasonal flooding was controlled by the building of dams in the twentieth century (Nabhan and de Wet 1984; Freckman and Lelong 2003). At least three other wild or semidomesticated *Panicum* species were used as grain by Native Americans (Doebley 1984). The *Panicum* CWR were reviewed recently by Bhandari et al. (2011), and their general crop status was reviewed recently by Dwivedi et al. (2012), Goron and Raizada (2015), and Upadhyaya et al. (2016).

2.7.1.2 Cultivation

As some of the most resilient of crops, the *Panicum* millets are valuable for providing agricultural stability during poor agricultural years. Their ability to yield in short (60–90 days) and dry seasons makes them useful as catch crops if a primary crop fails (Goron and Raizada 2015).

2.7.2 Crop Wild Relatives in North America

2.7.2.1 Gene Pools

All three cultivated millets have wild conspecific or almost conspecific relatives in North America (Table 2.5). *Panicum milliaceum* is naturalized (Freckman and Lelong 2003; Cavers and Kane 2016), and *P. hirticaule* is native in the southwestern United States and Mexico (Freckman and Lelong 2003; Valdés-Reyna et al. 2009). *Panicum psilopodium* Trin., which is present in North America as a very rare weed (Freckman and Lelong 2003), can be crossed with little millet (Hiremath et al. 1990) and is therefore in GP-1 for that millet species, as well as being in the wider gene pool for proso millet. The three *Panicum* millets have surprisingly closely related genomes (Hunt et al. 2014). Proso millet is an allotetraploid composed of genomes

Table 2.5 Germplasm accessions of millets (*Panicum* L.) and their close crop wild relatives in North America

Species	Native	Naturalized	Accessions in the NPGS of any geographic origin[a]	Accessions in GENESYS of any geographic origin, excluding NPGS accessions[b]	Provisional gene pool of *P. hirticaule*	Provisional gene pool of *P. miliaceum*	Provisional gene pool of *P. sumatrense*	Distribution[c]
Panicum capillare L.	Yes		1	20	GP-2?	GP-2	GP-3	Widespread in North America
Panicum hirticaule J. Presl	Yes		6	3	GP-1	GP-2?	GP-3	Grown as minor crop in northern Mexico, wild in southwestern United States and south, including South America and the West Indies
Panicum miliaceum L.	No	Yes	721	18,207	GP-2?	GP-1	GP-2	Grown as a crop in the United States High Plains and naturalized as a weed
Panicum philadelphicum Bernh. ex Nees	Yes		0	0	GP-3	GP-2	GP-3	Eastern United States and adjacent Canada, as far south as South Carolina
Panicum psilopodium Trin.	No	Yes, rarely	0	0	GP-3	GP-2	GP-1	Maryland as a very rare weed, but native to East Asia
Panicum repens L.	Uncertain	Yes	2	14	GP-3	GP-2	GP-2	Beaches near the Gulf of Mexico and pantropical
Panicum sumatrense Roth	No	No	212	482	GP-3	GP-2	GP-1	A crop in Asia and part of the genome of *P. repens* (Hunt et al. 2014)
Total			942	18,726				

[a] (USDA, ARS 2017)
[b] (Global Crop Diversity Trust 2017)
[c] (Freckman and Lelong 2003)

that are close to the genomes of *Panicum capillare* L. and *Panicum repens* L., which are both present in North America. The closeness of the *P. hirticaule* genome to *P. capilarie* in a dendrogram by Hunt et al. (2014) is the basis for a tentative placement of *P. hirticaule* in the GP-2 of proso millet. Little millet is not wild in North America but is included in the discussion both because of being a crop and because of its genomic relationship with *P. repens* (Hunt et al. 2014).

2.7.2.2 Useful Crop Wild Relative Traits

The wild species have not been used in crop improvement as far as we know. There should be no biological difficulty in crossing between these millets and their wild conspecifics. It is possible that crossing could be accomplished with wild species that have partially compatible genomes but different numbers of chromosomes (Hunt et al. 2014), although crossing may require special manipulation. The wild *Panicum* species' adaptations to both arid and hydric environments (Freckman and Lelong 2003; Valdés-Reyna et al. 2009) may be useful for the cultivated species. Resistance to atrazine has evolved in *P. capillare* (Heap 2017), which could be useful in a cultivar. Also, the wild species are potential sources of useful apomixes (Bhandari et al. 2011).

2.7.3 Wild Economic Species

Wild *Panicum* seeds are edible; they are used by wildlife, especially songbirds (Martin et al. 1951). The grain of at least five *Panicum* species was harvested for food by Southwestern Native Americans (Doebley 1984). In Florida, panicoid grass seeds in threshed condition (with the bracts removed) are present at prehistoric archeological sites and are thought to have been an important food. However, the term "panicoid" applies to many grass genera, including *Echinochloa* and *Setaria*, which with available archeological methods are indistinguishable (Hutchinson et al. 2016). Based on this evidence, it is possible that grain from *Panicum* was a staple prehistoric food in Florida, or perhaps only one of several edible grass seeds that were processed and eaten in similar ways. The *Panicum* CWR have recently been the subject of much research and are attracting interest since switch grass (*Panicum virgatum* L.) is a potential new biomass crop (Bhandari et al. 2011) and one of the popular low-input landscaping grasses (Thetford et al. 2011).

2.7.4 Conservation Status of North American Wild Relatives

The genus *Panicum* has about 100 species in the modern strict sense after reduction from about 450 species in recent revisions (Aliscioni et al. 2003). Within *Panicum*, reticulate allopolyploid evolution makes relationships between the species complicated (Triplett et al. 2012) and is a reason to accession broadly among species to evaluate understudied genomic relationships. Two endemic Hawaiian taxa, *Panicum fauriei* Hitchc. var. *carteri* (Hosaka) Davidse and *Panicum niihauense* H. St. John, are listed as endangered by the USFWS (2017), and neither is accessioned in the NPGS (USDA, ARS 2017) or in other gene banks included in GENESYS (Global Crop Diversity Trust 2017). The NPGS should also acquire more than the present one accession of *P. capillare* and two accessions of *P. repens* to allow expansion of genomic research to a larger number of samples (Hunt et al. 2014). *Panicum* is too large to make the entire genus a germplasm acquisition priority, and it is beyond the scope of this chapter to set acquisition priorities throughout the genus.

2.8 Quinoa (*Chenopodium quinoa* Willd.)

2.8.1 Introduction

2.8.1.1 Origin of the Crop and Brief History of Use

Quinoa (*Chenopodium quinoa* Willd.) is an Andean crop, grown for grain that is generally cooked in hot water, similar to rice. There are thought to be two centers of domestication, one in the Andean highlands and one in the southwestern South American costal lowlands (Jarvis et al. 2017). Quinoa is more nutritious than rice because of its high-protein content of about 16.5% and its beneficial ratios of amino acids (Wu 2015). There has been tremendous market growth and commercial excitement about quinoa since 2007 (Núñez De Arco 2015). Most quinoa production is still in the Andes where it originated; however, many countries outside South America now have quinoa development programs (Bhargava and Srivastava 2013; Bhargava and Ohri 2016); most of these based on cultivation of Chilean coastal-origin germplasm. Key features of this germplasm pool are insensitivity to daylength and partial tolerance of high temperatures during anthesis and seed set (E. Jellen, personal communication). Besides *Chenopodium quinoa* (Sauer 1993; Bhargava and Srivastava 2013), there are four other domesticated grain crops in the genus (USDA, ARS 2017): *C. berlandieri* Moq. subsp. *nuttalliae* (Saff.) H.D. Wilson & Heiser in Mexico (Wilson and Heiser 1979); *C. formosanum* Koidz. in Taiwan (Liu 1996); the white or brown-seeded *C. album* L. and *C. giganteum* D. Don in India (Partap et al. 1998); and *C. pallidicaule* Aellen in Bolivia (IPGRI PROINPA e IFAD 2005). All of these crops have varieties that produce a pale grain similar to quinoa.

2.8.1.2 Cultivation

Entrepreneurial farmers are rapidly changing the map of quinoa production. Much of the higher-quality Andean-origin quinoa is intolerant of temperate summer conditions during pollination, which is an impediment to wider adoption as a crop, especially in the United States. Presently quinoa is produced as a summer crop in regions with cool summers, such as high elevations in the Andes or Rocky Mountains, high latitudes (Peterson and Murphy 2015), and the Pacific Coast (Dunn 2016). It is grown as a winter crop in locations with warmer climates, such as Morocco or Pakistan (Hirich et al. 2014; Sajjad et al. 2014) and southern California (Mohan 2016). It flowers well in temperate summers, but for most available genotypes, there is very little seed set due to some combination of heat, humidity, and long days (Peterson and Murphy 2015). The closely related wild *C. berlandieri* Moq. sets seed and persists in the same locations; therefore, it is a genetic source (Peterson and Murphy 2015) and phenology model that agronomists can look to for climate adaptation. In our observation, the native central Iowan *C. berlandieri* mostly germinates in April, but does not flower until shorter daylengths and cool weather arrive in the fall (Clemants and Mosyakin 2003).

Some free-living populations of *C. berlandieri* may have no more heat tolerance at flowering than highland ecotypes of *C. quinoa*. As an example, *C. berlandieri* var. *zschackei* (Murr) Murr (interior continental) and *C. berlandieri* var. *macrocalycium* (Aellen) Cronquist (New England coastal) are considered ecotypes of *C. berlandieri* and are adapted to short days. They display what appears to be a heat-avoidance strategy by delaying flowering and fruit set until late summer-fall. An experimental delayed planting of *C. quinoa* was made in Ames, Iowa, on July 15, 2015 to test suitability for fall flowering. The plants flowered in mid-September and set seed, demonstrating that the fall flowering window is useful for successful seed set (Table 2.6). In the southern United States and Mexico, wild *C. berlandieri* has the climatic adaptation of spring flowering, which is documented by virtual herbarium specimens, including New York Botanical Garden accession 990,862 (NYBG 2017) and University of South Florida accession 101,046 (Wunderlin et al. 2017). The southern locations where *C. berlandieri* flowers in the spring are probably also suited to winter-grown quinoa that flowers and sets seeds in the spring. There have been successful quinoa plantings of this type in California's Imperial Valley but only starting in 2016 (Mohan 2016). Temperate and subtropical quinoa varieties and farming systems could be developed to optimize both planting and flowering times, mimicking the CWRs.

In contrast, populations of *C. berlandieri* var. *boscianum* (Moq.) Wahl (Gulf Coastal) (Fig. 2.4) and *C. berlandieri* var. *sinuatum* (Murr) Wahl (southwestern interior) ecotypes have been identified that are day-neutral and will flower and set seed in temperatures well in excess of 30 °C (E. Jellen, personal communication).

Table 2.6 Yield of *Chenopodium quinoa* Willd. planted July 15, 2015 and harvested Oct. 26, 2015 in Ames, Iowa (180 cm long rows on 90 cm spacing)

Accession	Number of plants	Grams/100 seeds	Grams of seed
Ames 13737	4	0.305	69.9
PI 510537	14	0.141	77.8
PI 614880	21	0.212	32.3
PI 634919	5	0.263	97.6

Fig. 2.4 Seeds of a population of the wild quinoa relative *Chenopodium berlandieri* Moq. subsp. *berlandieri* var. *boscianum* (Moq.) Wahl was collected with the collection number BYU 14113 by Jellen and Maughan, on a rocky ocean breakwater in Gulfport, Mississippi. Ocean breakwaters are a typical habitat for these plants. (Photo by Eric N. Jellen)

These plants are of particular interest for improving quinoa's heat tolerance, and efforts are underway at Brigham Young University and Washington State University to cross these sources of heat tolerance into cultivated quinoa germplasm.

2.8.2 Crop Wild Relatives in North America

2.8.2.1 Gene Pools

The *Chenopodium* CWR were reviewed recently (Jellen et al. 2011; Bhargava and Ohri 2016), but knowledge is developing rapidly. Good magnification is needed to see the diagnostic traits; consequently, even botanists often generalize about taxonomic identities. North America is rich in quinoa CWR (Table 2.7). The FNA treatment of *Chenopodium* (Clemants and Mosyakin 2003) is tremendously useful for checklisting and collection priority setting; however, it is outdated or incomplete in parts. Benet-Pierce and Simpson (2014) plan to revise the species level keys based on better use of flower and seed traits. Twelve of the 33 species classified as *Chenopodium* in the FNA (Clemants and Mosyakin 2003) are now in other genera

Table 2.7 Germplasm accessions of North American *Chenopodium* L. taxa that are closely related to *C. quinoa* Willd

Taxon	Accessions in the NPGS of any geographic origin[a]	Accessions in GENESYS of any geographic origin, excluding NPGS accessions[b]	Genome	Provisional gene pool of *Chenopodium quinoa*	Distribution[c]
Chenopodium berlandieri Moq. subsp. *nuttalliae* (Saff.) H. D. Wilson & Heiser	6	6	A and B	GP-1	Mexico (domesticated)
C. berlandieri Moq. subsp. *berlandieri* var. *berlandieri*	0	0	A and B	GP-1	South Texas and Mexico
C. berlandieri Moq. subsp. *berlandieri* var. *boscianum* (Moq.) Wahl	24	0	A and B	GP-1	Gulf Coast, narrow ocean shore distribution
Chenopodium berlandieri Moq. subsp. *berlandieri* var. *bushianum* (Aellen) Cronquist	1	0	A and B	GP-1	Northeastern United States
Chenopodium berlandieri Moq. subsp. *berlandieri* var. *macrocalycium* (Aellen) Cronquist	2	0	A and B	GP-1	Mid-Atlantic and north, narrow ocean shore distribution
Chenopodium berlandieri Moq. subsp. *berlandieri* var. s*inuatum* (Murr) Wahl	15	0	A and B	GP-1	Southwestern United States
Chenopodium berlandieri Moq. subsp. *berlandieri* var. *zschackei* (Murr) Murr	19	0	A and B	GP-1	Western Canada, United States, and Mexico
Chenopodium berlandieri Moq. (*s*ubspecific taxa unstated)[d]	15	11	A and B	GP-1	

(continued)

Table 2.7 (continued)

Taxon	Accessions in the NPGS of any geographic origin[a]	Accessions in GENESYS of any geographic origin, excluding NPGS accessions[b]	Genome	Provisional gene pool of *Chenopodium quinoa*	Distribution[c]
Chenopodium ficifolium Sm.	1	7	B	GP-2	Widespread, but infrequent, adventive
Chenopodium neomexicanum Standl.	11	0	A	GP-2	Southwestern United States and adjacent Mexico
Chenopodium standleyanum Aellen	4	1	A	GP-2	Eastern temperate United States
Total	98	25			

[a](USDA, ARS 2017)
[b](Global Crop Diversity Trust 2017)
[c](Clemants and Mosyakin 2003)
[d]These include accessions that are mixtures, difficult to classify in the Flora of North America key (Clemants and Mosyakin 2003), or never classified

(USDA, ARS 2017) based on a revision by Fuentes-Bazan et al. (2012). The gaps in the FNA include the species *Chenopodium littoreum* Benet-Pierce & M. G. Simpson and *C. nitens* Benet-Pierce & M. G. Simpson, which were described after the FNA's publication (Benet-Pierce and Simpson 2010, 2014), and the spring-flowering *C. berlandieri* found from Florida to California and south and not clearly described in the FNA, although it may correspond to variety *boscianum*. Recently, Benet-Pierce and Simpson (2017) revised *C. neomexicanum* Standl. and split this entity into seven taxa: *C. neomexicanum*, *C. arizonicum* Standl., *C. lenticulare* Aellen, *C. palmeri* Standl., *C. parryi* Standl., *C. sonorense* Benet-Pierce & M.G. Simpson, and the Baja California island isolate *C. flabellifolium* Standl. Frequent changes in *Chenopodium* nomenclature make the regularly updated GRIN Taxonomy (USDA, ARS 2017) the best source of current information.

Chenopodium quinoa is an allotetraploid composed of two CWR genomes, A and B. Identifying the *C. quinoa* genomes in diploid wild species was a terrific scientific achievement. Two wild species have the same two genomes as quinoa and are closely related: *C. hircinum* Schrad. in South America and *C. berlandieri* in North America. These two allotetraploid wild species with genomes A and B are of greatest interest for crop improvement because of genetic similarity and crossing fertility with *C. quinoa* (Matanguihan 2015), placing them in the GP-1. Crosses between quinoa cultivars and various wild *C. berlandieri* accessions have produced consistently fertile F_1s and F_2 populations with 70–90% fertility (E. Jellen, personal communication). The two constituent genomes correspond best to diploid genomes in either *C. neomexicanum* or *C. standleyanum* Aellen (genome A) and *C. ficifolium* Sm. (genome B) (Storchova et al. 2015; Walsh et al. 2015). These diploid A and B genome species are wild in North America: *C. neomexicanum* occurs in the southwestern United States and northern Mexico; *C. standleyanum* is a widespread eastern temperate native species; and *C. ficifolium* is an infrequent adventive species. The constituent species are in GP-2 since they may be used someday to make a synthetic allotetraploid that is cross-fertile with quinoa.

2.8.2.2 Useful Crop Wild Relative Traits

Pest and disease issues of quinoa were reviewed by Gandarillas et al. (2015) and by Peterson and Murphy (2015). Downy mildew is a problem for quinoa production, and *C. berlandieri* has resistance reviewed by Peterson and Murphy (2015). The CWR species are a potential source of resistance to leaf miners and downy mildew, as observed in weedy quinoa fields where the weedy species have essentially no damage (Jellen et al. 2011). The salt bladders, sometimes described as a farinaceous pubescence on foliage of *Chenopodium* and many related genera, are part of their defense against insects (LoPresti 2014) and may be useful for pest resistance breeding. *Chenopodium berlandieri* may be useful in both generating male sterile quinoa lineages and for restoring male fertility (Ward and Johnson 1993). A cross between quinoa and a large-seeded *C. berlandieri* var. *macrocalycium* accession from Maine (PI 666279, BYU 803) resulted in some interesting segregates (Matanguihan et al. 2015), but the full outcome is not reported.

2.8.3 Wild Economic Species

Both the wild and domesticated *Chenopodium* species have edible foliage and are used as vegetables (Bhargava et al. 2007). They are readily available and appreciated by wild food foragers (Gibbons 1962). The numerous wild species are mostly interchangeable for this purpose, although some *Chenopodium* species can have a dreadful dead fish smell resulting from the compound trimethylamine (Cromwell 1950) and are therefore unsuited to vegetable use. Among these are the native Gulf Coast ecotypes of *C. berlandieri* var. *boscianum* (Moq.) Wahl and A-genome diploids *C. watsonii* A. Nelson, *C. neomexicanum*, *C. palmeri*, *C. arizonicum*, and *C. sonorense* (Benet-Pierce and Simpson 2017) and especially *C. vulvaria* L. (Cromwell 1950). Native Americans used wild *Chenopodium* seeds and foliage as a food (Moerman 2017), and there is an archeological record of prehistoric Native Americans growing *C. berlandieri* as a grain crop (Smith and Yarnell 2009) similar to Mexican *C. berlandieri* Moq. subsp. *nuttalliae* (Saff.) H. D. Wilson & Heiser. The wild plants are also a wildlife food, especially for upland birds (Martin et al. 1951).

2.8.4 Conservation Status of North American Wild Relatives

The NPGS is actively acquiring *Chenopodium* CWR germplasm. The most active collectors, Eric Jellen and Jeff Maughan of Brigham Young University, have donated 92 wild *Chenopodium* accessions since 2004. Some C*henopodium* wild species are endangered in the wild, although most are locally common. Disturbance by people is generally good for wild *Chenopodium* species, since many thrive as urban or agricultural weeds. However, two *C. berlandieri* varieties, *boscanum* and *macrocalycium*, have narrow ocean shore distributions (Clemants and Mosyakin 2003) and are therefore at risk from ocean beach development and ocean pollution. One of these, variety *macrocalycium*, is represented in the NPGS by just two accessions (Table 2.7). Jellen and Maughan (personal communication) have noted on a 2014 USDA-funded collection expedition to the Mid-Atlantic Coast that most areas previously reported to harbor *C. berlandieri* now have healthy populations of *C. album* L., which suggests that the latter may be outcompeting the former due to its more aggressive weedy characteristics. Of the six *C. berlandieri* varieties treated in the FNA, five are represented in the NPGS (Table 2.7). The NPGS (USDA, ARS 2017) and the other gene banks whose accessions are included in GENESYS (Global Crop Diversity Trust 2017) lack examples of *C. berlandieri* Moq. var. *berlandieri*, which may correspond to the spring-maturing types from South Florida and South Texas. In parts of the genus that are not closely related to quinoa, *C. cycloides* A. Nelson, *C. foggii* Wahl, and *C. littoreum* are especially rare (Natureserve 2017). At least seven distantly related *Chenopodium* species native to North America are not represented in the NPGS or GENESYS collection: *C. albescens* Small, *C. cycloides*, *C. foggii*, *C. littoreum*, *C. nitens*, *C. pallescens* Standl., and *C. subglabrum* (S. Watson) A. Nelson (Global Crop Diversity Trust 2017; USDA, ARS 2017). They should be acquired to expand the available germplasm and provide ex situ conservation for the rare species. Some of the rare species may be acquired via partnerships with conservation biologists that monitor wild populations and could provide seeds.

2.9 Foxtail Millet (*Setaria italica* (L.) P. Beauv.)

2.9.1 Introduction

2.9.1.1 Origin of the Crop and Brief History of Use

Besides foxtail millet (*Setaria italica*), the most important *Setaria* P. Beauv. crop, 11 other *Setaria* species, including some North American natives, have been used as cereals on either on a wild-gathered or domesticated basis; and many are therefore represented in the archeological record (Austin 2006). Foxtail millet is present at 8,000-year-old archeological sites in China and is historically widespread in

Eurasia (Austin 2006). *Setaria italica* was domesticated repeatedly from *Setaria viridis* (L.) P. Beauv. in Eurasia (Lata et al. 2013). It differs from its wild progenitor in reduced seed abscission (Hodge and Kellogg 2016) and other traits (Darmency et al. 1987; Darmency and Dekker 2011). There is new scientific interest in *Setaria* for use as a small genome ($2n = 2x = 18$), model organism for C_4 bioenergy grasses (Brutnell et al. 2010; Lata et al. 2013; Huang et al. 2014; Muthamilarasan and Prasad 2015). A recent method paper describes how to make crosses in *Setaria viridis* (Jiang et al. 2013).

2.9.1.2 Cultivation

In North America there are two main limitations for use of foxtail millet in agriculture. First, foxtail is a typical minor crop without established markets and infrastructure. Second, wheat streak mosaic virus disease in foxtail millet can transfer to wheat, causing farmers in wheat-producing areas to be reluctant to use foxtail millet in crop rotations (Baltensperger 1996).

2.9.2 Crop Wild Relatives in North America

2.9.2.1 Gene Pools

The *Setaria* CWR (Darmency and Dekker 2011) and the crop (Dwivedi et al. 2012; Lata et al. 2013; Vetriventhan et al. 2015) were recently reviewed. The last taxonomic revision of *Setaria* was in 1962 (Rominger 1962), with some updates in the FNA (Rominger 2003). The gene pools of *S. italica* were delineated by Darmency and Dekker (2011), confirmed by Vetriventhan (2015), and expanded by Lata et al. (2013) based on their review of crossing and genomic in situ hybridization data. All of the GP-1 and GP-2 species are wild in North America (Table 2.8). Wild *S. viridis* can be considered conspecific with domesticated *S. italica* (Prasada Rao et al. 1987), and together they form GP-1. The secondary gene pool is composed of *Setaria adhaerens* (Forssk.) Chiov., *Setaria faberi* R. A. W. Herrm., *Setaria verticillata* (L.) P. Beauv, and *Setaria verticilliformis* Dumort. Layton and Kellogg (2014) confirm the Darmency and Dekker gene pool organization and provide genomic evidence to include *S. verticilliformis* in GP-2. Lata et al. (2013) expanded the list of GP-3 species to two that are present in North America, *Setaria grisebachii* E. Fourn. and *Setaria pumila* (Poir.) Roem. & Schult. and one that is native to Australia, *Setaria queenslandica* Domin. The other members of GP-3 are understudied and therefore indicated with a question mark in Table 2.8. Most of the species in the genus are presumed to be in GP-3.

Table 2.8 Germplasm accessions of foxtail millet (*Setaria* P. Beauv.) crop wild relatives in North America

Species	Native	Naturalized	Accessions in the NPGS of any geographic origin[a]	Accessions in GENESYS of any geographic origin, excluding NPGS accessions[b]	Provisional gene pool	Distribution[c]
Setaria adhaerens (Forssk.) Chiov.	Yes		1	0	GP-2	Throughout the world tropics and into Mexico and the southwestern United States
Setaria arizonica Rominger	Yes		0	0	GP-3?	Southern Arizona and adjacent Sonora
Setaria barbata (Lam.) Kunth		Yes	1	3	GP-3?	From Africa and naturalized in the West Indies
Setaria chapmanii (Vasey) Pilg.	Yes		0	0	GP-3?	Southern Florida, West Indies, and southeastern Mexico
Setaria corrugata (Elliott) Schult.	Yes		0	0	GP-3?	Florida and the costal southeastern United States into the West Indies
Setaria faberi R. A. W. Herrm.		Yes	5	4	GP-2	A widespread agricultural weed
Setaria grisebachii E. Fourn.	Yes		2	0	GP-3	Southwestern United States through Mexico into Guatemala
Setaria latifolia (Scribn.) R. A. W. Herrm	Yes		0	0	GP-3?	Mexico
Setaria leucopila (Scribn. & Merr.) K. Schum.	Yes		8	1	GP-3?	Southwestern United States and northern Mexico
Setaria liebmannii E. Fourn.	Yes		0	1	GP-3?	Pacific slope of Mexico into Arizona
Setaria longipila E. Fourn.	Yes		0	0	GP-3?	Southern Mexico and Central America

(continued)

Table 2.8 (continued)

Species	Native	Naturalized	Accessions in the NPGS of any geographic origin[a]	Accessions in GENESYS of any geographic origin, excluding NPGS accessions[b]	Provisional gene pool	Distribution[c]
Setaria macrosperma (Scribn. & Merr.) K. Schum.	Yes		0	0	GP-3?	Florida and the Bahamas
Setaria macrostachya Kunth	Yes		9	1	GP-3?	Mexico and adjacent United States
Setaria magna Griseb.	Yes		2	0	GP-3?	Coastal southeastern United States, Mexico and West indies
Setaria megaphylla (Steud.) T. Durand & Schinz		Yes	3	8	GP-3?	Africa and naturalized in Florida
Setaria palmeri Henrard	Yes		0	0	GP-3?	Baja California
Setaria palmifolia (J. Koenig) Stapf		Yes	4	4	GP-3?	Asia and naturalized in Florida and Mexico
Setaria paniculifera (Steud.) E. Fourn. ex Hemsl. (= *Setaria sulcata* Raddi)	Yes		1	0	GP-3?	Mexico and the Caribbean islands
Setaria parviflora (Poir.) Kerguélen	Yes		15	6	GP-3?	Mexico, West Indies, southeastern United States, and southern California
Setaria pumila (Poir.) Roem. & Schult.		Yes	26	64	GP-3	Very widespread and common but native in Eurasia and Africa
Setaria reverchonii (Vasey) Pilg.	Yes		0	0	GP-3?	Northeastern Mexico and nearby United States
Setaria scandens Schrad.	Yes		0	0	GP-3?	Southern Mexico, South America, and West Indies
Setaria scheelei (Steud.) Hitchc.	Yes		1	1	GP-3?	Texas and New Mexico into Central Mexico

Setaria setosa (Sw.) P. Beauv. (= *Setaria rariflora J. C. Mikan* ex Trin.)	Yes		3	2	GP-3?	Mexico, West Indies, and naturalized in South Florida
Setaria sphacelata (Schumach.) Stapf & C. E. Hubb.		Yes	113	172	GP-3?	Southern Mexico into South America
Setaria tenax (Rich.) Desv.	Yes		0	0	GP-3?	Mexico and the West Indies into South America
Setaria texana Emery	Yes		0	0	GP-3?	Texas and northern Mexico
Setaria variifolia (Swallen) Davidse	Yes		0	0	GP-3?	Southern Mexico and Central America
Setaria verticillata (L.) P. Beauv.		Yes	9	21	GP-2	Widely naturalized but especially in southern Canada and northern United States
Setaria verticilliformis Dumort.		Yes	0	0	GP-2	Infrequent urban weed in the United States
Setaria villosissima (Scribn. & Merr.) K. Schum.	Yes		0	0	GP-3?	Southwestern Texas and northern Mexico
Setaria viridis (L.) P. Beauv. (= *Setaria italica* subsp. *viridis* (L.) Thell.)		Yes	74	45	GP-1	A common weed in most of North America, but infrequent in Florida
Setaria vulpiseta (Lam.) Roem. & Schult.	Yes		1	2		Mexico and the West Indies
Total			278	335		

[a] (USDA, ARS 2017)
[b] (Global Crop Diversity Trust 2017)
[c] (Rominger 2003; Villaseñor 2016)

2.9.2.2 Useful Crop Wild Relative Traits

Setaria viridis is widespread and readily crosses with *S. italica* crop plants (Huang et al. 2014). However, unlike many crops, *S. italica* is already genetically diverse because of its heritage of multiple domestications; therefore, there is little incentive for breeders to use wild germplasm (Darmency and Dekker 2011). There are two forms of *S. viridis* in the United States, one is found north and the other south of 44° north latitude (Rominger 2003; Schröder et al. 2017). The widespread local adaptations found in wild *S. viridis* make it a likely source of special adaptations for particular environmental challenges, such as herbicide tolerance (Heap 2017), drought tolerance, and salt tolerance (Darmency and Dekker 2011). Herbicide tolerance from wild *S. viridis* is already incorporated in one elite cultivar (Darmency and Dekker 2011). Also, since *S. italica* and *S. viridis* cross spontaneously at a frequency of 0.3–4% (Till-Bottraud et al. 1992), hybrids may be present in many existing seed lots, and F_1 hybrids can be identified visually (Darmency et al. 1987). A potentially useful male sterility was obtained from a cross between *S. verticilliata* and *S. italica*, but it is little used, and instead male sterility from within *S. italica* is generally used in China (Darmency and Dekker 2011).

2.9.3 Wild Economic Species

Setaria species may be the most common plants in temperate North America but mostly as weeds. They are used as forage by domesticated animals (Lawrence et al. 1989; Rominger 2003) and are outstanding in importance to wild seed-eating animals (Martin et al. 1951). The grain of at least three wild *Setaria* species was used as cereals by indigenous North Americans, and probably seeds from all the available species were used (Austin 2006). The plains bristle grass 'Stevan' (*Setaria leucopila* (Scribn. & Merr.) K. Schum., PI 552568) and other named cultivars were developed for revegetation use in the southwestern United States; they are adapted for emergence from deep planting and are apomictic (Pater 1995).

2.9.4 Conservation Status of North American Wild Relatives

The widespread temperate weedy *Setaria* species naturalized in North America are generally already represented in the NPGS (USDA, ARS 2017) (Table 2.8) and some of the other gene banks represented in GENESYS (Global Crop Diversity Trust 2017), and their genomes have been analyzed (Layton and Kellogg 2014). However, many of the wild non-weedy species lack representation in germplasm collections and should be accessioned. For example, germplasm of *Setaria corrugata* (Elliott) Schult., an annual wild species in Florida that closely resembles *S. viridis* (Rominger 2003), is absent from germplasm collections. Similarly, *Setaria* *arizonica* Rominger, which has a vulnerable conservation status (Natureserve 2017) because of its limited distribution in Arizona and adjacent Sonora, is not represented in these collections. There is no information available on the crossing ability or genomes of either of these species.

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Chapter 3
Wildrice (*Zizania* L.) in North America: Genetic Resources, Conservation, and Use

Raymond Porter

Abstract Wildrice (*Zizania* spp.) is an annual aquatic grain, occurring naturally in shallow waters of lakes and streams. *Zizania palustris* is found mainly in the Great Lakes region of the USA and Canada. This species of wildrice has been harvested from natural stands for many centuries (and still is) by certain groups of Native Americans who consider it sacred. It has also been cultivated in paddies since 1950 and is still undergoing domestication as a crop. Two other species are present in North America: *Z. aquatica* and *Z. texana*. The former occurs throughout the Great Lakes, St. Lawrence Seaway, Atlantic Coast, and Gulf Coast regions. The latter is endangered, being present only in a small stretch of the San Marcos River in Texas, as well as in several refugia populations. Genetic studies suggest *Z. palustris* has a strong syntenic relationship to *Oryza sativa*. Genetic diversity varies widely among and within stands but is generally high, although inbreeding is higher than expected in certain populations. A recently identified potential threat is the toxic effects of sulfide in sediments under certain conditions. Major preservation concerns include declining or disappearing stands due to hydrology issues and shoreland development, difficulty storing seeds either short term or long term, and narrow stratification and seed moisture requirements to break dormancy. There are no accessions currently being conserved in the US National Plant Germplasm System. Development of ex situ storage protocols should continue while pursuing strategic preservation and restoration of natural stands, guided by knowledge of their population genetics.

Keywords Wildrice · *Zizania*

R. Porter (✉)
Huntington University, Huntington, IN, USA
e-mail: rporter@huntington.edu

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3.1 Introduction

Early voyageurs and settlers who encountered this plant called it “wildrice” because it grew in water, similar to *Oryza sativa*. This is how it is commonly identified in the marketplace, although it may not be wild and is not strictly rice (Oelke and Porter 2016). In some scientific literature, a single word is used (e.g., Hayes and Stucker 1989) to avoid confusion with wild species of *Oryza*, a convention that we will use here. Wildrice is an annual aquatic grain, occurring naturally in shallow waters of lakes and streams, primarily of the Great Lakes region of the USA and Canada, but also extending along the St. Lawrence Seaway and along the Eastern Seaboard and Gulf Coast of the USA (Aiken et al. 1988; Terrell et al. 1997). Wildrice tolerates a wide range of water depths (0.05–2.50 m), sediments (clay to peat), and latitudes (30° to 56°N) (Aiken et al. 1988).

Taxonomically, four species are recognized in the genus *Zizania*. Three are native to North America—*Z. aquatica* L. (Fig. 3.1), *Z. palustris* L. (Fig. 3.2), and *Z. texana* Hitch. (Fig. 3.3); the fourth, *Z. latifolia* (Griseb.) Turcz. ex Stapf, is native to eastern Asia. *Zizania palustris*, an annual plant, has larger grains than the

Fig. 3.1 Panicle of *Zizania aquatica* L., showing spreading female branches. (University of Florida/IFAS Center for Aquatic and Invasive Plants)

Fig. 3.2 Wild *Zizania palustris* L. is still harvested from natural stands into canoes. (Eli Sagor, University of Minnesota)

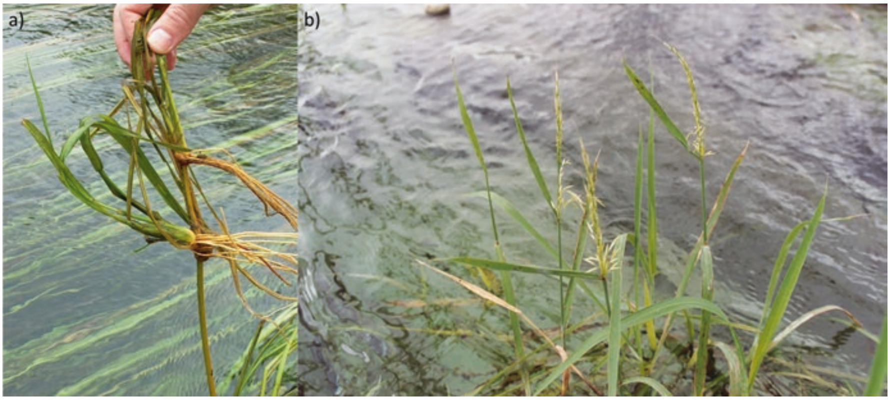

Fig. 3.3 (**a**) Submerged and (**b**) emergent plants of endangered *Zizania texana* Hitch. in the San Marcos River, Texas (**a**: Chris Richards, USDA-ARS. **b**: Ervin Oelke, University of Minnesota, retired)

other three and is the species that has been harvested in the wild and domesticated as a crop. Two botanical varieties of *Z. palustris* occur naturally in North American waters: var. *palustris* and var. *interior* (Fig. 3.4). *Zizania aquatica* is also annual, but the grains are of smaller size and are not harvested for food. The two varieties

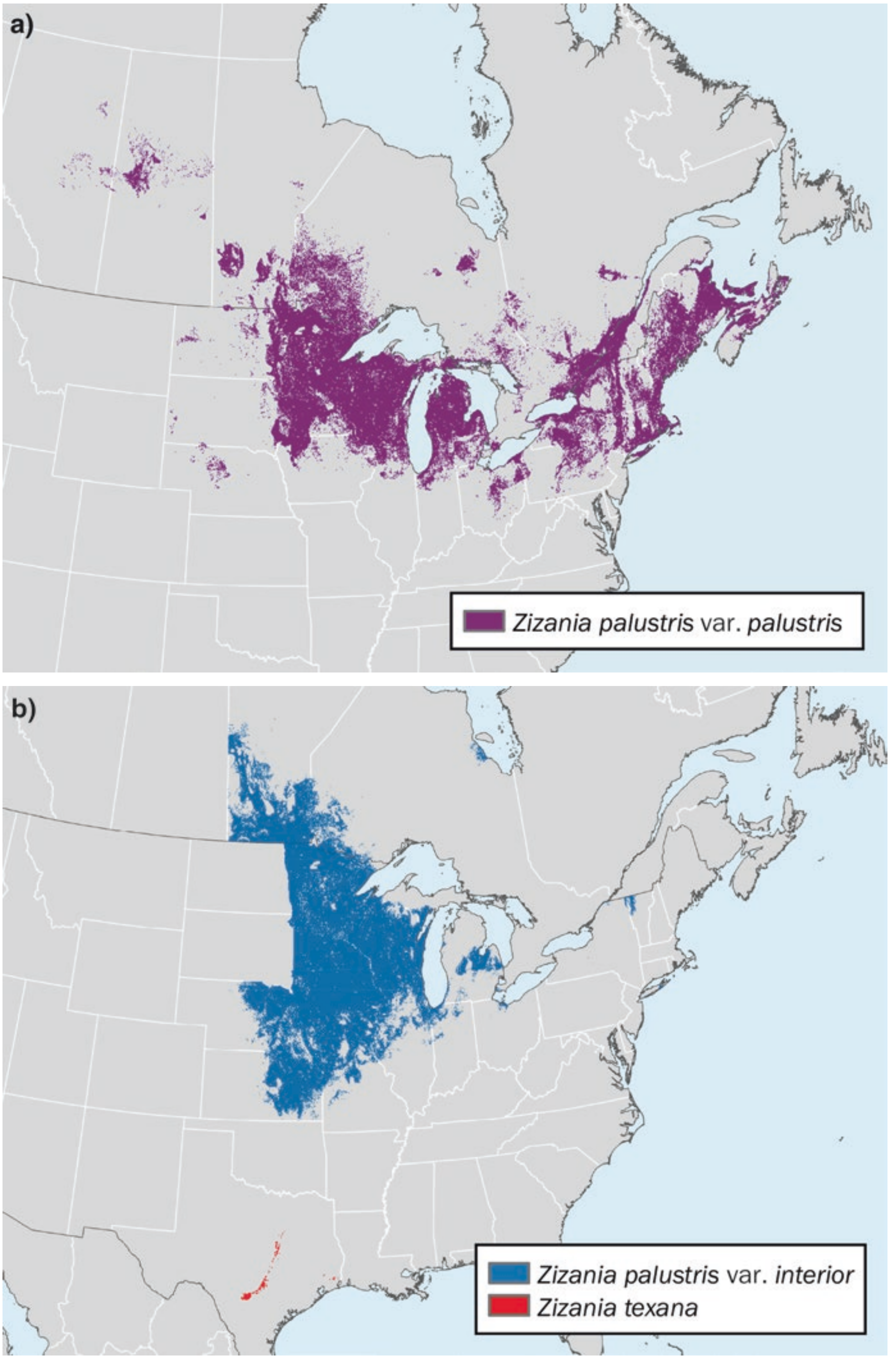

Fig. 3.4 Modeled potential distribution of (**a**) *Zizania palustris* L. var. *palustris* and (**b**) *Z. palustris* L. var. *interior* (Fassett) Dore and *Z. texana* Hitchc., based on climatic and edaphic similarities with herbarium reference localities. Full methods for generation of maps and data providers are given in Appendix 1

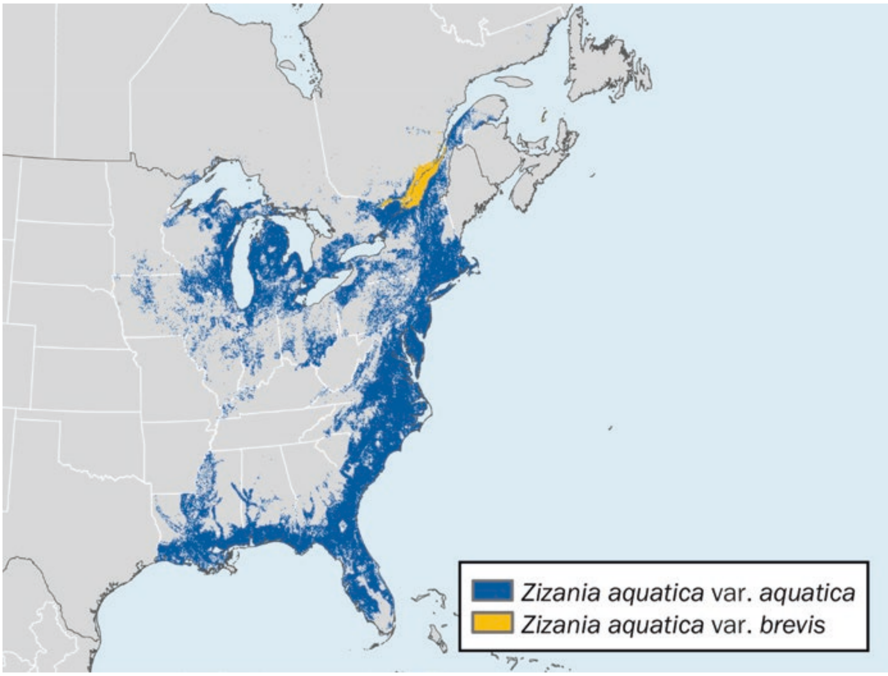

Fig. 3.5 Modeled potential distribution of *Zizania aquatica* L. var. *aquatica* and *Z. aquatica* L. var. *brevis* Fassett, based on climatic and edaphic similarities with primarily herbarium reference localities. Full methods for generation of maps and data providers are given in Appendix 1

of *Z. aquatica* are var. *aquatica* and var. *brevis* (Fig. 3.5). *Zizania texana* and *Z. latifolia* are also small-seeded, but unlike *Z. aquatica*, they are perennial (Terrell et al. 1997). Cultivated or harvested wildrice that is now known as *Z. palustris* was often called *Z. aquatica* in older scientific literature; Fassett (1924) recognized one species, *Z. aquatica,* with four varieties, and Gleason and Cronquist (1963) continued that convention. Aiken et al. (1988) and Terrell et al. (1997) described the four distinct species that are currently widely accepted. *Zizania palustris* and *Z. aquatica* in particular have been distinguished as separate species on the basis of spikelet anatomy (Duvall and Biesboer 1988a), allozymes (Warwick and Aiken 1986), crossability (Duvall and Biesboer 1988b), and plastid DNA restriction sites (Duvall et al. 1993).

3.1.1 Recent Cultivation, Domestication, and Breeding

Cultivation in paddies began in northern Minnesota in the early 1950s, with selection for domestication traits following in the late 1960s. The cultivated crop subsequently spread to California, mainly in the Sacramento Valley and Fall River

Valley, and on a limited basis in the Willamette Valley of Oregon and along the St. Joe and St. Maries Rivers near Coeur d'Alene, Idaho (Oelke 2007).

In parts of Canada, lakes without wildrice have been seeded with wild-type (shattering) seeds collected from other lakes, and the resulting stands are managed for wildrice production. Canadian lake populations are typically harvested by airboat (Aiken et al. 1988). Wildrice has also been established and grown on a limited basis in New South Wales, Australia, and in eastern Hungary (Oelke 2007).

General reviews of wildrice include Aiken et al. (1988), Oelke (2007), and Oelke and Porter (2016). Domestication of wildrice has been reviewed by de Wet and Oelke (1978) and by Hayes and Stucker (1989). Breeding has been reviewed by Grombacher et al. (1997). Domestication appears to have been initiated by the discovery of qualitative "nonshattering" in a paddy-grown wild population around 1969, permitting the grain to remain on the plant long enough to be harvested in one pass by a combine (Fig. 3.6). Elliott and Perlinger (1977) concluded that the nonshattering phenotype appears to be controlled by two complementary genes. There is quantitative variability for shattering resistance beyond these two or three genes (Everett and Stucker 1983).

Comparative genetic studies have indicated a strong syntenic relationship with *Oryza sativa*; all ten rice linkage groups are represented in wildrice, with three being duplicated in wildrice (Kennard et al. 2000; Hass et al. 2003). Kennard et al. (2002) found that three QTLs had major effects for shattering, possibly orthologous to the shattering loci in *Oryza*. Inbred lines have been developed and crossed to produce hybrid varieties, facilitated by a cms-restorer system

Fig. 3.6 Cultivated wildrice (*Zizania palustris* L.) retains seeds on the plant throughout the ripening period, allowing it to be harvested with a combine. (Dave Hansen, Minnesota Agricultural Experiment Station)

(Foster 1998; Foster and Zhu 1999). Some hybrid varieties have been grown for commercial production in California. Crosses between specific breeding populations in Minnesota have shown evidence of hybrid vigor for grain yield, indicating possible heterotic groupings (Porter and Kahler 2010).

3.1.2 Seed Storage Issues

Lack of reliable seed storage has hampered breeding progress, as well as both short- and long-term seed preservation. Wildrice seeds don't appear to tolerate drying well, although factors such as heterogeneous seed maturity or development of dormancy during desiccation may affect their response to drying. But even if dormancy is broken to remove it as a germination-inhibiting factor (Probert and Longley 1989) and freshly harvested seeds are tested at different developmental stages (Probert and Brierley 1989), seeds still do not tolerate drying.

Although seeds can retain viability for up to 6 months when stored at temperatures as high as 30 °C and seed moistures down to 30% (fwb), stratification is still necessary to break dormancy. Conversely, hydrated seeds can be frozen to −10 °C without damage but still require stratification at temperatures between 0 °C and 10 °C to break dormancy (Kovach and Bradford 1992a). Kovach and Bradford (1992b) found that the reported desiccation intolerance of wildrice can be mitigated by proper control of temperature of dehydration (>25 °C) and temperature and rate of rehydration (10–25 °C over at least 3 weeks). They were able to maintain viability by dehydrating seeds in this way to a seed and embryonic axis moisture content as low as 6–8% (fwb). They conclude the classification of wildrice as recalcitrant is unwarranted. Vertucci et al. (1995) flash dried excised embryos at 35 °C or room temperature to different moisture contents. More mature embryos survived to lower temperatures (−50 °C) than the least mature embryos (−18 °C). They concluded that long-term preservation of wildrice seeds is possible at −20 °C, depending on the maturity of the embryo.

3.2 Wild Relatives of the Crop

Genetic diversity within and among wild populations of *Z. palustris*, the source from which the crop was selected, has been of particular interest for research aimed at conservation efforts. Using 13 isozyme markers, Lu et al. (2005) found the overall genetic diversity of 17 Wisconsin populations to be moderate (0.15) compared with other wind-pollinated species but low compared to the mean of Poaceae. Population size and degree of isolation were major factors contributing to genetic variability; gene diversity in turn showed significant positive correlations with several fitness traits that were measured. Gene flow between populations was low. Inbreeding within populations (f) was also low, averaged among the populations studied, but varied greatly, with a high of 0.52, suggesting differences in outcrossing rates, disturbance, and human influence. Kern and Kahler (2011) found higher-than-expected levels of inbreeding in two large wildlife refuge populations in Minnesota, especially compared with other natural populations. They also found greater genetic diversity and less inbreeding in river populations within the refuge than in their respective lake populations. When Kern and Kahler (2014) studied genetic diversity of six separated bays within the St. Louis River estuary, they found two of the sites were genetically differentiated from each other and from the other four, possibly a result of historical reseeding efforts using seed from elsewhere, and different sedimentation and water chemistries.

Biesboer et al. (2014) sought to document genetic diversity using SSR markers in a large study of 70 wild *Z. palustris* populations across Minnesota. They found a high degree of heterozygosity within wildrice populations, averaging 0.54 with a range of 0.37–0.73. Based on allele frequencies, the populations were grouped into four major clades and ten sub-clades. Genetic distance coefficients (Nei83) ranged from 0.22 to 0.83, indicating a wide amount of genetic variability among populations. Using Wright's Fixation Index (F_{ST}) to compare heterozygosity of each population to the expected total heterozygosity across all populations, they identified six clades.

Counts and Lee (1987, 1988a, b, and 1990) grew wildrice populations from various lakes in Ontario, Canada, together in a common greenhouse or lake environment, to study the responses of a number of morphological and phenological traits to various environmental and cultivation factors. Their results suggested that phenotypic plasticity in wildrice buffers the populations from directional selection pressures. Counts (1993) followed with a study of genetic variability (using isozymes) and phenotypic plasticity among two *Z. palustris* and four *Z. aquatica* populations collected along the Atlantic seaboard and grown together in varying greenhouse conditions. She observed no relationship between heterozygosity and degree of phenotypic plasticity of stem size, flowering, and reproductive traits, but *Z. palustris* populations responded to temperature differences with greater plasticity than *Z. aquatica* populations.

Because of its endangered status, *Z. texana* has received research attention aimed at its preservation. Richards et al. (2007) assessed its genetic diversity using microsatellite markers. The larger, demographically stable stands along its 4-km range of the San Marcos River in Texas contained the greatest genetic diversity. Stratified sampling of such stands captured all the microsatellite alleles in fewer individuals, where random sampling did not. The population had a high degree of heterozygosity overall.

3.2.1 Use of Wild Relatives for Crop Improvement

Anecdotally, wildrice cultivars may trace their origins from few or a single lake population. Wildrice breeders have collected accessions from many natural stands, primarily from Minnesota lakes, to form gene pools as a source of breeding materials (Elliott 1980; Porter et al. 2001), but these have not been a major source of new traits or varieties. Varietal development efforts have relied heavily on recurrent phenotypic selection within already adapted open-pollinated populations, in order to maintain genetic diversity within populations and because of the limited ability to reliably store seeds for several generations. Kahler et al. (2014) used highly polymorphic SSR markers derived from *Z. texana* (Richards et al. 2004; Kern et al. 2011) to confirm these relationships among advanced breeding populations by constructing a phylogenetic tree based on Nei's genetic distances; one breeding population appearing to have a closer genetic distance to several natural populations than to the other breeding populations.

Nonshattering phenotypes are occasionally found in *Z. palustris* stands. Seed size is generally greater in lake populations than in river populations (Eule-Nashoba et al. 2012). Some lake populations are known anecdotally by ricers (hand harvesters) for their greater size. Wild populations vary in many morphological traits but have not been explicitly sought for introgression of traits, because considerable genetic diversity still exists within breeding populations (R. Porter, personal observation).

Other species may have traits of interest, but they have not been extensively utilized. Grombacher et al. (1997) described previously unpublished work in which accessions of *Z. aquatica* from Florida were crossed successfully with several *Z. palustris* lines, using *Z. aquatica* as the female parent (*per* Duvall and Biesboer 1988b). Reduced dormancy was introgressed into several breeding populations by backcrossing; nondormancy appeared to be dominant and simply inherited (Porter 1998). Grombacher et al. (1997) also suggest that *Z. aquatica* var. *brevis* could be a source of short awns, short seeds, short height, and salinity tolerance due to its adaptation to tidal habitats. *Z. texana* and *Z. palustris* were crossed successfully by Duvall and Biesboer (1988a), for phylogenetic studies, but not for utilization. In the future, *Z. texana* could be a source of perenniality, if this were to become a breeding objective.

3.3 Wild Utilized Species

For wildrice, the wild relatives have a longer history of use than cultivated wildrice. Native Americans continue to harvest the grain from natural stands (Fig. 3.2); their treaty-recognized right to do so both on-reservation and in ceded territories has been upheld by the US Supreme Court (Minnesota v. Mille Lacs 1999). Others can obtain state permits in Minnesota or Wisconsin to harvest the crop from public waters. The Minnesota Department of Natural Resources (Minnesota DNR 2008) estimated that 4,000 to 5,000 individuals participate in wildrice harvesting annually, 3,000 of whom are tribal members. Individual tribal departments of natural resources and inter-band agencies such as the Great Lakes Indian Fish and Wildlife Commission (GLIFWC) study and manage the health of natural stands of wildrice, mostly in Minnesota and Wisconsin. Reservation wildrice committees, as well as the departments of natural resources of key states like Minnesota and Wisconsin, regulate wildrice harvesting and educate the public on the allowed method and harvest season. The Minnesota DNR has frequently assessed and published the stand densities of a number of key lakes. Recent assessments found over 64,000 acres of wildrice stands in Minnesota on 1,200 lakes and rivers (Minnesota DNR 2008).

Some Native American groups have expressed concern that cultivated wildrice pollen flow to natural stands could occur and affect their genetic integrity or even cause a genetic collapse. A comprehensive study to identify threats to natural wildrice concluded that conventional breeding does not pose such a threat, since no novel genes or alleles have been brought into cultivars from outside the natural *Zizania* gene pool (Minnesota DNR 2008). Also, limited pollen travel studies suggest there is a significant decrease in the amount of gene flow at distances of up to 2 miles from wildrice paddies (Cregan 2004). Therefore, it seems unlikely that any genetic migration from paddies would change the genetic structure of natural stands.

3.3.1 Archaeological Record of Utilization

McAndrews (1969) estimated wildrice pollen in a Minnesota lake beginning about 1935 years ago. Huber (2000) summarized a number of studies of pollen in Minnesota lake sediments and concluded that wildrice was present in those lakes in the last 10,000 years "in quantities large enough to provide a considerable subsistence component" to the Paleoindian cultures present during that time. Mather and Thompson (2000) reviewed archaeological evidence for the use of wildrice as a food and cited evidence (in the form of wildrice phytoliths) of periods of "intensified use" of wildrice approximately 2000 years before European contact at Mille Lacs Lake in Minnesota. Valppu (2000) also cited evidence of the beginnings of wildrice processing on Big Rice Lake, St. Louis Co., Minnesota, about 2000 years ago.

3.3.2 Cultural Significance for Native Americans

Wildrice has been harvested by Native Americans from natural stands for centuries, having been recognized as a valuable source of nutrition. It is called *manoomin* by the Ojibwe (Anishinaabe); considered a sacred grain, it is a very important part of their cultural activities (Vennum 1988). It is still harvested the traditional way: while one person poles a canoe through a stand, another dislodges the ripe grains from the plants by tapping the stems with ricing sticks, allowing the grains to fall into the canoe. The grains are then parched to gelatinize the starch, allowing for long-term storage. It is boiled like rice to be consumed as a whole grain in various ways (Oelke and Porter 2016).

3.4 Conservation Status of CWR and WUS

Decline and disappearance of historic wildrice stands have been a concern for some time, although natural stands do fluctuate from year to year. One case documented a return of wildrice after at least a 5-year absence, following a major flooding event that resulted in significant sediment disturbance (Dukerschein 2000).

Threats to wildrice were identified and reported under mandate of the Minnesota State Legislature (Minnesota DNR 2008). The primary threats include "changes in local hydrology due to dams and channelization, water-based recreation and shoreland development, and mining and other industrial activities," but hydrology issues and shoreland development were identified as especially important at the local level. The study also identified the statewide and regional threats of most importance as loss of genetic integrity, invasive species, and climate change.

More recently, the Minnesota Pollution Control Agency was authorized to more closely study the possible impact on wildrice of sulfate-containing effluents from mining or municipal sources (MPCA 2014). Research was funded to investigate the issue through extensive field surveys of wildrice stands and sediments, laboratory hydroponics studies, outdoor container experiments simulating natural conditions, analysis of sediments from the rooting zones of wildrice lakes, and laboratory sediment incubation experiments to observe sulfate movement and conversion to sulfide. Sulfate per se was determined to have minimal effect on wildrice growth but could prove toxic under conditions where it is converted to sulfide. Results of these studies are being used to refine rulemaking about allowable sulfide levels in specific sediment conditions. Data from this comprehensive study (particularly the field survey) should prove useful as a baseline for understanding other factors affecting natural wildrice stands, aiding in conservation efforts.

In the study of threats to wildrice, possible effects of climate change were discussed (Minnesota DNR 2008). Seed set could be reduced if hot, dry conditions coincided with pollination. Carp and invasive plant species could spread into wildrice habitats with warming waters. Warm, humid weather favors certain plant diseases such as *Bipolaris* spp. that occur naturally in wild populations. Severe weather could damage stands during the more vulnerable floating leaf and seed production stages. The southern edge of the species' natural range may already be shifting northward.

Zizania texana is listed as endangered (USFWS 1978, 2013). Its range is limited to the upper 2 miles of the San Marcos River in central Texas (Terrell et al. 1978, 1997; Figs. 3.3 and 3.4). Conservation efforts include both in situ preservation and maintaining ex situ refugia populations collected from—and adequately representing the genetic diversity of—the extant San Marcos River population (Wilson et al. 2017). Pollen longevity is short (10–60 min) and is released between 0200 and 0400, limiting sexual reproduction of this perennial species (Power and Oxley 2004); by comparison, pollen longevity in cultivated *Z. palustris* has been estimated to be less than 2 h after another extrusion (Page and Stucker 1990).

Currently there are no *Zizania* accessions in the US National Plant Germplasm System. More work is needed to develop reliable protocols for long-term storage of whole seeds (Christina Walters, personal communication). Accessions have been collected directly from public waters at various times by the Minnesota wildrice breeding program. Since short- to medium-term seed storage has been unreliable for plant breeders and other researchers, individual accessions have had to be maintained by being grown out. Those that were not grown out eventually lost seed viability in storage. As another approach to utilization, many were allowed to inter-mate in research paddies each year in a "common garden" approach to maintaining a dynamic germplasm pool.

Conservation efforts should focus on improving ex situ preservation methodology—both short-term and long-term—but also on maintaining or improving in situ population health. Regarding fitness-related traits in natural stands, "Higher levels of genetic variability may translate into improved population persistence for wildrice in natural environments" (Lu et al.). In situ preservation of populations, particularly those that are recognized as declining, should recognize the dynamic nature of this outcrossing species. Seeding new lakes or reseeding declining or disappeared populations has been done by agencies such as GLIFWC, as well as tribal and state DNRs. Restoration efforts may need to take into consideration the need for an adequate population size and the addition of new alleles from other populations in order to reverse inbreeding of isolated stands in particular.

Biesboer et al. (2014) gave recommendations to guide wildrice preservation and restoration. For preservation, priority should be placed on populations that have a high degree of genetic variability as a potential source of seed for restoration of other stands. For restoration, they identified two distinct issues. First, genetic accuracy is the goal, but where populations have disappeared, judgment is needed to determine what might be the closest match. Second, the aim of restoration should be a functional population, perhaps employing a range of genotypes to maximize the likelihood of success. They cite Falk et al. (2001) as providing good principles to guide restoration efforts. Finally, they point out that restoration of the population must be preceded by understanding and correcting the reasons for the decline.

For this iconic North American grain, preservation as both a CWR and WUS is affected by its unique features: its aquatic habitat, its seed storage difficulties, its recent history of domestication, and its cultural importance to Native Americans. All these make its conservation challenging but not impossible.

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Chapter 4
Wild Beans (*Phaseolus* L.) of North America

Sarah Dohle, Jorge Carlos Berny Mier y Teran, Ashley Egan, Theodore Kisha, and Colin K. Khoury

Abstract The wild relatives of the five domesticated species of bean (*Phaseolus* L.) are widely distributed across the tropics and subtropics of the New World, with taxa extending from the Canadian border to Argentina, and on the Caribbean Islands, Bermuda, and the Galapagos Islands. Mesoamerica holds the largest concentration of species, particularly in the highlands of central Mexico, northward along the Sierra Madre Occidental, and south to Chiapas. The progenitors and close relatives of all five domesticates are also concentrated in this region. Plant breeding involving the use of wild relatives has almost entirely been directed toward the improvement of common bean (*Phaseolus vulgaris* L.), the most widely cultivated species, and successful contributions have mostly come from its progenitor (*Phaseolus vulgaris* L.) and a few other taxa. Wild relatives are considered to possess novel useful genetic variation that has not yet been fully explored.

S. Dohle
Department of Plant Sciences, Delaware Valley University, Doylestown, PA, USA
e-mail: sarah.dohle@delval.edu

J. C. Berny Mier y Teran
Department of Plant Sciences, University of California, Davis, CA, USA
e-mail: jcberny@ucdavis.edu

A. Egan
Smithsonian Institution, National Museum of Natural History, Department of Botany, Washington, DC, USA
e-mail: ashegan2@gmail.com

T. Kisha
USDA Agricultural Research Service, Western Regional Plant Introduction Station, Pullman, WA, USA
e-mail: theodore.kisha@ars.usda.gov

C. K. Khoury (✉)
USDA, Agricultural Research Service, Center for Agricultural Resources Research, National Laboratory for Genetic Resources Preservation, Fort Collins, CO, USA

International Center for Tropical Agriculture (CIAT), Cali, Colombia
e-mail: colin.khoury@ars.usda.gov

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A number of wild *Phaseolus* are rare endemics that are threatened in their natural habitats and are insufficiently protected in situ. Significant ex situ collections of wild *Phaseolus* are maintained at the International Center for Tropical Agriculture (CIAT), the USDA-ARS National Plant Germplasm System, within the Sistema Nacional de Recursos Fitogenéticos para la Alimentación y la Agricultura (SINAREFI) Conservation Centers Network in Mexico, and at the Botanic Garden Meise, Belgium. Unfortunately, over 26% of *Phaseolus* taxa are not represented at all in these ex situ conservation facilities, and another 29% are represented by less than ten accessions, making over half of the species highly underrepresented in genebanks. Further efforts to enhance the protection of vulnerable species in their natural habitats, and further collecting to fill critical gaps in germplasm collections, are warranted.

Keywords Genetic resources · Ex situ conservation · In situ conservation · Grain legumes

4.1 Introduction

Beans (*Phaseolus* L.) have been cultivated for over 7000 years in the neotropics and continue to be a critical source of plant protein, dietary fiber, iron, zinc, and other micronutrients for human nutrition (Broughton et al. 2003; Ramírez-Villegas et al. 2010). The plants are also important to sustainable agricultural production practices due to their ability to enrich soil nitrogen by way of their symbiotic association with nitrogen-fixing rhizobia bacteria (Rubiales and Mikic 2015).

The genus *Phaseolus* has five domesticated species; each of the product of independent domestication processes from different wild progenitor species: common bean (*Phaseolus vulgaris* L), lima bean (*P. lunatus* L.), runner bean (*P. coccineus* L.), tepary bean (*P. acutifolius* A. Gray), and year bean (*P. dumosus* Macfady) (Bitocchi et al. 2017). Both common bean and lima bean were in fact domesticated more than once from different populations of their wild progenitor taxa, in Mesoamerica and in the Andes (Gepts 1998; Motta-Aldana et al. 2010; Bitocchi et al. 2013).

Common bean is the world's most important legume for direct human consumption, comprising more than 50% of the grain legumes eaten worldwide, holding primary importance in the staple diet of over 500 million people, and being cultivated on over 23 million hectares, on every inhabitable continent (Gepts 2001; McClean et al. 2004; CGIAR 2017). Major production areas include Brazil, Mexico and Central America, the Iberian Peninsula, Central-Eastern and Southern Africa, China, and India (Bitocchi et al. 2017).

The other four domesticated species have more distinct and somewhat narrower ecological adaptations (Debouck and Smartt 1995; Bitocchi et al. 2017). Lima bean grows in the warm humid tropics, from sea level to over 2000 m asl

(Baudoin 1988; Bitocchi et al. 2017; Serrano-Serrano et al. 2012). Runner bean is adapted to cool highland conditions and is now cultivated primarily in climatically appropriate regions of Spain, Italy, the UK, the Netherlands, and other northern European countries with cooler growing season temperatures (Rodino et al. 2007). Tepary bean, the most drought tolerant of cultivated *Phaseolus*, is adapted to arid and semiarid conditions, with high temperatures, low and variable precipitation, and alkaline soils (Pratt and Nabhan 1988; Porch et al. 2013a). Tepary bean is still predominantly grown only in its region of origin in the warm deserts of Mexico and the USA, although it is the subject of increasing interest in similar agroecological regions of Africa and South Asia (Small 2014). Year bean is the domesticated form of a species that is the result of a naturally occurring hybridization event between the progenitors of common and runner bean (Mina-Vargas et al. 2016). Year bean is cultivated in Central America (particularly in the highlands of Guatemala), the Caribbean, and in the Northern Andes from Venezuela south to Peru, especially in climatic zones where common bean is highly susceptible to anthracnose, *Ascochyta* blight, and root rot (Mina-Vargas et al. 2016; USDA, ARS, National Plant Germplasm System 2017b; D. Debouck personal communication 2017).

Even with the incredible expansion and success of *Phaseolus* beans worldwide, a wide range of challenges to their cultivation exist. Common beans are vulnerable to drought and heat, which are likely to be exacerbated by climate change (Beebe et al. 2011; Jarvis et al. 2012). Major diseases for the crop include root rot, *Xanthomonas* blight, downy mildew, rust, angular leaf spot, anthracnose, web blight, white mold, halo blight, bean common mosaic virus (BCMV), and a variety of other viruses. Major insect pests include red spider, mealybug, white fly, leafhoppers, weevils, various caterpillars, flea beetles, *Diabrotica*, and Mexican bean beetles (Beebe 2012).

Lima bean insect pests include thrips, aphids, leaf miners, *Heliothis*, and chrysomelid beetles. They are also susceptible to mycoplasmas (Freytag and Debouck 2002) and white mold (Boland and Hall 1994). Runner beans are primarily affected by rust, as well as angular leaf spot, anthracnose, and *Ascochyta* leaf spot, and by Apion pod weevil, chrysomelid beetles, thrips, flea beetle, and leafhoppers. Tepary beans are susceptible to powdery mildew, root rots, white mold, rust, and viruses including alfalfa mosaic, bean yellow mosaic, BCMV, bean golden mosaic, curly top, pod mottle, and four whitefly-transmitted viruses (Freytag and Debouck 2002). Insect pests of tepary bean include leafhopper, leaf-eating beetles, leaf miners, flea beetles, and leaf-eating caterpillars (Debouck 1999; Freytag and Debouck 2002).

This chapter provides an overview of the identities and relationships, distributions, genetic resource potential, and conservation status of the North American wild relatives of *Phaseolus* beans. We focus on the progenitors and close relatives of the domesticated species, as they are considered the most promising taxa with regard to successful present and future uses as genetic resources (Harlan and de Wet 1971). We also provide details on *Phaseolus polystachios* (L.) Britton et al., a distant relative of lima bean which is the most northerly occurring wild species in the genus, known by the authors to be declining in portions of its natural habitat. We conclude with a discussion of the key steps needed to improve the conservation of North American *Phaseolus* crop wild relatives.

4.2 Crop Wild Relatives of *Phaseolus* Beans and the Relationships Between Wild Taxa and the Domesticated Species

Phaseolus is a monophyletic genus native to the New World, comprising some 70–85 species and ca. 30 infraspecific taxa, which are currently parsed into eight phylogenetic groups within two clades (Freytag and Debouck 2002; Delgado-Salinas et al. 2006; Ramírez-Villegas et al. 2010) (Fig. 4.1). The total number of species may reach 100 or more with thorough fieldwork in understudied areas of the neotropics in combination with phylogenetic analyses, in further search of narrow endemic taxa (D. Debouck personal communication 2017).

The *vulgaris* group includes all cultivated species except *P. lunatus*, along with four other noncultivated species, including the newly described *Phaseolus debouckii* A. Delgado, segregated from *P. vulgaris* based on genome-wide single nucleotide polymorphisms (Rendón-Anaya et al. 2017a, b). The *lunatus* group includes at least five wild species, while its sister clade, the *polystachios* group, includes nine or more taxa (Fig. 4.1).

Phaseolus species have been organized into genetic relative categories, or “genepools,” based on crossing studies and phylogenetic analyses (Smartt 1981; Singh and Jauhar 2005; Rendón-Anaya et al. 2017a, b; The Harlan and de Wet Crop Wild Relative Inventory 2017; USDA, ARS, National Plant Germplasm System 2017b). The primary genepool of domesticated species includes both cultivated forms and wild populations, hybrids of which are generally fully fertile with no major reproductive barriers (Harlan and de Wet 1971) (Table 4.1).

The secondary genepool is comprised of related species that may be crossable with the cultivated forms, but with extra effort needed to overcome reproductive barriers and to eliminate linkage drag (Prohens et al. 2017; Miller and Khoury 2018). Common bean has been successfully crossed with species in its secondary genepool; lima and tepary bean may be less capable of gene exchange with their secondary relatives, although their potential has not been as comprehensively studied (Debouck 1999; D. Debouck personal communication 2017). Tertiary relatives and other distantly related taxa within the genus are not considered in detail here, as their potential for utilization as genetic resources is constrained by major biological barriers to interfertility, although advancing techniques may make utilization of distant relatives more feasible in the future (Zhang et al. 2014; Miller and Khoury 2018).

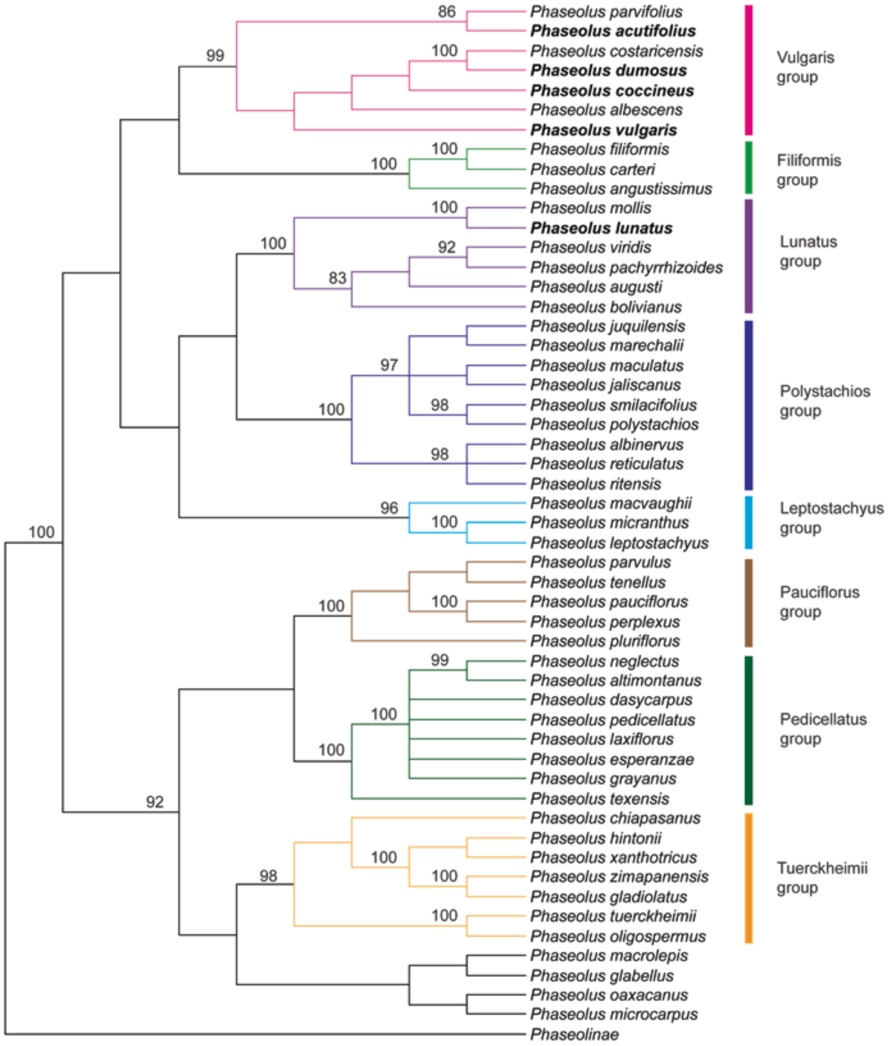

Fig. 4.1 Phylogenetic tree of *Phaseolus* groups, modified from the trnK-ITS maximum parsimony analysis of Delgado-Salinas et al. (2006), with the nodal supports value noted above key clades. Groups defined as in Delgado-Salinas et al. (1999). Domesticated species are in bold

4.3 Distribution of Wild *Phaseolus* in North America

The genus *Phaseolus* originated in the tropics and subtropics of the New World. Wild species belonging to the genus are naturally distributed from the USA south to Argentina (Ramírez -Villegas et al. 2010). Taxa are not known from Chile nor from Canada (Freytag and Debouck 2002), although Sousa and Delgado-Salinas (1993)

Table 4.1 Genepools of *Phaseolus* domesticated species

Common bean – *Phaseolus vulgaris* L., *Phaseolus vulgaris* L. var. *vulgaris*		
Primary relatives	**Secondary relatives**	**Tertiary relatives**
Phaseolus vulgaris L. (including *Phaseolus vulgaris* L. var. *aborigineus* (Burkart) Baudet and *Phaseolus vulgaris* L. var. *mexicanus* A. Delgado)	*Phaseolus albescens* McVaugh ex R. Ramírez & A. Delgado	*Phaseolus acutifolius* A. Gray
	Phaseolus coccineus L.	*Phaseolus acutifolius* A. Gray var. *acutifolius*
	Phaseolus costaricensis Freytag & Debouck	*Phaseolus acutifolius* A. Gray var. *tenuifolius* A. Gray
	Phaseolus dumosus Macfady	*Phaseolus angustissimus* A. Gray
	Phaseolus debouckii A. Delgado	*Phaseolus carteri* Freytag & Debouck
	Phaseolus persistentus Freytag & Debouck	*Phaseolus filiformis* Benth.
		Phaseolus maculatus Scheele subsp. *ritensis* (M. E. Jones) Freytag
		Phaseolus parvifolius Freytag
Runner bean – *Phaseolus coccineus* L.		
Primary	**Secondary**	**Tertiary**
Phaseolus coccineus L.	*Phaseolus albescens* McVaugh ex R. Ramírez & A. Delgado	*Phaseolus acutifolius* A. Gray
	Phaseolus costaricensis Freytag & Debouck	
	Phaseolus dumosus Macfady	
	Phaseolus vulgaris L.	
Year bean – *Phaseolus dumosus* Macfady		
Primary	**Secondary**	**Tertiary**
Phaseolus dumosus Macfady	*Phaseolus albescens* McVaugh ex R. Ramírez & A. Delgado	*Phaseolus parvifolius* Freytag
	Phaseolus coccineus L.	
	Phaseolus costaricensis Freytag & Debouck	
	Phaseolus vulgaris L.	
Tepary bean – *Phaseolus acutifolius* A. Gray		
Primary	**Secondary**	**Tertiary**
Phaseolus acutifolius A. Gray var. *acutifolius*	*Phaseolus parvifolius* Freytag	*Phaseolus albescens* McVaugh ex R. Ramírez & A. Delgado

(continued)

Table 4.1 (continued)

Phaseolus acutifolius A. Gray var. *tenuifolius* A. Gray		*Phaseolus carteri* Freytag & Debouck
		Phaseolus coccineus L.
		Phaseolus costaricensis Freytag & Debouck
		Phaseolus dumosus Macfady
		Phaseolus filiformis Benth.
		Phaseolus persistentus Freytag & Debouck
		Phaseolus vulgaris L.
Lima bean – *Phaseolus lunatus* L.		
Primary	**Secondary**	**Tertiary**
Phaseolus lunatus L.	*Phaseolus augusti* Harms	*Phaseolus acinaciformis* Freytag & Debouck
	Phaseolus longiplacentifer Freytag	*Phaseolus albinervus* Freytag & Debouck
	Phaseolus mollis Hook. f.	*Phaseolus jaliscanus* Piper
	Phaseolus pachyrrhizoides Harms	*Phaseolus juquilensis* A. Delgado
	Phaseolus viridis Piper	*Phaseolus lignosus* Britton
		Phaseolus maculatifolius Freytag & Debouck
		Phaseolus maculatus Scheele
		Phaseolus marechalii A. Delgado
		Phaseolus nodosus Freytag & Debouck
		Phaseolus novoleonensis Debouck
		Phaseolus polystachios (L.) Britton et al.
		Phaseolus reticulatus Freytag & Debouck
		Phaseolus rotundatus Freytag & Debouck
		Phaseolus salicifolius Piper
		Phaseolus scrobiculatifolius Freytag
		Phaseolus sonorensis Standl.
		Phaseolus venosus Piper
		Phaseolus xolocotzii A. Delgado

Adapted from USDA-ARS National Plant Germplasm System (2017b), The Harlan and de Wet Crop Wild Relative Inventory (2017), Rendón-Anaya et al. (2017a, b), and D. Debouck personal communication (2017) report wild populations in southern Quebec and Ontario. Members also occur on the major Caribbean Islands (*Phaseolus dumosus* Macfady, *Phaseolus lunatus* L., and possibly *P. polystachios* [Liogier (1988)]), Bermuda (*Phaseolus lignosus* Britton), and the Galapagos Islands (*Phaseolus mollis* Hook. f.) (Ramírez -Villegas et al. 2010; Arani et al. 2017; Debouck 2017; USDA, ARS, National Plant Germplasm System 2017b).

The main areas of richness of species are Mesoamerica (from southern USA, Mexico, and Central America down to Panama), the northern Andean region (Colombia to northern Peru), and the central Andes (northern Peru, Bolivia, and northwest Argentina). Of these, the Mesoamerican center is the richest in number of taxa, reaching the highest concentrations in the highlands of central Mexico, northward along the Sierra Madre Occidental, and south to Chiapas (Nabhan 1990; Debouck 2000; Freytag and Debouck 2002; Ramírez-Villegas et al. 2010) (Fig. 4.2). Numerous rare endemic species are distributed in North America, especially in the Sierra Madre Occidental and Sierra Madre Oriental of Mexico.

The distributions of the primary and secondary relatives of the cultivated species are detailed below.

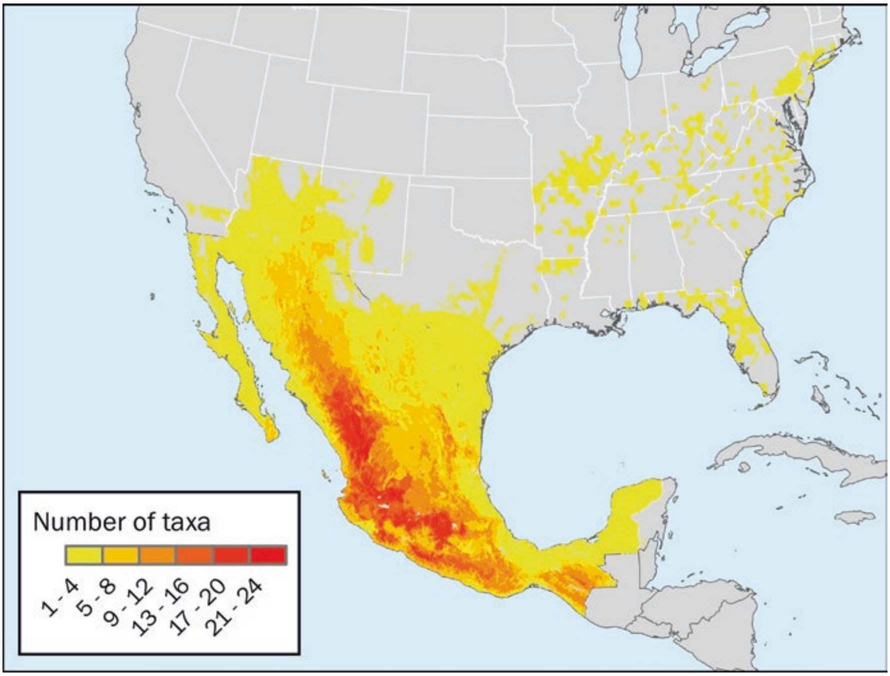

Fig. 4.2 Species richness map of modeled potential distributions of 57 North American *Phaseolus* taxa. The map displays overlapping potential distribution models for assessed taxa. Potential distribution models are based on climatic and edaphic similarities with herbarium and genebank reference localities and reflect potential for occurrence rather than confirmed presence. Warmer colors indicate areas where greater numbers of taxa potentially occur in the same geographic localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

4.3.1 Distributions of Close Relatives of Common Bean

Wild common bean (*P. vulgaris* L.) occurs from southern Chihuahua, Mexico, south through Central America and the Andes to Argentina (Nabhan 1985; USDA, ARS, National Plant Germplasm System 2017b) (Fig. 4.3). Populations are found from very arid conditions to over 100 cm annual precipitation (Gentry 1969; Freytag and Debouck 2002). The plant is often found growing over or in shrubs on the edges and within open pine-oak forests and woodlands, usually from 800 to 2000 m asl (Freytag and Debouck 2002). Wild common bean is usually found in shallow, often friable but sometimes heavy, soils, derived from limestone, schist, granite, lava, or tufa (Freytag and Debouck 2002). The plant is a short-lived perennial, generally producing seeds during its first year of growth on indeterminate climbing vines reaching over 3 meters long (Gentry 1969). The species produces vegetative growth during the rainy season, developing pods during the dry season, which varies by region, indicating a strong population-level adaptation to local climates (Gentry 1969). Wild common bean has been separated into multiple varieties, including *P. vulgaris* L. var. *aborigineus* [Burkart] Baudet and *Phaseolus vulgaris* L. var. *mexicanus* A. Delgado based on geographic and morphological differences. Here we follow Freytag and Debouck (2002) in treating the plants as one continuum within the species.

Fig. 4.3 Occurrence localities of North American *Phaseolus* primary and secondary wild relatives within the common bean (*P. vulgaris* L.), runner bean (*P. coccineus* L.), and year bean (*P. dumosus* Macfad.) genepools. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

Secondary relative *Phaseolus albescens* McVaugh ex R. Ramírez & A. Delgado is known from 16 populations distributed in montane forests in central Mexico, in the states of Colima, Guerrero, Jalisco, and Michoacan (Ramírez-Delgadillo and Delgado-Salinas 1999; Debouck 2017; USDA, ARS, National Plant Germplasm System 2017b) (Fig. 4.3). *Phaseolus costaricensis* Freytag & Debouck occurs in Costa Rica and Panama (USDA, ARS, National Plant Germplasm System 2017b), the newly described *Phaseolus debouckii* A. Delgado is distributed in Ecuador and northern Peru (Rendón-Anaya et al. 2017a), and *Phaseolus persistentus* Freytag & Debouck occurs in Guatemala (USDA, ARS, National Plant Germplasm System 2017b). Wild *Phaseolus coccineus L.* and *P. dumosus* are covered in the sections below. North American occurrences of these species are mapped in Fig. 4.3.

4.3.2 Distributions of Close Relatives of Runner Bean

Wild runner bean (*P. coccineus*) occurs from southern Chihuahua, Mexico south to Matagalpa, Nicaragua; reports outside that range are likely to be escapes from cultivation or misidentifications (Nabhan 1985; Freytag and Debouck 2002; USDA, ARS, National Plant Germplasm System 2017b; D. Debouck personal communication 2017) (Fig. 4.3). Wild runner bean is a climbing perennial with large red flowers that can vine up to 5 m. The species has been assigned several subspecies, some of which have purple flowers; white flowers are generally restricted to cultivated types (Freytag and Debouck 2002). Wild runner bean is normally found from 1500 to 2500 m asl in mixed forests of pine, oak, juniper, liquidambar, and hawthorn, growing over shrubs and herbs (Freytag and Debouck 2002). The various subspecies and varieties of wild *coccineus* appear to be adapted to specific climates and habitats, from cloud forest to desert and from rich to poor soils (Freytag and Debouck 2002). Some types are quite rare, such as *Phaseolus coccineus* L. subsp. *coccineus* var. *griseus* (Piper) Freytag, occurring in dry conditions of southern Oaxaca in scrub oak and mesquite (Freytag and Debouck 2002).

4.3.3 Distributions of Close Relatives of Year Bean

Wild year bean (*P. dumosus*) is distributed in Chiapas in southern Mexico and in Guatemala and is naturalized in other regions of Central America as well as in the Caribbean (USDA, ARS, National Plant Germplasm System 2017b) (Fig. 4.3). Only four populations are known in Mexico (Freytag and Debouck 2002; Debouck 2017), in humid pine-oak forests, growing on very steep slopes and along streams, mostly in open places, often over weeds and small trees, in deep, moist, well-drained, often sandy or rocky, humic soil derived from volcanic ash (Freytag and Debouck 2002).

4.3.4 Distributions of Close Relatives of Tepary Bean

Wild tepary bean (*Phaseolus acutifolius* A. Gray) mostly occurs at elevations of 335–2000 m asl from Arizona and New Mexico, USA, and south to Jalisco in central Mexico (Freytag and Debouck 2002; USDA, ARS, National Plant Germplasm System 2017b) (Fig. 4.4). Populations may extend into Texas and Baja California (Freytag and Debouck 2002). Wild tepary beans are annuals, with fibrous roots and small slender climbing vines. Plants are generally found along dry washes, streambeds, canyon bottoms, and floodplains in pine-oak forest and along trails, abandoned fields, and fence rows in drier areas (Freytag and Debouck 2002). *Phaseolus acutifolius* A. Gray var. *acutifolius* is somewhat sympatric with *Phaseolus acutifolius* A. Gray var. *tenuifolius* A. Gray, although variety *acutifolius* is thought to occur in drier conditions and generally more westerly in the Sierra Madre and lowlands, whereas variety *tenuifolius* occurs in the higher parts of the mountains and eastward (Freytag and Debouck 2002; D. Debouck personal communication 2017). A wild *Phaseolus acutifolius* A. Gray var. *latifolius* Freeman has been described as occurring from northwest Mexico and the southwestern USA (Freytag and Debouck 2002). Here we follow USDA-ARS National Plant Germplasm System (2017b) in considering it a synonym of var. *acutifolius*. Secondary relative *Phaseolus parvifolius* Freytag is distributed from Sonora and Baja California Sur, Mexico, south to Guatemala (Fig. 4.4).

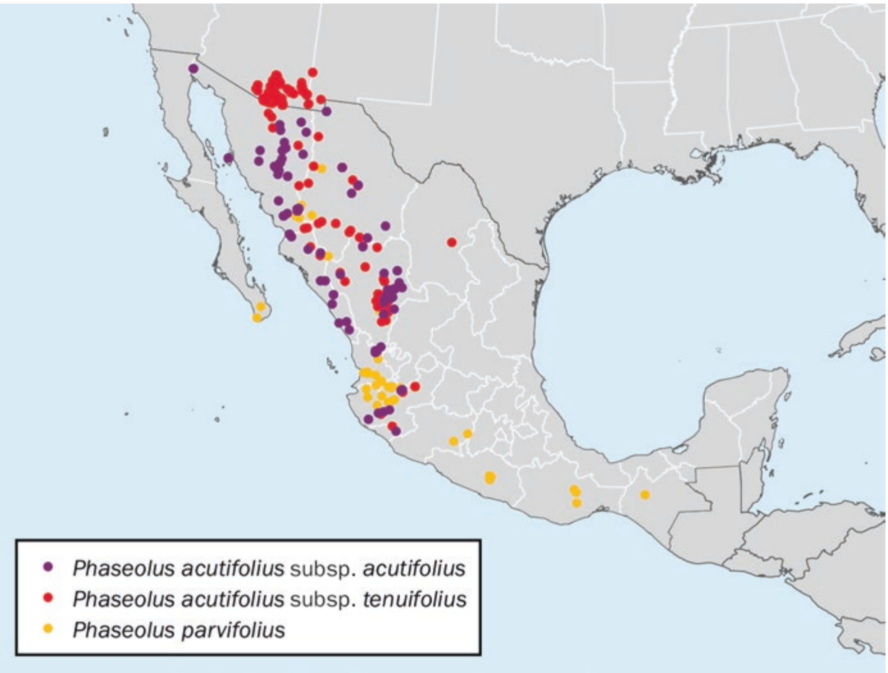

Fig. 4.4 Occurrence localities of North American *Phaseolus* primary and secondary wild relatives within the tepary bean (*P. acutifolius* A. Gray) genepool. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

4.3.5 Distributions of Close Relatives of Lima Bean

Wild lima bean (*P. lunatus* L.) is distributed from Sinaloa, Mexico, south through Central America to Brazil and Argentina (Freytag and Debouck 2002; USDA, ARS, National Plant Germplasm System 2017b) (Fig. 4.5). One population is known from Baja California Sur, Mexico. Wild lima bean is a climber, with vines up to 8 m long and with perennial, fibrous, and sometimes fleshy roots. The plant is mostly found along stream banks or other moist areas of pine-oak forests between 0 and 1600 m asl (Freytag and Debouck 2002). Wild lima bean often grows over shrubs and small trees in areas cleared for coffee, sugarcane and other crops, and is more abundant in areas inaccessible to grazing. The plant is adapted to a wide range of soil types derived from volcanic rock and ash, metamorphic schists, limestones, and basalt, from black clay to brown friable rock, and even in sand dunes (Freytag and Debouck 2002).

Phaseolus longiplacentifer Freytag is a narrow endemic species described by the senior author in Freytag and Debouck (2002), known only from its type collection north of Orizaba, Veracruz, Mexico. Delgado-Salinas et al. (2006) assigned *longiplacentifer* as a synonym of *Phaseolus viridis* Piper (1926), which is found in scattered places in Veracruz, Oaxaca, and Chiapas, Mexico, and in Alta Verapaz, Guatemala (Debouck 2017), while the senior author in Freytag and Debouck (2002)

Fig. 4.5 Occurrence localities of North American *Phaseolus* primary and secondary wild relatives within the lima bean (*P. lunatus* L.) genepool. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

considered *P. viridis* a synonym of (wild) *P. lunatus*. *Phaseolus augusti* Harms is distributed in Ecuador, Peru, Bolivia, and Argentina; *Phaseolus pachyrrhizoides* Harms occurs in Peru; and *P. mollis* is distributed only in the Galapagos Islands (USDA, ARS, National Plant Germplasm System 2017b).

4.4 Utilization of Wild *Phaseolus*

4.4.1 Utilization of Wild Phaseolus *as Genetic Resources*

Considerable genetic variation in cultivated common bean has existed historically as the result of multiple domestication events as well as further naturally occurring gene flow between wild progenitors and early domesticates, resulting in six to seven "races" within two main "genepools" with clear genetic structure (Acosta-Gallegos et al. 2007). The diversity in major commercial common bean varieties has been considered to be relatively narrow, though, and numerous authors have recommended a widening of this genetic base (e.g., Adams 1977; Singh 1992; Sonnante et al. 1994; Beebe et al. 1995; Singh 1999; Métais et al. 2002; Rosales-Serna et al. 2004).

Interspecific crosses are possible between domesticated *P. vulgaris*, *P. coccineus*, *P. dumosus*, and *P. acutifolius* (Fig. 4.6). *Phaseolus coccineus* and *P. dumosus* readily cross with *P. vulgaris* without embryo rescue, although the progeny have reduced viability when using *P. vulgaris* as the male parent (Al-Yasiri and Coyne 1966; Debouck 1999). *Phaseolus acutifolius* has been utilized in interspecific crosses with common bean, mostly through congruity crosses (alternate backcrossing), using embryo rescue with *P. vulgaris* as the cytoplasm source (Waines et al. 1988; Mejía-Jiménez et al. 1994; Anderson et al. 1996).

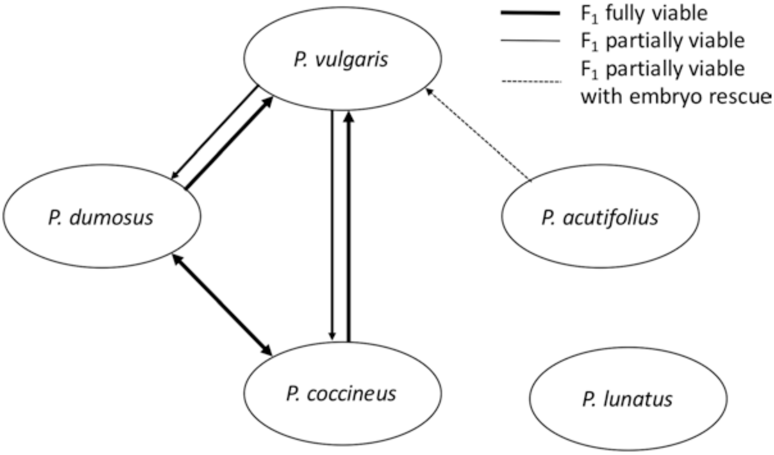

Fig. 4.6 Viability of interspecific crosses of the five domesticated species of *Phaseolus* based on Al-Yasiri and Coyne (1966), Smartt (1970), and Debouck (1999). The arrow points toward the female in the cross

Runner bean accessions have been employed in common bean breeding as new sources of resistance to bean golden yellow mosaic virus (Osorno et al. 2007), white mold (Schwartz et al. 2006; Singh et al. 2009; Vasconcellos et al. 2017), and common bacterial blight (Freytag et al. 1982; Miklas et al. 1999). Year bean accessions have been researched for resistance to anthracnosis (Mahuku et al. 2002), *Ascochyta* leaf blight (Schmit and Baudoin 1992), and white mold (Hunter et al. 1982) as well as to enhance nutritional quality (Blair 2013). Tepary bean accessions have contributed new sources of resistance to common bacterial blight, leafhopper, and bruchid (Singh et al. 1998), and the species has been explored for drought and heat tolerance (Rao et al. 2013). Although attempts to cross *P. vulgaris* and *P. lunatus* have mostly been unsuccessful (Al-Yasiri and Coyne 1966; Smartt 1970), viable but infertile plants have been reported (Mok et al. 1978), although not replicated (Debouck 1999).

Practical limitations constrain the use of wild germplasm for common bean cultivar improvement, as breeding is mainly restricted to the variation within market classes (Kelly et al. 1998; Singh 2001). The complexity of inheritance and genetic linkage of traits of commercial importance, such as seed color, seed size, and growth habit, has hindered the introgression of novel variation (Koinange et al. 1996; Kelly et al. 1999; Singh 2001; McClean et al. 2002; Blair et al. 2006; Moghaddam et al. 2016). The lack of useful characterization and evaluation data on wild accessions has also been considered a constraint. Wild accessions are avoided because of the limited power of evaluation of the germplasm for agronomically useful traits, due to attributes such as vigorous growth habits, long growing cycles, photoperiod sensitivity, and dehiscence (Singh 2001; Acosta-Gallegos et al. 2007). Finally, a simple lack of readily available wild germplasm may have constrained its use in bean breeding, particularly prior to the 1970s (Freytag and Debouck 2002).

That said, *Phaseolus* wild relatives are considered to possess valuable traits that may be difficult to find in domesticated materials (Porch et al. 2013b; Rao et al. 2013). Target traits in common bean research with focus on wild *vulgaris* germplasm have included resistance to storage insects, leafhoppers, *Ascochyta* blight, common bacterial blight, white mold, BCMV, *Fusarium* root rot, and rust, and tolerance to abiotic stresses and low soil fertility, as well as early maturity, adaptation to higher latitudes, upright plant type, pod quality, seed size, seed yield, protein digestibility, and nodulation traits (Kornegay and Cardona 1991; Shellie-Dessert and Bliss 1991; Kipe-Nolt et al. 1992; Kornegay et al. 1993; Delgado-Salinas et al. 1999; Singh 2001; Acevedo et al. 2006; Blair et al. 2006; Acosta-Gallegos et al. 2007; Cortés et al. 2013; De Ron et al. 2015; Blair et al. 2016; Rodriguez et al. 2016).

Wild *P. vulgaris* has been successfully used in common bean breeding as a source of resistance to bruchids (Osborn et al. 1988, 2003; Kornegay et al. 1993), common bacterial and web blight (Beaver et al. 2012), white mold (Mkwaila et al. 2011), and for yield (Acosta-Gallegos et al. 2007; Wright and Kelly 2011; Porch et al. 2013b). In addition, wild *P. acutifolius* has been utilized in common bean breeding as a source of resistance to bruchids (Singh et al. 1998; Kusolwa et al. 2016),

Table 4.2 Accessions of wild *Phaseolus* published as utilized in common bean breeding. For accession codes, G refers to International Center for Tropical Agriculture (CIAT) collections and PI to USDA-ARS National Plant Germplasm System accessions

Trait	Source species	Accession	References
Bruchids	*P. vulgaris* L.	G12882, G12866, G12952, G02771	Osborn et al. (1988, 2003) and Kornegay et al. (1993)
Bruchids	*P. acutifolius* A. Gray	G40199	Singh et al. (1998) and Kusolwa et al. (2016)
Cold and drought	*P. acutifolius* A. Gray	PI 638833	Souter et al. (2017)
Common bacterial blight	*P. vulgaris* L.	PI 417662	Beaver et al. (2012)
Web blight	*P. vulgaris* L.	PI 417662	Beaver et al. (2012)
White mold	*P. vulgaris* L.	PI 318695	Mkwaila et al. (2011)
White mold	*P. costaricensis* Freytag & Debouck	G40604	Singh et al. (2009), Schwartz and Singh (2013)
Yield	*P. vulgaris* L.	G24423	Acosta-Gallegos et al. (2007)

low temperatures, and drought tolerance (Souter et al. 2017). *Phaseolus costaricensis* has contributed white mold resistance (Singh et al. 2009; Schwartz and Singh 2013). Wild *Phaseolus* accessions published as sources of traits utilized in common bean plant breeding programs are listed in Table 4.2.

Secondary relative *P. costaricensis* has also been noted as belonging to a germplasm group potentially having resistance to angular leaf spot, anthracnose, *Ascochyta* blight, bean golden mosaic virus, bean yellow mosaic virus, common bacterial blight, and *Fusarium* root rot, as well as cold tolerance (Singh 2001). Some distant relatives of common bean have been recorded as possessing interesting characteristics of potential value to breeding, although successful introgression would be difficult. Examples include *Phaseolus leptostachyus* Benth. for its determinate growth habit (Freytag and Debouck 2002), *Phaseolus angustissimus* A. Gray for cold tolerance (Balasubramanian et al. 2004), and the Mexican restricted endemic *Phaseolus leptophyllus* G. Don, whose unique leaf morphology may provide protection from water loss during drought stress (Freytag and Debouck 2002).

Widening of genetic diversity in the other *Phaseolus* crop species may also prove important, as species such as tepary bean are thought to possess relatively low levels of genetic variation in cultivated forms (Schinkel and Gepts 1988; Garvin and Weeden 1994; Munoz et al. 2006). With regard to lima bean, tertiary relatives *Phaseolus jaliscanus* Piper, *Phaseolus maculatus* Scheele, *Phaseolus maculatus* Scheele subsp. *ritensis* (M. E. Jones) Freytag, *P. polystachios*, and *Phaseolus salicifolius* Piper have been noted for their disease resistance (van der Maesen and Somaatmadja 1992).

4.4.2 *Direct Uses of Wild* Phaseolus *Species*

The seeds of wild common and lima beans are used as food by indigenous peoples in times of scarcity but are not regularly consumed (Gentry 1969; Freytag and Debouck 2002; Zizumbo-Villareal et al. 2012). Kaplan (1965) noted that the roots of wild runner bean are poisonous, but that tubers which form on the roots are occasionally boiled for consumption. Wild *vulgaris*, *coccineus*, and *acutifolius* var. *tenuifolius* are known to be grazed by cattle and goats (Freytag and Debouck 2002). A number of additional wild *Phaseolus* species were probably occasionally consumed and possibly even cultivated, including *P. polystachios* (possibly cultivated) (Kaplan 1965), *P. leptostachyus*, and *Phaseolus glabellus* Piper (Freytag and Debouck 2002).

4.5 Conservation of Wild *Phaseolus* in North America

4.5.1 *In Situ Conservation of Wild* Phaseolus *in North America*

NatureServe has published conservation assessments for 17 currently accepted *Phaseolus* taxa (NatureServe 2017). Of these only *Phaseolus texensis* A. Delgado & W. R. Carr is listed as a threatened species (i.e., G1 or G2), assigned a G2 (imperiled) status. The species is narrowly endemic to rocky canyons in the eastern and southern parts of the Edwards Plateau of Texas and is known from only a few localities (Delgado-Salinas and Carr 2007). *Phaseolus supinus* Wiggins & Rollins is also listed imperiled and is also present (although not listed) in the US Fish and Wildlife Service Environmental Conservation Online System (USFWS 2017), but this species is no longer an accepted *Phaseolus* taxon, having been reassigned as *Macroptilium supinum* (Wiggins & Rollins) A. Delgado et al. (USDA, ARS, National Plant Germplasm System 2017b).

The IUCN Red List of Threatened Species lists *P. lignosus*, the Bermuda endemic, as Critically Endangered (Copeland et al. 2014). The species is restricted to six populations due to habitat loss and invasive species, and surveys completed in 2004 counted a total of only 29 mature individuals, which may be all that are left of naturally occurring plants. Surveys conducted in 2014 were successful in finding populations only within Walsingham Natural Reserve, although it may also occur in three other protected areas in Bermuda. *Phaseolus lignosus* is listed as Critical Risk B1, C, at Level 3 in Bermuda, under the Protected Species Order 2012, and benefits from a recovery plan led by Bermuda Department of Environment Protection, including habitat protection and restoration as well as ex situ conservation. Seeds are in long-term storage at the International Center for Tropical Agriculture and at Kew’s Millennium Seed Bank, and propagation efforts have translocated the species to five sites, where populations appear to be viable (Copeland et al. 2014; Debouck 2015).

The Red List also covers *P. polystachios* and *Phaseolus xanthotrichus* Piper, both as species of Least Concern, assessed as widespread species with generally stable populations (Contu 2012; Groom 2012). Recent efforts by authors Kisha and Egan to document the extant range of *P. polystachios* relative to historical collections have revealed a striking decline in range and commonality therein, particularly along northern and western range boundaries (T. Kisha & A.N. Egan personal observations 2017). Furthermore, while *P. polystachios* has a wide range within North America, it is now declared extirpated from Michigan (MI DNR 2017), Connecticut (CT DEEP 2015), and Pennsylvania (PA Natural Heritage Program Species Lists 2014) and imperiled in several others (NatureServe 2017).

The IUCN Red List and NatureServe programs currently offer no information on a large number of endemic and otherwise rare North American *Phaseolus* taxa, including *Phaseolus polystachios* (L.) Britton et al. subsp. *smilacifolius* (Pollard) Freytag occurring in Florida; *Phaseolus carteri* Freytag & Debouck in Baja California Sur, *Phaseolus amabilis* Standl. in Chihuahua; *Phaseolus reticulatus* Freytag & Debouck in Durango; *Phaseolus albiflorus* Freytag & Debouck, *Phaseolus albiviolaceus* Freytag & Debouck, *Phaseolus altimontanus* Freytag & Debouck, *Phaseolus maculatifolius* Freytag & Debouck, *Phaseolus novoleonensis* Debouck, *Phaseolus neglectus* F. J. Herm., and *Phaseolus trifidus* Freytag in Nuevo Leon, Tamaulipas, and/or Coahuila; *Phaseolus purpusii* Brandegee in San Luis Potosi; *P. jaliscanus*, *Phaseolus esperanzae* Seaton, *Phaseolus magnilobatus* Freytag & Debouck, *Phaseolus marechalii* A. Delgado, and *Phaseolus rotundatus* Freytag & Debouck in central Mexico; *Phaseolus leptophyllus* G. Don in Guerrero; and *Phaseolus chiapasanus* Piper in southern Mexico. Conservation status and threat assessment information are needed for such species to be able to prioritize conservation action.

Aside potentially from the populations of wild *Phaseolus* monitored in the Sierra de Manantlan Biosphere Reserve in Jalisco and Colima, Mexico (Vázquez-García 1995), no active management of wild *Phaseolus* in protected areas is known by the authors to be ongoing in North America. And even in the Biosphere Reserve, the mention by Vázquez-García et al. (1995) of two unidentified species clearly indicates that the first limiting factor for in situ conservation is that protected areas lack a complete inventory of plants (D. Debouck personal communication 2017).

In situ conservation is certainly occurring in federal, state, provincial, Native American, Indigenous Peoples, nongovernmental, and privately managed protected areas without inventories, active management plans, or regularly scheduled monitoring. But information on these populations is not available. Outside of these areas, wild *Phaseolus* populations are considered to be vulnerable to habitat destruction (Freytag and Debouck 2002) and potentially (for progenitor species) to genetic contamination due to gene flow with cultivated forms (Papa and Gepts 2003).

4.5.1.1 Remarks on *Phaseolus polystachios* (L.) Britton et al.

Phaseolus polystachios, the North American wild kidney bean or thicket bean, is the only *Phaseolus* species native to temperate North America, with a distribution from Texas to Connecticut, USA. As such, it has evolutionarily adapted to different climatic, ecological, and pest conditions compared to most of its congeners and may thus harbor unique genetic traits that could prove useful for *Phaseolus* breeding efforts. The thicket bean is an herbaceous, perennial vine with tuberous roots that overwinter. Thicket bean is known to have hypogeal germination wherein the seed and cotyledons can stay below ground through germination, a trait that may have enabled *P. polystachios* to flourish in colder latitudes (Dhaliwal and Pollard 1962).

Phaseolus polystachios has a documented distribution reaching from New England to Florida, west to the eastern edges of Texas, and north to Michigan. The plant favors the edges of forests, roads, and streams where it has garnered its name by twining into thickets in rather open areas, particularly on slopes with southwestern, southern, and southeastern aspects. The thicket bean can establish colonies on open forest slopes, but it much prefers well-drained soils and full-sun conditions (Allard 1947). The thicket bean prefers an intermediate day length, with too-short or too-long days hampering its growth. Depending on latitude, *P. polystachios* will flower between June and September and fruit between August and November.

Thicket bean's wide range may have been historically augmented by indigenous gathering, caching, or even cultivation. Seeds or phytoliths of *P. polystachios* have been identified at the Parkin site in Arkansas, dating from the fifteenth to sixteenth centuries (Scarry and Reitz 2005) and much earlier from the Hunter's Home site in New York, with potential dates as early as 2500 B.C. (Hart et al. 2008). That said, even with its wide distribution, the thicket bean is not commonly found within its range and seems to be on the decline. The plant is considered extirpated in Michigan, where it was historically documented from the Detroit River International Wildlife Refuge, Pennsylvania, where author A.N. Egan failed to find any extant populations at 21 historical localities, and in Connecticut, listed as special concern by state agencies as of November 2017 (see above). Thicket bean's decline may be due to competitive exclusion from nonnative, introduced vines, habitat destruction from urban development (e.g., there are old herbarium records of populations located within what are now highly urbanized New York City and Washington DC [D. Debouck personal communication 2017]), quarrying, mowing, herbicide use, and fire suppression around human-built structures (A.N. Egan, personal observation 2017). Authors A.N. Egan and T. Kisha have completed extensive locality studies across its range, visiting over 200 locations in efforts to collect plants, but averaged about a 25% success rate of finding extant populations from historical collection locality information or firsthand knowledge of state and federal botanists.

The closest cultivated relative of *P. polystachios* is lima bean, which is susceptible to white mold (*Sclerotinia sclerotiorum* (Lib.) de Bary), leading to flower drop, emergence issues, and pod set failure. Through coevolution in its natural habitat, *P. polystachios* may have acquired true resistance to the ubiquitous pathogen.

Further, transfer of the hypogeal germination trait to lima bean may be useful. Several decades ago, successful crosses between the two species were made, but hybrids showed high pollen sterility, likely due to meiotic irregularities due to chromosomal and genetic differences (Dhaliwal and Pollard 1962). With advances in plant breeding and genetics techniques, renewed efforts to tap into the *P. polystachios* genome may be fruitful for lima bean improvement. One *P. lunatus* x *P. polystachios* hybrid accession (G40503) is represented in the CIAT collection, originating from the work of Albert P. Lorz of the University of Florida (D. Debouck personal communication 2017).

The USDA-ARS National Plant Germplasm System (NPGS) safeguarded until recently only 13 accessions of *P. polystachios*, six of which were collected in 2013 in Florida. Recent explorations supported by the NPGS have augmented the holdings. A trip throughout Ohio in 2015 by authors Egan and Kisha increased holdings by 11 accessions, and a 2016 trip to Virginia, North Carolina, and South Carolina by Egan increased holdings by 19 accessions. In 2017, trips by Egan to Alabama, Arkansas, Mississippi, and Louisiana yielded 25 more accessions, while a trip by Kisha to Kentucky and Tennessee yielded an additional 10. Enrichment of germplasm collections from across the range of *P. polystachios* will enable a much more comprehensive assessment of genetic diversity within the species, providing valuable knowledge to in situ conservation efforts, and may in addition help to reveal further traits of value for crop improvement. Genetic diversity studies are currently underway by Kisha and Egan.

4.5.2 Ex Situ Conservation of Wild Phaseolus *in North America*

Significant ex situ collections of wild *Phaseolus* are maintained at the International Center for Tropical Agriculture (CIAT), Colombia (ca. 2000 accessions); the USDA-ARS National Plant Germplasm System (ca. 900 accessions), within the Sistema Nacional de Recursos Fitogenéticos para la Alimentación y la Agricultura (SINAREFI) Conservation Centers Network in Mexico (ca. 400 accessions); and the Botanic Garden Meise, Belgium (ca. 400 accessions).

Counts of accessions of *Phaseolus* taxa are provided in Table 4.3. Of 94 taxa, 25 (26.6%) are not represented at all in these ex situ conservation facilities, and another 27 (28.7%) are represented by less than ten accessions, making over half of *Phaseolus* taxa highly underrepresented in these genebanks. Given that some duplication exists between the major collections as a result of collaborative collecting missions and recent repatriation (e.g., repatriation of 915 wild Mexican *Phaseolus* accessions maintained at CIAT to the Centro Nacional de Recursos Genéticos [CNRG] of the Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias [INIFAP]) (F. de la Torre personal communication 2017), the number of unique accessions held in these facilities is likely even less than the total counts for most taxa.

Table 4.3 Counts of accessions in major wild *Phaseolus* collections databases

Taxon	CIAT	USDA-ARS NPGS	Mexico SINAREFI	Botanic Garden Meise	BGCI	GENESYS
Phaseolus acinaciformis	1					
Phaseolus acutifolius		53 (33)	101*		10*	1130*
Phaseolus acutifolius var. *acutifolius*	81	36 (16)		34	2	92
Phaseolus acutifolius var. *tenuifolius*	84	55 (50)	2	10	2	75
Phaseolus albescens	1		1			
Phaseolus albicarminus	1					
Phaseolus albiflorus	7	1 (1)	1	1	1	9
Phaseolus albinervus						
Phaseolus albiviolaceus	2		6			
Phaseolus altimontanus	1	1 (0)	2	1	1	3
Phaseolus amabilis						
Phaseolus amblyosepalus						
Phaseolus angustissimus	5	4 (2)		3	2	13
Phaseolus anisophyllus						
Phaseolus augusti	29	16 (1)		2	1	59
Phaseolus campanulatus						
Phaseolus carteri	1	2	1	1		4
Phaseolus chiapasanus	4	1		2	1	5
Phaseolus coccineus	168	74 (18)	716*	46	44*	2871*
Phaseolus coccineus subsp. *coccineus*		5 (0)				154
Phaseolus coccineus var. *coccineus*		17 (1)				243
Phaseolus coccineus var. *griseus*		2 (0)			1	2
Phaseolus coccineus var. *tridentatus*		1 (0)			1	1
Phaseolus costaricensis	27	6			1	18
Phaseolus dasycarpus						
Phaseolus dumosus	9	6 (3)	24*	2	2*	604*
Phaseolus esperanzae	7			1		8
Phaseolus esquincensis						
Phaseolus filiformis	36	19 (15)	4	10	4	97
Phaseolus glabellus	8	5 (1)	3	5	1	22
Phaseolus gladiolatus						
Phaseolus grayanus	2	18 (0)		5	2	25
Phaseolus hintonii	5	5 (2)	3	8	2	21
Phaseolus hygrophilus	1					
Phaseolus jaliscanus		2 (0)	1	1	1	3

(continued)

Table 4.3 (continued)

Taxon	CIAT	USDA-ARS NPGS	Mexico SINAREFI	Botanic Garden Meise	BGCI	GENESYS
Phaseolus juquilensis						
Phaseolus laxiflorus						
Phaseolus leptophyllus						
Phaseolus leptostachyus	105	31 (23)	45		2	144
Phaseolus leptostachyus var. *leptostachyus*		1 (0)		43	1	43
Phaseolus lignosus	2				1	1
Phaseolus longiplacentifer						
Phaseolus lunatus	220	74 (46)	280*	62	25*	6223*
Phaseolus macrolepis	2	2 (0)			1	3
Phaseolus maculatifolius			3			
Phaseolus maculatus	1	18 (0)		10	5	33
Phaseolus maculatus subsp. *maculatus*		1 (0)				2
Phaseolus maculatus subsp. *ritensis*		23 (4)		8		32
Phaseolus macvaughii	2	1	4	2	1	5
Phaseolus magnilobatus	4	1		1	1	3
Phaseolus marechalii	5	2 (0)		3	2	12
Phaseolus micranthus	1	1 (0)	2	2	1	4
Phaseolus microcarpus	29	17 (6)	19	15	3	76
Phaseolus mollis						
Phaseolus neglectus		1 (0)	2	2	1	5
Phaseolus nelsonii						
Phaseolus nodosus	1					
Phaseolus novoleonensis	1		2	1		1
Phaseolus oaxacanus	1					
Phaseolus oligospermus	13	2 (1)		6	1	21
Phaseolus opacus						
Phaseolus pachyrrhizoides	21	8		3	1	31
Phaseolus parvifolius	20	2 (0)	9	1	1	46
Phaseolus parvulus		12 (1)		3	2	15
Phaseolus pauciflorus				2		2
Phaseolus pedicellatus	7	3 (0)	12	3	2	12
Phaseolus perplexus		1 (0)			1	1
Phaseolus persistentus						
Phaseolus plagiocylix						
Phaseolus pluriflorus	1	3 (0)	1	3	1	7
Phaseolus polymorphus	1					1

(continued)

Table 4.3 (continued)

Taxon	CIAT	USDA-ARS NPGS	Mexico SINAREFI	Botanic Garden Meise	BGCI	GENESYS
Phaseolus polystachios	3	57 (1)			2	8
Phaseolus polystachios subsp. *polystachios*		7 (0)		3	1	10
Phaseolus polystachios subsp. *sinuatus*		3			1	2
Phaseolus purpusii						
Phaseolus reticulatus		1 (0)			1	1
Phaseolus rotundatus	2	2	6		1	4
Phaseolus salicifolius	1	1 (0)		1	1	2
Phaseolus scabrellus						
Phaseolus scrobiculatifolius						
Phaseolus smilacifolius						
Phaseolus sonorensis						
Phaseolus talamancensis	2	1 (0)			1	4
Phaseolus tenellus		2 (0)			1	2
Phaseolus teulensis						
Phaseolus texensis	1	1 (0)				1
Phaseolus trifidus						
Phaseolus tuerckheimii	13	2		1	1	6
Phaseolus venosus						
Phaseolus vulgaris	1032	176 (156)	3995*	99	33*	83092*
Phaseolus vulgaris var. *aborigineus*		112 (81)		7	2	225
Phaseolus xanthotrichus	41	8 (3)		11	1	55
Phaseolus xolocotzii				1		1
Phaseolus zimapanensis	8	8 (4)	12	7	2	24

Data from CIAT (2017); USDA-ARS National Plant Germplasm System (2017a), R. González Santos personal communication (2017), Botanic Garden Meise (2017), BGCI (2017), and Data Providers and the Crop Trust (2017)

CIAT, USDA-ARS NPGS, and Botanic Garden Meise databases were queried only for accessions noted as wild; Mexico SINAREFI, BGCI, and GENESYS database counts for *P. acutifolius*, *P. coccineus*, *P. dumosus*, *P. lunatus*, and *P. vulgaris* are likely to include cultivated forms and are marked with an "*." The GENESYS database includes information from over 400 institutes, mainly in the CGIAR, USDA-ARS NPGS, and European genebank systems (Data Providers and the Crop Trust 2017) and thus replicates the information from CIAT and USDA-ARS NPGS. For USDA-ARS NPGS, counts of currently available accessions are given in parentheses

Moreover, many of these accessions are unavailable to researchers due to a lack of adequate seed for distribution.

Ramírez-Villegas et al. (2010) assessed the comprehensiveness of major ex situ collections with regard to taxonomic, geographic, and environmental or ecological niche gaps (i.e., the degree of representation of the range of climates that wild

Phaseolus species occupy). Of 85 assessed taxa, they assigned 48 (56.5%) a high priority for further collecting due to being completely absent or highly underrepresented in major genebanks. Seventeen taxa were assigned medium priority for further collecting, 15 low priority, and only 5 assessed as adequately represented ex situ. Geographic hotspots for further collecting were concentrated in central Mexico, although various narrow endemic species occurring in other parts of the country were also prioritized (Ramírez-Villegas et al. 2010). Gap analyses for close relatives of common and lima bean performed more recently corroborated these results (Castañeda-Álvarez et al. 2016).

4.6 Final Remarks

The wild relatives of the five domesticated species of *Phaseolus* beans are clearly a very diverse group of plants extending widely across the New World. The majority of these species appear to be fairly well resolved and understood with regard to their taxonomy and distributions. Further research is still needed to clarify the identities and relationships among an additional dozen or more taxa, particularly with regard to narrow endemic species.

Aside from the progenitor of common bean and a few studies involving other relatives, the wild members of the bean crop genepools are still largely unexplored, despite indications that novel useful diversity may be found within them. Given the relative sensitivity of common bean to heat, drought, and other effects of climate change, numerous promising wild species, as well as domesticates such as *P. acutifolius*, may play an increasing role as contributors of valuable genetic resources to the crop. Contributions from wild relatives to improving agronomic and market-related traits in the other domesticated species would also be valuable to increasing their importance worldwide.

But these contributions can only be made if these resources are well conserved and available to plant breeders and other researchers. A number of wild *Phaseolus* are rare endemics that are threatened in their natural habitats and are insufficiently protected in situ. Aside perhaps from the progenitors and a few other species, the wild taxa are also largely underrepresented in major genebanks. Further efforts to enhance protection of vulnerable species in their natural habitats, and further collecting to fill critical gaps in germplasm collections, are highly warranted.

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Part II
Vegetables

Chapter 5
Wild *Lactuca* Species in North America

A. Lebeda, E. Křístková, I. Doležalová, M. Kitner, and M. P. Widrlechner

Abstract This chapter presents a brief history of the uses of lettuce (*Lactuca sativa* L.) and its wild North American relatives and reviews the agricultural importance of lettuce and challenges in its cultivation, in relation to nutritional quality, diseases, pests, and edaphic and climatic limitations. The evolution and taxonomy of the genus *Lactuca* are presented, with a primary focus on the wild *Lactuca* species of North America, their characterization, biogeography and distribution, habitat ecology, and genepools. Specific examples of phenotypic variability, genetic diversity, and disease resistance of wild *Lactuca* taxa from both published reports and recent evaluations conducted in our laboratory are also presented. The past (and future) exploitation of wild *Lactuca* relatives in lettuce breeding is examined and discussed in the broader context of crop improvement. The current status of in situ and ex situ conservation of wild and weedy North American *Lactuca* is reviewed, along with recommendations on how these genetic resources could be better conserved and utilized.

Keywords Wild lettuce · Genetic resources · Taxonomy · Biogeography · Genetic diversity · Conservation

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A. Lebeda (✉) · E. Křístková · M. Kitner
Department of Botany, Faculty of Science, Palacký University in Olomouc,
Olomouc, Czech Republic
e-mail: ales.lebeda@upol.cz

I. Doležalová
Department of Genetic Resources for Vegetables, Medicinal and Special Plants of Crop
Research Institute in Olomouc, Olomouc, Czech Republic

M. P. Widrlechner
Departments of Horticulture and of Ecology, Evolution and Organismal Biology,
Iowa State University, Ames, IA, USA

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5.1 Introduction

5.1.1 Origin of the Crop and Brief History of Use Worldwide

As one of the earliest domesticated vegetables (4000–8000 years BP), lettuce belongs to a core group of ancient crops (Hancock 2012). The center of diversity of related *Lactuca* species is in Southwestern Asia (Kuang et al. 2008), with lettuce likely originating from this region (Zohary and Hopf 1993). The earliest known artifacts related to lettuce originate from the tomb decorations in Egypt's Nile Valley. These decorations are similar to modern stalk or stem lettuce (Lebeda et al. 2007a). More recently, romaine lettuce probably arose in Italy in the thirteenth or fourteenth century. Head types of lettuce were noted for the first time in Southern Europe in the sixteenth century (Lebeda et al. 2007a). Domesticated lettuce was probably brought to the Americas on the second voyage of Columbus in 1494 (Hedrick 1972).

Lettuce (*Lactuca sativa* L.) is considered to be of polyphyletic origin and likely was selected from the genepool of *L. serriola* L. (Lebeda et al. 2007a; Kuang et al. 2008) (probably *L. serriola* f. *integrifolia* (Gray) S.D. Prince & R.N. Carter), followed by introgression of traits from other closely related *Lactuca* species (Lebeda et al. 2012b; Kitner et al. 2015) and similar DNA sequence profiles; it is highly probable that some *Lactuca* species (*L. azerbaijanica* Rech. f., *L. altaica* Fisch. & C.A. Mey., *L. aculeata* Boiss. & Kotschy, and *L. scarioloides* Boiss.) (Zohary 1991; Koopman et al. 1998) and probably also *L. dregeana* DC. (van Herwijnen and Manning 2017) played important roles in the evolution of cultivated lettuce.

The ongoing process of lettuce domestication (and breeding) is connected to the loss of typical features of wild *Lactuca* species. Systematic improvement and breeding of lettuce started in the second half of the nineteenth century in Europe and at the beginning of the twentieth century in North America (Lebeda et al. 2007a; Mikel 2007). The most important modifications include the absence of leaf trichomes, changes in leaf shape and structure, the formation of heads, delayed bolting and flowering, a reduced content of latex, and reduced bitterness (Lebeda et al. 2007a, 2009a). Recent breeding has been especially focused on leaf shape, shelf life, disease resistance, pest resistance, abiotic tolerance, nutritional quality, low nitrate content, and color variability (Lebeda et al. 2007a, 2009a, 2014).

Various species of wild lettuce have been prized for medicinal and dietetic purposes by indigenous North American people (Borchers et al. 2000). For example, *L. biennis* (Moench) Fernald was used to ease lactation by the Ojibwa Indians (Smith 1932), and the latex of *L. canadensis* L. was used as phytotherapy for warts by the Ojibwa (Densmore 1928) and skin inflammation (including eczema) by the Menominee Indians (Lewis and Elvin-Lewis 2003). Native Americans used the roots of blue lettuce (*L. tatarica* (L.) C.A. Mey. subsp. *pulchella* (Pursh) Stebbins) as chewing gum (Reagan 1929); an infusion of it was made to treat diarrhea (Turner et al. 1980); and the young leaves were eaten as a green vegetable (Anonymous 2011), as were the leaves of *L. canadensis* (Hamel and Chiltoskey 1975) and *L. ludoviciana* (Nutt.) Riddell (Chamberlin 1911). In more recent times, an introduced species, opium, or acrid lettuce (*L. virosa* L.) has been used by indigenous people for treating gastroenteritis (Hocking 1956) and for sedative purposes, especially for nervous complaints, but also as an aid in seeking meditative trances and visions (Anonymous 2016a, b). The health benefits of *L. virosa* tea have long been suspected (Anonymous 2016a, b). These examples, which are not meant to be exhaustive, demonstrate that wild *Lactuca* taxa have played an important role in the lives of the native people of North America and suggest potential modern applications.

5.1.2 Modern-Day Use

Lettuce is one of the most important vegetable crops and the most popular leafy vegetable crop. It is almost exclusively used as a fresh, uncooked product with moderate dietetic value. Lettuce is diverse, occurring in at least seven distinct types (crisphead, cos (romaine), butterhead, leaf, latin, stem (stalk), and oilseed) (Lebeda et al. 2007a). However, recently new morphotypes (e.g., red leaf, baby lettuce) have been developed that do not fit into pre-existing categories. Currently, at least eight horticultural types divided on the basis of head shape and size, the shape, size and texture of the leaves, stem length, and seed size are under wide cultivation (Simko et al. 2014a, b). All these forms, except for two (stem and oilseed), are typically consumed raw (Rubatzky and Yamaguchi 1997; Welbaum 2015).

Lettuce is produced on a commercial scale in many countries worldwide but is also frequently grown in small gardens. As a commercial crop, it is very important in Asia, North and Central America, and Europe (Lebeda et al. 2007a), and, recently, lettuce production has been increasing in Australia (FAOSTAT 2016). About 80% of lettuce world production in 2011 (24.3 million tons) originated from four countries: China (52.3%), the USA (16%), India (4.4%), and Spain (3.6%) (Simko et al. 2014b; FAOSTAT 2013). In North America, lettuce production is concentrated in the USA, especially in California and Arizona, but there is also some production near Toronto and Montreal in Canada. In 2015, lettuce (head, leaf, and romaine) for fresh market was planted on ~100,000 ha in the USA, with a total production of 3,667,910 metric tons and a cash value of nearly $3 billion (USDA – NASS 2016). In Canada, the total area of harvested lettuce and chicory in 2013 was 3642 ha, with total production of ca 75,000 metric tons (FAOSTAT 2016).

5.1.3 Challenges in Cultivation

5.1.3.1 Diseases, Pests, and Edaphic and Climatic Limitations

It is well known and widely accepted that wild crop relatives may serve as suitable sources of resistance against biotic and abiotic stressors (Burdon and Jarosz 1989). Understanding the genetic diversity of wild *Lactuca* species is a crucial phenomenon for future progress in lettuce improvement (Lebeda et al. 2007a, 2009a, 2014). The breeding of lettuce resistant to biotic (pathogens and pests) and abiotic (edaphic and climatic factors) stressors is currently most often achieved by combining desirable resistance alleles from sexually compatible wild *Lactuca* species (Lebeda et al. 2009a, 2014; Simko 2013). Our knowledge of wild *Lactuca* species as donors (sources) of important resistance traits and of existing gaps has been summarized in detail by Lebeda et al. (2007a, 2009a, 2014) and Simko (2013).

During recent decades, lettuce breeding projects have been increasingly focused on developing complex resistance to pathogens and pests (Pink and Keane 1993; Ryder 1999; Lebeda et al. 2007a, 2014; Mou 2008). There is also increasing interest for breeding to overcome certain abiotic factors and physiological disorders (e.g., salinity, soil characteristics, different photoperiod regimens, cold injury) and nutrient deficiencies (Lebeda et al. 2007a; Simko et al. 2014b). In all cases, the availability of wild *Lactuca* germplasm with suitable traits is crucial for breeding (Lebeda et al. 2007a, 2014).

There are large numbers of pathogens, pests, and various physiological disorders that damage lettuce (Davis et al. 1997a; Barkai-Golan 2001; Capinera 2001; Blancard et al. 2003; Chamont et al. 2010). However, our knowledge of diseases and pests on wild *Lactuca* taxa is limited (Lebeda et al. 2008; Lebeda and Mieslerová 2011), especially on *Lactuca* taxa occurring in North America (Lebeda et al. 2012a). Some diseases and pests have global distribution and significant economic impacts; others are damaging only on a local scale (Barrière et al. 2014). Economically important diseases and insect pests affecting the yield components of lettuce in North America were summarized by Simko et al. (2014b) (Table 5.1). However, the situation is very dynamic; some pathogens are moving into new areas, and new strains and races arise that overcome resistance in modern cultivars (Lebeda et al. 2014).

Wild *Lactuca* germplasm includes resistance to various diseases, pests, and abiotic stresses, having been widely used in lettuce resistance breeding since the 1930s (Lebeda et al. 2002, 2007a; Parra et al. 2016; Lebeda et al. 2014; Petrželová et al. 2011; van Treuren et al. 2013). However, our current knowledge about these interactions is small and covers only a limited part of the potential variation in host-pathogen/pest and environmental (edaphic and climatic factors) interactions. We clearly need more field studies and collecting activities, as well as screening large collections of well-defined wild *Lactuca* germplasm for resistance to the most important lettuce pathogens and pests (Lebeda et al. 2011, 2012a, 2014).

5.1.3.2 Nutritional, Functional Use

Traditionally, lettuce was harvested and directly marketed as whole fresh heads and generally consumed raw. However, during the last three decades, three important changes occurred (Ryder 1999) which have a major influence on the storability, quality, and nutritional value of lettuce: (1) the development of plastic-wrap

Table 5.1 Economically important diseases and insect pests affecting lettuce yield components (survival, weight, architecture/appearance) in North America (modified following Simko et al. (2014b)) and availability of adequate resistance sources in wild *Lactuca* species germplasm (modified following Lebeda et al. 2009a, 2014)

Disease, pathogen, or pest	Wild *Lactuca* species as donors of resistance
Big-vein (*Mirafiori lettuce big-vein virus*)	*L. virosa* L.
Lettuce dieback (*Tomato bushy stunt virus* and *Lettuce necrotic stunt virus*)	*L. serriola* L., *L. saligna* L., *L. virosa* L.
Lettuce mosaic (*Lettuce mosaic virus*)	*L. serriola* L., *L. saligna* L., *L. virosa* L., *L. perennis* L., *L. tatarica* (L.) C.A. Mey.
Tomato spotted wilt virus and	*L. serriola* L., *L. saligna* L.
Impatiens necrotic spot virus	
Bacterial leaf spot (*Xanthomonas campestris* pv. *vitians*	
(Brown) Vauterin, Hoste, Kersters & Swings)	n.p.
Corky root (*Rhizomonas suberifaciens* van Bruggen et al.)	*L. serriola* L., *L. saligna* L., *L. virosa* L.
Lettuce downy mildew (*Bremia lactucae* Regel)	*L. serriola* L., *L. saligna* L., *L. virosa* L., *L. indica* L., *L. quercina* L., *L. aculeata* Boiss. & Kotschy, *L. biennis* L., *L. tatarica* (L.) C. A. Mey., *L. viminea* (L.) J. Presl & C. Presl
Lettuce powdery mildew (*Golovinomyces cichoracearum* s.str. (DC) VP Gelyuta)	*L. serriola* L., *L. saligna* L., *L. virosa* L., *L. perennis* L., *L. quercina* L., *L. sibirica* (L.) Benth. ex Maxim., *L. aculeata* Boiss. & Kotschy, *L. tatarica* (L.) C. A. Mey., *L. tenerrima* Pourr., *L. viminea* (L.) J. Presl & C. Presl
Verticillium wilt (*Verticillium dahliae* Kleb.)	*L. serriola* L., *L. virosa* L.
Fusarium wilt (*Fusarium oxysporum* f. sp. *lactucae*)	n.p.
Lettuce drop (*Sclerotinia minor* Jagger and *Sclerotinia sclerotiorum* (Lib.) de Bary)	*L. serriola* L., *L. virosa* L.
Phoma basal rot (*Phoma exigua* Desm.)	n.p.
Bottom rot (*Rhizoctonia solani* J.G. Kühn)	n.p.
Lettuce aphid (*Nasonovia ribisnigri* Mosely)	*L. serriola* L., *L. virosa* L., *L. perennis* L.
Leaf miners (*Liriomyza langei* Frick, *L. trifolii* Burgess, and *L. sativae* Blanchard)	*L. serriola* L., *L. saligna* L., *L. virosa* L.

n.p. none yet published

packaging for crisphead lettuce, (2) chopping or shredding the heads and packaging in plastic bags, and (3) the development of mesclun and other salad mixes containing several types of lettuce and/or other leafy vegetables (Rubatzky and Yamaguchi 1997).

As consumption of salad mixes becomes more popular, lettuce can contribute to the nutritional content of human diets (Kenny and O'Beirne 2009). The consumption of salads consisting of first leaves (cotyledons) or seedlings (baby leaf) has been gaining popularity as a culinary trend, which has been driven both by the growers' marketing strategies for higher profit and the consumers' increased demands (Kim et al. 2016). However, the potential nutritional contributions of lettuce have been underestimated from the perspectives of research on lettuce germplasm and breeding, as well as in growing and marketing (Lebeda et al. 2007a).

Lettuce has a high water content (95%); has few calories, fat, and sodium; and is good source of fiber, iron, folate, vitamin C, and other health-beneficial bioactive compounds (e.g., carotenoids and phenolics). The nutritional quality of lettuce differs significantly among the various horticultural types. Leaf and romaine lettuces have much higher vitamin and mineral contents than do the crisphead type (Mou 2008). Leaf and romaine lettuces also contain folate (vitamin B_9) concentrations. Baby green romaine is high in vitamin C, while butterhead, romaine, and leaf lettuces are high in β-carotene and lutein (Kim et al. 2016). Recent studies have shown anti-inflammatory, cholesterol-lowering, and antidiabetic activities and gastroprotective effects attributed to the bioactive compounds in lettuce (Chadwick et al. 2016).

Unfortunately, we have few detailed analytical studies focused on the content of nutrients in wild *Lactuca* germplasm. Mou (2005) reported that *L. serriola*, *L. saligna*, *L. virosa*, and primitive forms of lettuce had higher β-carotene and lutein contents than do modern cultivated lettuce. However, our knowledge on the content of other bioactive compounds in wild *Lactuca* species is very limited, with the exception of sesquiterpene lactones, which cause bitterness (Zidorn 2008; Chadwick et al. 2016).

5.1.3.3 Climate Change and Lettuce Growing

Global climate change may affect agriculture more through water availability than temperature (Leafy Vegetable Crop Germplasm Committee 2015, Wilson et al. 2016; Zhang et al. 2016). All lettuce production in California and Arizona is irrigated, but water availability for growers is expected to decrease. Limits for irrigation water can lead to restrictions on leafy vegetable production for farms in the San Joaquin Valley (Leafy Vegetable Crop Germplasm Committee 2015).

Most leaf and iceberg lettuce is planted by using pelleted seed, and precision irrigation systems supply optimal water throughout the growing period (Smith et al. 2016; Turini et al. 2016). Lettuce is moderately salt sensitive, and excess salinity results in poor seed germination and reduced growth (Smith et al. 2016). Thus, an increasing need for suitable irrigation water will increase the cost of inputs related to the management of irrigation systems. In lettuce breeding and cultivation, we must seriously consider recent (and impending) climate changes described above from at least these three perspectives:

First, lettuce cultivation technologies must ensure that this activity minimizes negative impacts on the local environment.

Second, new adaptation strategies for cultivation need to be developed focusing on water conservation (Wolfe 2013).

Third, wild *Lactuca* species should be phenotyped and used in lettuce breeding programs (Lebeda et al. 2007a, 2009a, b, 2014). Our field observations confirmed *L. serriola* and *L. virosa* surviving under extreme conditions (Lebeda et al. 2012a), and these traits are fixed genetically (Sect. 5.2.2.2).

5.2 Wild Relatives of Lettuce

5.2.1 Evolution and Taxonomy

5.2.1.1 Taxonomic Position of the Tribe Lactucae and the Genus *Lactuca*

The genus *Lactuca* L. is grouped within the subtribe Lactucinae Dumort of the tribe Lactucae (Funk et al. 2009), which is part of the subfamily Cichorioideae within the Asteraceae. Recently, molecular data representing the entire Lactucae led to a revised treatment of the Cichorieae (Kilian et al. 2009; Wang et al. 2013); this phylogeny suggests the tribe Cichorieae contains five clades, with the fourth clade containing five subclades (Hypochaeridinae, Chondrillinae, Crepidinae, Hyoseridinae, and Lactucinae). The subclade Lactucinae includes the genera *Lactuca*, *Cicerbita* Wallr., and *Notoseris* C. Shih.

Uncertainties about the generic limits and phylogenetic relationships of the genus *Lactuca* still remain, due to its broad variability of morphological characters and the existence of spatially separated groups of species (Lebeda et al. 2007a; Wei et al. 2017). The taxonomic delimitation of this genus has ranged from an extremely broad (Bentham 1873; Hoffman 1890–1894) to extremely narrow (Tuisl 1968; Shih 1988a, b; Kadereit and Jeffrey 2007). Intergeneric transfers have involved species of related genera from subtribe Lactucinae (*Cephalorrhynchus* Boiss., *Steptorhamphus* Bunge), Sonchinae (*Launaea* Cass., *Prenanthes* L., *Sonchus* L.), and Crepidinae (*Ixeris* Cass., *Youngia* Cass.). Some genera, including *Scariola* F.W. Schmidt, *Mulgedium* Cass., *Cicerbita* Wallr., and (rarely) *Mycelis* Cass., may be kept separate from *Lactuca* but are sometimes included.

Moderately wide concepts of *Lactuca* were established by Stebbins (1937a, b, 1939) and Feráková (1977), which are widely used in classification of European *Lactuca*, who divided the genus *Lactuca* into four sections (*Lactuca*, *Phaenixopus*, *Mulgedium*, and *Lactucopsis*) with two subsections within section *Lactuca*: *Lactuca* and *Cyaniacae*. Lebeda (1998), Lebeda and Astley (1999), and Lebeda et al. (2004b, 2007a, 2009a) elaborated on this classification of *Lactuca* and divided the genus into seven sections, *Lactuca* (with *Lactuca* and *Cyaniacae*), *Phaenixopus*, *Mulgedium*, *Lactucopsis*, *Tuberosae*, *Micranthae*, and *Sororiae*, and two geographical groups (African and North American) (Table 5.2). Lebeda et al. (2004b) showed that at least 98 wild *Lactuca* spp. had been described: 51 species in Asia, 43 in Africa, 17 in Europe, 12 in America, and 3 in Australia.

Table 5.2 Taxonomy of the genus *Lactuca* L.: sections, subsections, and geographical groups (Lebeda 1998; Lebeda et al. 2004b, 2007a; Wei et al. 2017)

Sections/subsections
Lactuca L. (98 wild and one cultivated species)
subsect. *Lactuca* L. (*L. aculeata*, *L. altaica*, *L. azerbaijanica*, *L. dregeana*, *L. georgica*, *L. livida*, *L. saligna*, *L. sativa*, *L. scarioloides*, *L. serriola*, *L. virosa*)
subsect. *Cyanicae* DC. (*L. perennis*, *L. tenerrima*, *L. undulata*)
Phaenixopus (Cass.) Bentham (*L. viminea*)
Mulgedium (Cass.) C.B. Clarke (*L. tatarica*, *L. sibirica*, *L. taraxacifolia*)
Lactucopsis (Schultz Bip. ex Vis. et Pančić) Rouy (*L. quercina*)
Tuberosae Boiss. (*L. indica*)
Micranthae Boiss. (*L. auriculata*, *L. dissecta*, *L. rosularis*)
Sororiae Franchet (*L. sororia*)
Groups (geographical view)
North American (*L. biennis*, *L. canadensis*, *L. floridana*, *L. graminifolia*, *L. hirsuta*, *L. ludoviciana*)
African (*L. capensis*, *L. dregeana*, *L. homblei*)

Molecular markers have been applied to these classification problems. Koopman et al. (2002) determined 2C DNA contents in 23 *Lactuca* species and related genera and found significant intraspecific variation in DNA content for 6 species. They detected four groups with (partially) overlapping DNA content ranges, partly conforming to accepted classifications. Wang et al. (2013) constructed a DNA-based phylogenetic tree of *Lactuca* focusing on the Chinese center of diversity. The most comprehensive study of relationships within *Lactuca* based on chloroplast DNA sequence comparison was that of Wei et al. (2017), who included 34% of known *Lactuca* species and 40% of the total endemic African species, demonstrating distinctions among the "crop clade" of *Lactuca* and the *Pterocypsela* clade with Asian *Lactuca* species, while the North American species, *L. canadensis*, and Asian and widespread species formed distinct clades. They proposed *L. indica* L., *L. orientalis* (Boiss.) Boiss., and *L. viminea* as novel potential genetic resources for lettuce breeding. We still lack a comprehensive analysis of the diversity of autochthonous American *Lactuca* species.

5.2.1.2 Botanical Characterization of the Genus *Lactuca* L.

A morphological characterization of the genus *Lactuca* with respect to North American species generally follows Strother's (2006b) description:

> Annual, biennial, or perennial, 15–450+ cm; taprooted. Stems usually one, usually erect, branched distally or throughout, glabrous or hairy (sometimes hispid to setose). Leaves basal and cauline or mostly cauline (at flowering); sessile or petiolate; blades orbiculate, ovate, oblong, or lanceolate to oblanceolate, linear, or filiform; margins entire or denticulate to pinnately lobed (faces glabrous or hairy,

> often ± setose). Heads borne singly or in corymbiform to paniculiform arrays. Peduncles not inflated distally, sometimes bracteate. Calyculi of 3–10+, deltate to lanceolate bractlets in 2–3 series (sometimes intergrading with phyllaries). Involucres campanulate to cylindric, 2–5(−8+) mm diameter. Phyllaries 5–13+ in ±2 series (erect or reflexed in fruit), lanceolate to linear, usually subequal to equal, margins sometimes scarious, apices obtuse to acute. Receptacles flat to convex, pitted, glabrous, epaleate. Florets 6–50+; corollas yellow to orange, bluish to purplish, or whitish. Cypselae reddish brown, tan, whitish, or purplish to blackish, bodies compressed to flattened, elliptic to oblong, beaks stout (0.1–1 mm, gradually or weakly set off from bodies) or filiform (2–6 mm, sharply set off from bodies), ribs 1–9 on each face, faces often transversely rugulose, usually glabrous; pappi persistent (borne on discs at tips of cypselae or beaks), obscurely double, each a minute, erose corona 0.05–0.2 mm subtending 40–80+, white or fuscous, ± equal, barbellate to barbellulate bristles in 1–2 series, or simple of 80–120+, white, ± equal, barbellulate to nearly smooth bristles in 2–3+ series.

Generally, the genus *Lactuca* includes annual, biennial, and perennial herbs (and rarely shrubs), with abundant latex, distributed in temperate and warmer regions mostly in the Northern Hemisphere (Feráková 1977; Lebeda et al. 2004b). Sections *Phoenixopus*, *Mulgedium*, *Lactucopsis*, *Tuberosae*, *Micranthae*, and *Sororiae* (Table 5.2) include mostly biennial or perennial species (Lebeda and Astley 1999). Species of subsection *Lactuca* are annual, winter annual, or biennial herbs, while perennial species belong to subsection *Cyanicae*. Species of the genus *Lactuca* have various ecological requirements and can be found in diverse habitats. The most widespread species, *L. serriola*, *L. saligna* L., and *L. virosa*, are weedy and occur on waste places and ruderal habitats, mainly along roads, highways, and ditches (Lebeda et al. 2001, 2004b, 2007a, 2011, 2012a). Most of European *Lactuca* species are calciphiles (i.e., *L. perennis* L., *L. viminea*, *L. graeca* Boiss., and *L. tenerrima* Pourr.) and found in limestone and dolomite areas, often on rocky slopes.

The African species are annual or perennial herbs or subshrubs. This group is heterogeneous and represents species mostly occurring in tropical East Africa and Madagascar (Jeffrey 1966; Jeffrey and Beentje 2000), scandent, liana-like endemic species of the central African mountains (Stebbins 1937b, Dethier 1982), and species which are more widely distributed (i.e., *L. serriola*, *L. saligna*). *Lactuca* species recorded from Asia are mostly representatives of sections *Tuberosae*, *Micranthae*, and *Sororiae*, except for the abovementioned, widespread species from section *Lactuca* (Lebeda and Astley 1999; Lebeda et al. 2004b, 2007a).

The North American group includes autochthonous wild *Lactuca* species distributed from Canada to Florida and Mexico. These species are in most cases biennial; however, *L. tatarica* (L.) C.A. Mey. subsp. *pulchella* (Pursh) Stebbins is perennial (McGregor et al. 1986). Germplasm variation of selected wild and weedy *Lactuca* species, with an emphasis on their distribution and ecology, has been studied through field research in North America by Lebeda et al. (2011, 2012a). The autochthonous North American species (except for *L. tatarica* subsp. *pulchella*), reported as geographically and cytologically isolated from the others, are characterized by the haploid chromosome number *n* = 17 (Babcock et al. 1937) and are of an amphidiploid origin (Feráková 1977). In these species, higher contents of nuclear DNA have been established in comparison with Eurasian taxa (Doležalová et al. 2002b).

5.2.1.3 Wild *Lactuca* Species in North America, Their Characterization, Biogeography and Distribution, and Habitat Ecology

Information about the biogeography and distribution of wild and weedy *Lactuca* species in North America (Figs. 5.1, 5.2, 5.3, and 5.4) and their habitats (Figs. 5.1, 5.2, 5.3, and 5.4) is still incomplete, and the North American continent has been underestimated as a source of wild *Lactuca* species (Lebeda et al. 2004a, b, 2009a, b, 2011, 2012a, b). Our previous search, based on the available literature, provided an overview of the distribution of 12 wild and weedy *Lactuca* species in the New World, with 11 of them being described from North America (Lebeda et al. 2004b). However, according to Strother's (2006b) most recent treatment in *Flora North America*, only nine wild and weedy *Lactuca* species occur. Three weedy species (*L. serriola*, *L. saligna*, and *L. virosa*) are synanthropic and cosmopolitan

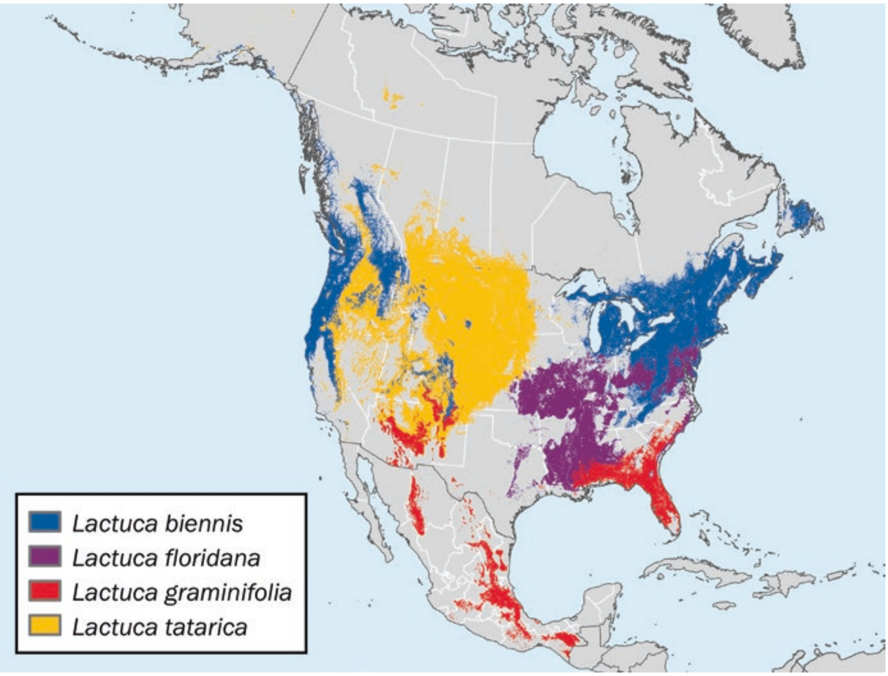

Fig. 5.1 Modeled potential distribution of *L. biennis* (Moench) Fernald, *L. floridana* (L.) Gaertn., *L. graminifolia* Michx., and *L. tatarica* (L.) C. A. Mey., based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

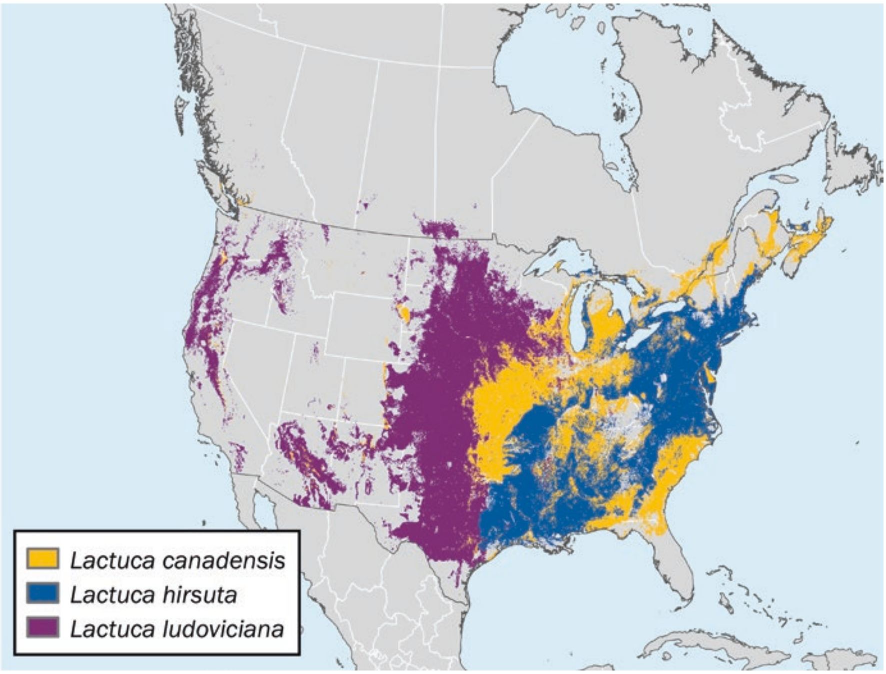

Fig. 5.2 Modeled potential distribution of *L. canadensis* L., *L. hirsuta* Muhl. ex Nutt., and *L. ludoviciana* (Nutt.) Riddell, based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

(Steyermark 1963; Nessler 1976; Strausbaugh and Core 1978; Cronquist 1980; McGregor et al. 1986; Chung 2006; Strother 2006b). Another six wild *Lactuca* taxa have been reported as autochthonous for North America (north of Mexico): *L. canadensis* L., *L. graminifolia* Michx., *L. biennis* (Moench) Fern., *L. floridana* (L.) Gaertn., *L. ludoviciana* (Nutt.) Ridd., and *L. hirsuta* Muhl. ex Nutt. (Strother 2006b). Two additional taxa, *L. terrae-novae* Fern. and *L. tatarica* subsp. *pulchella* (Pursh) Stebbins, are listed in the *Synonymized Check List of the Vascular Flora of the United States, Canada and Greenland* (Kartesz 1994); however, they are not reported in the recent flora of North America (Strother 2006b). Of these, Strother (2006a,b) noted that *L. terrae-novae* is "probably conspecific with" *L. biennis*, and, following Bremer (1994), he treated section *Mulgedium* as a separate genus, transferring *L. tatarica* subsp. *pulchella* to *M. pulchellum* (Pursh) G. Don. We concur with Koopman et al. (1998) and Chung (2006), retaining section

Mulgedium within *Lactuca*:
For all *Lactuca* species occurring in North America, their scientific (ordered alphabetically) and common names, botanical descriptions, and information about variability, distribution and ecology are given below. Basic description of species follows Strother (2006b), with some information taken from Fernald (1950), Steyermark (1963), Cronquist (1980), McGregor et al. (1986), and Chung (2006),

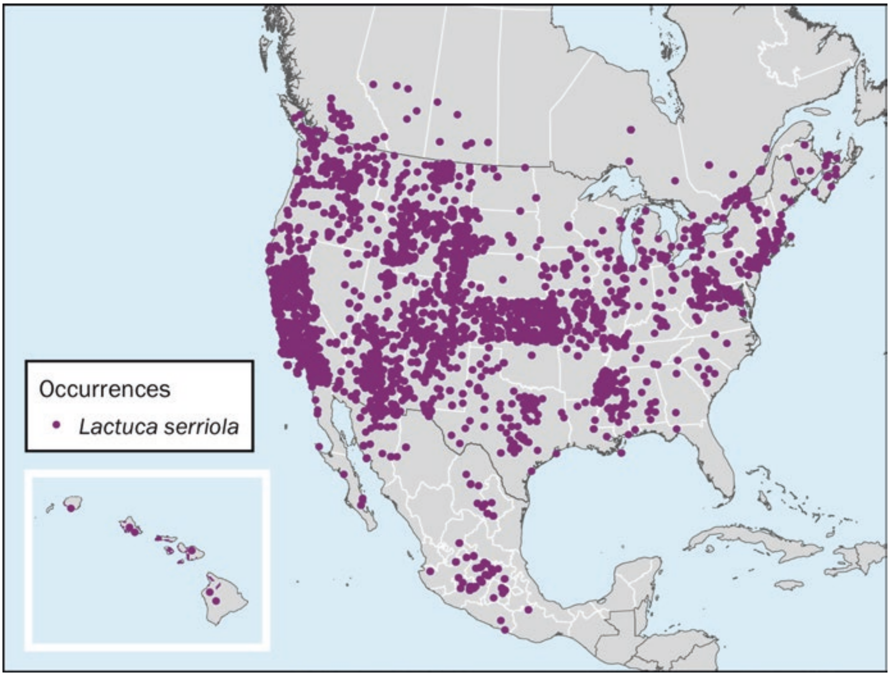

Fig. 5.3 Reference localities for *Lactuca serriola* L. from herbarium records and genebank passport data. Data may cause certain regions (such as the Upper Midwest) to be underrepresented. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

and others from the present authors' own observations (Lebeda et al. 2012a). *Recently accepted names of provinces and states of Canada and USA are used following* ISO 3166-1 *standards for geographic subdivisions* (http://en.wikipedia.org/wiki/ISO_3166-2:CA; http://en.wikipedia.org/wiki/ISO_3166-2:US); *European and Asian* countries are specified following codes used for plant genetic resources documentation (van Hintum 1995).

Lactuca biennis (Moench) Fern.
Tall blue lettuce, blue wood lettuce, or wild blue lettuce is an annual or biennial, (15-)75–200(−300+) cm. Leaves on proximal 2/3–3/4 of each stem; blades of undivided cauline leaves ovate to lanceolate, margins entire or denticulate, midribs sometimes sparsely piloso-setose. Heads in paniculiform arrays. Involucres 7–12+ mm. Phyllaries usually reflexed in fruit. Florets (15-)20–30(−50+); corollas bluish or whitish, sometimes yellowish, seldom deliquescent. Cypselae: bodies brown (often mottled), ± compressed-ellipsoid, 4–5+ mm, beaks ± stout, 0.1–0.5+ mm, faces (4-)5–6-nerved; pappi ± fuscous, 4–6+ mm. It can hybridize with L. canadensis, and an apparent hybrid has been called *L.* × *morssii* Robinson (Gleason and Cronquist 1991). It is broadly distributed across the USA and Canada flowering from July to

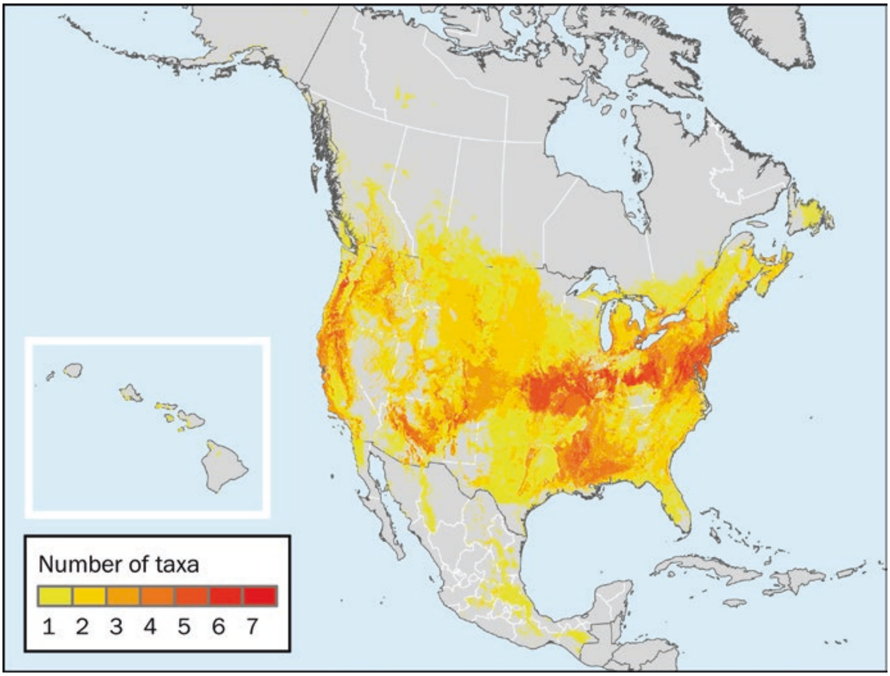

Fig. 5.4 Species richness map of modeled potential distributions of North American *Lactuca* taxa, based on climatic and edaphic similarities with herbarium and genebank reference localities. Warmer colors indicate areas where greater numbers of taxa potentially occur in the same geographic localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

October, growing in moist woods and shrub thickets, along streams, anthropogenic habitats, forest edges, meadows, and fields at elevations of 900–1500 m.

Lactuca canadensis L.
Canada lettuce, wild lettuce is a biennial, (15-)40–200(−450+) cm. Leaves on proximal 1/2–3/4 of each stem; blades of undivided cauline leaves oblong, obovate, or lanceolate to spatulate or lance-linear, margins entire or denticulate, midribs sometimes sparsely pilose. Heads in ± corymbiform to paniculiform arrays. Involucres 10–12+ mm. Phyllaries usually reflexed in fruit. Florets 15–20+; corollas orange-yellow (according Strother (2006b) also bluish), usually deliquescent. Cypselae: bodies brown (often mottled), ± flattened, elliptic, 2.5–3.5 mm, beaks ± filiform, 1–3 mm, faces 1(−3)-nerved; pappi white, 5–6 mm. There are two geographically distinct types based on flower color in this species. In the Great Plains, the flower color is always reddish or orange, but farther east the flower color is brilliant yellow. The areas of sympatry of these two phases have not yet been determined. *L. canadensis* is known to hybridize with *L. biennis* and presumed hybrids, with intermediate characters (Fernald 1950), are apparently quite scarce in Michigan

(Reznicek et al. 2011). It is found throughout the entire USA and Canada. It flowers from June to October and occurs in open woodland, rocky slopes along bluffs, prairie openings, alluvial thickets, borders of fields, muddy banks, and gravel bars along streams, roadsides, and along railroad, up to 2200 m.

Lactuca floridana (L.) Gaertn.
Woodland lettuce, Florida lettuce, or Florida blue lettuce is an annual or biennial, 25−150(−200+) cm. Leaves on proximal 2/3–3/4 of each stem; blades of undivided cauline leaves oblong, ovate, or elliptic, margins entire or denticulate, midribs sometimes sparsely pilose. Heads in (± pyramidal) paniculiform arrays. Involucres (8−)10−12+ mm. Phyllaries usually reflexed in fruit. Florets 10−15(−25+); corollas bluish or whitish, seldom deliquescent. Cypselae: bodies brown (often mottled), ± compressed-lanceoloid to compressed-fusiform, 4–5 mm, beaks ± stout, 0.1−0.5(−1) mm, faces 5-6-nerved; pappi white, 4–5 mm. Plants with leaves that are usually more or less deeply lobed or parted have been treated as var. floridana, but those with leaves that are usually only toothed, not lobed, have been named var. villosa (Jacquin) Cronquist. It is widely distributed *across the USA and also found in Manitoba and Ontario. It flowers* June–October and grows in open woods, thickets, low rich or alluvial woods, ravines, disturbed sites, waste ground, streambanks, roadsides, and along railroads at 10–200 m (Strother (2006b). However, in Ames (Iowa), it was observed at about 300 m (M.P. Widrlechner, pers. observation), and certain states and provinces where it has been reported are exclusively above 200 m.

Lactuca graminifolia Michx.
Grassleaf lettuce is a biennial, 25−90(−150+) cm. Leaves on proximal 1/3–1/2 of each stem; blades of undivided cauline leaves spatulate to lance-linear, margins entire or denticulate, midribs sometimes setose. Heads in ± paniculiform arrays. Involucres 12−20+ mm. Phyllaries usually reflexed in fruit. Florets 15−20+; corollas bluish to purplish, usually deliquescent. Cypselae: bodies brown (often mottled), ± flattened, elliptic, 5–6 mm, beaks ± filiform, 2–4 mm, faces 1(−3)-nerved; pappi white, 5–9 mm. There are three recognized varieties: *graminifolia*, *arizonica* McVaugh (plants of western populations), and *mexicana* McVaugh (known from Mexico). It is distributed in the Southern and Southwestern USA and throughout Mexico flowering from February to September occurring on sandy ridges, in pine forests, and in canyons at elevations 10–1700 m.

Lactuca hirsuta Muhl. ex Nutt.
Downy lettuce, hairy lettuce, is a biennial, 15–80(−120) cm. Leaves on proximal 1/3–2/3 of each stem; blades of undivided cauline leaves ± ovate, margins denticulate (sometimes ± ciliate), midribs usually piloso-setose. Heads in corymbiform to paniculiform arrays. Involucres 12–18+ mm. Phyllaries usually reflexed in fruit. Florets 12–24+; corollas usually yellow, sometimes drying bluish, usually deliquescent. Cypselae: bodies brown, ± flattened, elliptic, 4.5–5+ mm, beaks ± filiform, 2.5–3.5 mm, faces 1(−3)-nerved; pappi white, 6.5–8(−10+) mm. Plants with the lower part of stem hairy, and the lower and middle cauline leaves hairy on both surfaces have been treated as var. *hirsuta* (Bigelow) Fernald but those with more-or-less glabrous stems and only the midrib of the lower surface of the leaves hairy as var. *sanguinea*

(Bigelow) Fernald. It is broadly distributed across the USA and Canada, flowering time July–September. It grows in dry rocky woods and borders of upland sinkhole ponds, usually in acidic soils, along roadsides and openings at elevations 10–100 m (Strother (2006b). However, this range of elevations seems to be in error, as it is too low for many of US states where this species is distributed.

Lactuca ludoviciana (Nutt.) Riddell
Biannual lettuce, Louisiana lettuce, or western wild lettuce is a biennial, 15–150 cm. Leaves on proximal 1/2–3/4 of each stem; blades of undivided cauline leaves obovate or oblanceolate to spatulate, margins denticulate (piloso-ciliate), often prickly, midribs usually piloso-setose. Heads in paniculiform arrays. Involucres 12–15+ mm. Phyllaries usually reflexed in fruit. Florets 20–50+; corollas usually yellow, sometimes bluish, usually deliquescent. Cypselae: bodies brown to blackish (usually mottled), ± flattened, elliptic, 4.5–5+ mm, beaks ± filiform, 2.5–4.5 mm, faces 1(−3)-nerved; pappi white, 5–7(−11) mm. This taxon has several phases defined by variation in flower color or leaf morphology. The blue-flowered phase has been called f. *campestris* (Greene) Fern. Most plants have cauline leaves pinnate-lobed to sinuate and upper cauline leaves ovate and unlobed to sinuate. This is probably an intermediate between the two more “distinct” but less common phases with all leaves obovate, unlobed, or all leaves pinnatifid. Some degree of natural hybridization with *L. canadensis* may be expected. It is broadly distributed in the Western USA and Canada. Flowering from June–September, occurring in openings in woods, stream banks, rather moist places, native to the prairies and plains at 100–1400 m.

Lactuca saligna L.
Willow-leaved lettuce or least lettuce is an annual 15−70(−100+) cm. Leaves on proximal 1/2–3/4+ of each stem; blades of undivided cauline leaves ± linear to filiform, margins entire or denticulate, midribs usually prickly setose. Heads in racemiform to spiciform arrays. Involucres 6−9(−13+) mm. Phyllaries usually erect in fruit. Florets 6−12(−20+); corollas yellow (sometimes abaxially bluish), usually deliquescent. Cypselae: bodies pale brown, ± flattened, elliptic to oblanceolate, 2.5–3.5 mm, beaks ± filiform, (2−)5−6 mm, faces 5–7-nerved; pappi white, 5–6 mm. Two varieties based on leaf shape are recognized: var. saligna with middle cauline leaves non-lobed and var. runcinata Gren. & Godr. with the middle cauline leaves pinnatifid to pinnatisect. It is broadly distributed in the USA and in Eastern Canada. It flowers August–October, preferring warm, fertile, semiarid, slightly saline soils. The common habitats include waste places, woodland borders, riverbanks, and arable fields. L. saligna is a characteristic weedy species of both lowland and hilly areas (Europe to 1000 m in Italy, Cyprus to 1680 m; Turkey to 2400 m) (Lebeda et al. 2004b, 2016). In the recent Flora of North America, *L. saligna* was reported from most US states (Strother 2006b); however, Lebeda et al. (2012a) recorded *L. saligna* var. *saligna* only one time at abandoned, small garden in Salinas (California), confirming that this species is rather rare not only in California but across the USA. During recent decades, a few new records of L. saligna have been reported from various parts of the USA (Page County, Iowa; Texas) (Wilson 1992; O´Kennon et al. 1998).

Lactuca serriola L.
Prickly lettuce or wild lettuce is an annual (perhaps persisting in frost-free areas), (15−)30–70(−100+) cm. Leaves on proximal 1/2–3/4 of each stem; blades of undivided cauline leaves usually ± oblong, sometimes obovate to lanceolate, margins denticulate, usually prickly, midribs usually prickly setose, rarely smooth. Heads in paniculiform arrays. Involucres 9–10(−12) mm. Phyllaries usually reflexed in fruit. Florets 12–20; corollas yellow, usually deliquescent. Cypselae: bodies pale grayish to tan, ± flattened, oblanceolate, 2.5–3.5 mm, beaks ± filiform, 2.5–4 mm, faces (3−)5–9-nerved; pappi white, (3−)4–5 mm. There are two main forms recognized within *L. serriola* based on leaf shape: *L. serriola* f. *serriola* with pinnate-lobed leaves and *L. serriola* f. *integrifolia* (S.F. Gray) S.D. Prince & R.N. Carter with entire rosette and cauline leaves. This latter leaf form is also mentioned in the literature under the synonyms, *L. serriola* var. *integrata* Gren. & Godr., *L. augustana* All., *L. dubia* Jord., and *L. integrata* A. Nels. Plants with a densely setose inflorescence and spinose-ciliate leaves have been described as var. *coriacea* (Sch. Bip.) Rech. f. (Feráková 1977). It is found in every US state and Canadian province except Arkansas. It flowers May–October. In North America, *L. serriola* was recorded from 6 m (Longview, Washington) all the way up to 2325 m (Mesa Verde National Park, Colorado) and 2358 m (Yellowstone Lake, Wyoming), and there is evidence for elevational differentiation between the two botanical forms of *L. serriola*; *L. serriola* f. *serriola* was recorded more often from higher elevations, whereas f. *integrifolia* was common mostly in lower sites, the highest being at Chinquapin, California, at 1830 m (Lebeda et al. 2012a). It grows mostly in sunny exposures preferably on fertile, carbonate-rich soil, but its ecological amplitude is rather wide. It is also found in some unusual habitats, such as asphalt and concrete cracks and along house walls in highly urbanized areas, extreme desert conditions (Utah and Arizona), and stony slopes close to sulfur steam at Yellowstone National Park. It is very rare in Nevada, where *L. serriola* f. *serriola* was repeatedly recorded in Las Vegas but, however, only single plant in the Nevada desert (Mesquite) (Lebeda et al. 2012a). Recently, *L. serriola* has spread as an invasive weed along the roads, occupying ruderal places, town suburbs, new city parts, and uncultivated edge of field crops (Lebeda et al. 2001, 2004b, 2007b; Weaver and Downs 2003), and its increasing occurrence is frequently interpreted in concert with climate changes (D'Andrea et al. 2009).

Lactuca tatarica (L.) C.A. Mey. subsp. *pulchella* (Pursh) Stebbins
Blue lettuce is a perennial, 30–100 cm with think rhizomes, vertical with numerous underground stolons. Stem glabrous, erect, branched in the upper part. Basal leaves petiolate, pinnatisect. Cauline leaves of the same shape, sessile, base semi-amplexicaul, rarely undivided, all glaucous, rigid, margins denticulate. Heads in spiciform or corymbiform arrays.

Involucres 12−(13)−15 mm. Florets 19–21; corollas blue to violet, rarely white. Cypselae: bodies yellowish, olive to blackish, slightly compressed, 4.5–6.5 mm, beaks stout, 1–1.5 mm, faces 4–6-nerved; pappi white, 8–9 mm. The most common phase has oblong leaves with the lower cauline leaves possessing 1–3 pairs of linear lobes close to the leaf base. Of the two less common phases, one has totally linear leaves, and the other has ovate-runcinate leaves. It has a small distribution in the USA and Canada. It flowers June–September. It grows in dry to moist alluvial valleys and open meadows at elevations up to 2400 m (USGS 2016).

Lactuca terrae-novae Fern.
Newfoundland lettuce closely resembles *L. biennis* in both its vegetative and involucral characteristics. However, it differs from *L. biennis* in having a bright white pappus and orange to orange-brown achenes that are all firmly beaked (Fernald 1950). Strother (2006b) believed the type of *L. terrae-novae* Fernald to probably be conspecific with that of *L. biennis*. It is only found in Newfoundland, Canada, and occurs on meadows and limestone escarpments.

Lactuca virosa L.
Opium lettuce or poisonous lettuce is a biennial, 20–120(−200+) cm. Leaves on proximal 1/2–2/3 of each stem; blades of undivided cauline leaves obovate to spatulate, margins denticulate, midribs usually prickly setose. Heads in paniculiform arrays. Involucres 12–15 mm. Phyllaries usually reflexed in fruit. Florets 10–15; corollas yellow, usually deliquescent. Cypselae: bodies purplish to blackish, ± flattened, ± elliptic, 3.5–4 mm, beaks ± filiform, 2.5–3.5 mm, faces 5–7-nerved; pappi white, 5–6 mm. Within *L. virosa* the following infraspecific taxa are recognized: var. *virosa* with non-lobed leaves and var. *cruenta* with the leaves pinnatilobed to pinnatisect. The subsp. *cornigera* (Pau & Font Quer) Emb. & Maire has been described from Morocco (Meusel and Jäger 1992). It is found in Alabama, California, and Washington. It flowers May–October and can be found in ruderal habitats; however, it may occur on limestone in the northern part of its distribution area. This species was introduced as a medicinal plant to North America, where it became naturalized. *L. virosa* is a thermophilous species distributed from lowland to submontane regions (Central France to 1000 m, Wallis (Switzerland) to 1560 m, Morocco to 2300 m) (Feráková 1977; Hegi 1987; Meusel and Jäger 1992). Strother (2006b) reported this species in an elevational range of 10–400 m in North America. In California, its occurrence was reported by Hickman (1993) at elevations of ca 760 m, which is consistent with authors' recent observations made in Redwoods National Park (California). The record of *L. virosa* in the southern part of Washington along Road 504 to Mt. St. Helens (780 m) (Figs. 5.5 and 5.6) is a new state record for the USA (Lebeda et al. 2012a).

5.2.2 Genepools of Lactuca sativa L. *and Their Diversity*

5.2.2.1 Genepools and Species Concepts of *Lactuca sativa* L.

Cultivated lettuce is a member of the genus *Lactuca* (Asteraceae), which includes ~100 wild species (Lebeda et al. 2004b, 2007a). The taxonomic delimitation of the genus *Lactuca* is dynamic, and not fully elaborated (Lebeda et al. 2007a;

Fig. 5.5 Variation among *Lactuca serriola* L. habitats in the USA. (**a**) Large, dense population on a grassy slope near Road 152, Casa de Fruta, Santa Clara Valley, California; (**b**) a small population in a grassy place near Road 142, Old Highway, entrance to Catheys Valley, California; (**c**) a few individual plants in a grassy place in Virgin Port, Zion, Utah; (**d**) a few individual plants on a stony, sandy slope near the road, Red Canyon, Hatch, Utah; (**e**) a few individual plants among rocks near the Portal View Road, Yosemite, California; (**f**) single plant on a stony slope near sulfur steam, near the road around Yellowstone Lake, Wyoming (Lebeda et al. 2012a, b)

Doležalová 2014). During the last eight decades, four different concepts (Stebbins 1937a; Tuisl 1968; Feráková 1977; Lebeda and Astley 1999; Lebeda et al. 2007a) have been proposed for the classification of *Lactuca* species. More recently new views on *Lactuca* have emerged, based on phylogenetic studies (Wang et al. 2013; Wei et al. 2017). Nevertheless, according the last taxonomic/geographical concept

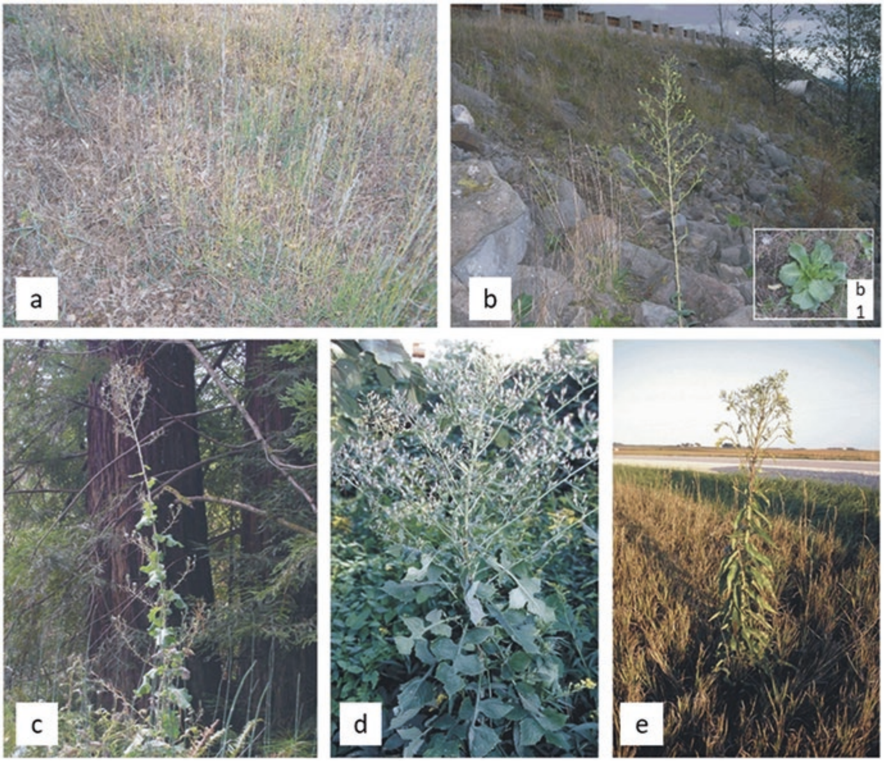

Fig. 5.6 Variation in habitats of four *Lactuca* species. (**a**) *L. saligna* L., weedy garden in Salinas, CA; (**b**) *L. virosa* L., stony embankment below the road above Hoffstadt Bridge (near Mount St. Helens National Volcanic Monument), WA; (**c**) *L. virosa* L., two individual plants in Redwood National Park, CA; (**d**) *L. floridana* (L.) Gaertn., Ames, IA; (**e**) *L. canadensis* L., close to Ames, IA. (Photos by I. Doležalová and A. Lebeda)

(Lebeda et al. 2007a), the North American autochthonous species are reported as a separate geographical group, which is cytologically (n = 17) well isolated from all other *Lactuca* species (Doležalová et al. 2002b).

Currently, there are two different concepts of the lettuce genepool (Lebeda et al. 2007a). The traditional concept (Harlan and de Wet 1971) of the primary genepool of *L. sativa* is represented by cultivars and landraces and those wild *Lactuca* taxa without any crossing barriers with *L. sativa*. The primary genepool is represented by prickly lettuce (*L. serriola*), which has been considered as its wild progenitor (Lebeda et al. 2007a, Kuang et al. 2008). *Lactuca serriola* has been used since the 1930s in lettuce breeding as a source of resistance genes against *Bremia lactucae* (Lebeda et al. 2002; Lebeda and Zinkernagel 2003; Mikel 2007; Parra et al. 2016) and many other pathogens and pests (Lebeda et al. 2014). The remaining components of lettuce's primary genepool include *Lactuca* species from Southwestern Asia and East Africa (Zohary 1991). *Lactuca saligna* can be included in the secondary genepool (Zohary, 1991; McGuire et al. 1993) and has been heavily exploited in lettuce breeding as a source of resistance to *B. lactucae* (Lebeda et al. 2002, 2014, 2016; Jeuken 2012; Parra et al. 2016). Lettuce's tertiary gene pool is represented by *Lactuca virosa* L. and other wild *Lactuca* taxa that are difficult to cross with *L. sativa* (Lebeda et al. 2007a). *Lactuca virosa* is an important source of resistance to various pathogens and pests (Lebeda et al. 2002, 2014). Recently, it has been frequently used in interspecific hybridization and lettuce breeding; fertile hybrids have been obtained and exploited (Lebeda et al. 2009a, 2014).

A divergent view of the lettuce genepool concept was proposed by Koopman et al. (1998) based on analysis of ITS-1 sequences and supported by data from crossing experiments (Lebeda et al. 2007a). According to Koopman et al.'s (1998) concept, the *Lactuca* species of section *Lactuca* subsection *Lactuca* comprise the primary and secondary genepools, while species of sections *Phaenixopus*, *Mulgedium*, and *Lactucopsis* (Lebeda et al. 2007a) comprise the tertiary genepool. The categorization of many *Lactuca* species, including North American species, is still unclear (Lebeda et al. 2007a; Wang et al. 2013; Wei et al. 2017). However, we hypothesize that all autochthonous North American *Lactuca* taxa, with the exception of *L. tatarica* subsp. *pulchella* (see Sect. 5.2.1.3), would fall outside the tertiary genepool, for they are not crossable with lettuce and other taxa in the primary genepool but still are considered the part of the genus *Lactuca*. *Lactuca* t*atarica* subsp. *pulchella* is a member of section *Mulgedium*.

5.2.2.2 Phenotypic Variability of *Lactuca sativa* L. and Wild *Lactuca* spp.

The variability of cultivated lettuce is expressed in various arrangements of leaf rosettes, shapes of leaf heads and blades, and combinations of yellow, green, and purple colors (Rodenburg 1960; de Vries and Raamsdonk 1994; Rijk Zwaan 2016). In contrast to cultivated lettuce, little is known about variation in the morphologic traits and phenological characteristics of wild *Lactuca* species from the North America.

Our recent description of phenotypic variability of North American wild *Lactuca* species is based on detailed observations and measurements of various morphological traits on rosette and stem leaves, stems, flowers and inflorescences, and fruits and of developmental characteristics of plants during their cultivation in the greenhouse. A descriptor list elaborated by Doležalová et al. (2002a) was used to standardize descriptions and the definitions of expression for each particular morphologic trait. Seedlings and young plants of biennial species (except for *L. floridana*) were vernalized (Prince 1980) to induce the flowering in the first year of growth.

5.2.2.2.1 Autochthonous American Species

Lactuca biennis (Moench) Fernald

L. biennis was represented by one sample from Canada and two samples from the USA (Iowa and North Carolina) (Lebeda et al. 2012a). All plants had divided rosette leaves (pinnatipart to pinnatisect) with rounded apices in plants from the USA and obtuse apices in those from Canada. Stem leaves were pinnatipart to pinnatisect with acute and obtuse apices. These traits fit the description of this species given by McGregor et al. (1986). Rosette leaves and divided stem leaves were not described by Strother (2006b). Pyramidal paniculate inflorescences were produced by plants from the USA; this trait was not assessed for plants from Canada. Leaves and stems lacked anthocyanin pigmentation. White to light blue floral ligules were recorded in all samples, generally corresponding to data given by Strother (2006b) and McGregor et al. (1986) for this species.

Lactuca floridana

All plants of nine samples originated from a relatively small area near Ames, Iowa (Lebeda et al. 2012a). They had divided (pinnatisect) rosette leaves with acute, subacute, or obtuse apices. This leaf shape fits the description given by McGregor et al. (1986). Anthocyanin was distributed on the lower side of the main veins of rosette leaves in five samples, on the upper side in two samples, and on both sides in one sample. One sample lacked anthocyanin coloration on its rosette leaves. Plants were not assessed at the stage of bolting or flowering. Rosette leaves were not described by Strother (2006b).

Lactuca ludoviciana

Within five samples collected near Ames, Iowa (Lebeda et al. 2012a), plants of four samples had similar phenotypes, with pinnatipart rosette leaves and rounded to obtuse apices. They were free of anthocyanin coloration. Plants of the fifth sample had pinnatipart rosette leaves with subacute apices, and, moreover, anthocyanin coloration was recorded on both sides on the main vein, and it was diffusely distributed on the leaf blade. Rosette leaves were not described by Strother (2006b). Stem leaves of this sample were pinnatipart, contrary to remaining four samples with pinnatisect stem leaves. The apex shape varied from acute to subacute and mucronate. Strother (2006b) mentioned neither divided stem leaves nor the presence of anthocyanins on leaves. However, our observations of rosette and stem leaves do correspond to those given by McGregor et al. (1986).

Pyramidal paniculate inflorescences with light purple floral ligules with white bases were recorded in all four “anthocyanin-free” samples. As the description of this trait can be influenced by the evaluator, there is not a strong contrast between our data and those of Strother (2006b), who mentioned that its ligules can be sometimes bluish. Our observations of ligule color and inflorescence type correspond to those given by McGregor et al. (1986).

Lactuca canadensis

L. canadensis was represented by 44 samples collected in Iowa and North Carolina (Lebeda et al. 2012a). Divided (pinnatisect) rosette leaves were recorded in 43 of the samples; entire (oblong) rosette and stem leaves were recorded in a single sample from North Carolina. The shape of apex of rosette leaves varied from acute to subacute and obtuse within this set of samples, and there were no associations of this trait with samples’ geographic origins. Anthocyanin pigmentation could be found on both the upper and lower sides of the main vein of the rosette leaves on samples from Iowa and North Carolina. Fourteen samples from Iowa and one sample from North Carolina lacked anthocyanin on their rosette leaves. We found no clear association of this trait with the specific expression of any other traits. Plants of two samples from North Carolina did not form leaf rosettes, and, in contrast to the flat leaf surface of other samples, their lower stem leaves expressed vertical undulation. The presence of trichomes on rosette leaves was consistent for the set of plant samples assessed, except for the sample with entire leaves from North Carolina, which lacked trichomes and moreover expressed vertical undulation. Rosette leaves were not described by Strother (2006b).

Stem leaves were deeply divided (pinnatisect) for the majority of samples assessed; only in one sample from Iowa were they pinnatipart and for another sample from Iowa pinnatifid. Stem leaves of two samples from North Carolina, which did not form leaf rosettes, differed by their subacute apices from all the remaining 42 samples, which displayed acute apices of the stem leaves. Trichomes on the lower side of the stem leaves were present in a majority of samples, but stem leaves of five samples from North Carolina and one from Iowa lacked them. Anthocyanin coloration on the midrib of stem leaves was recorded on three samples from North Carolina and on eight from Iowa. Plants with divided stem leaves were not noted nor as the presence of anthocyanin on leaves mentioned by Strother (2006b).

Pyramidal panicles were the predominant inflorescence type in this set of 44 *L. canadensis* samples. However, corymbose panicles were observed in nine samples from Iowa. One sample from North Carolina was heterogeneous in this trait, with both inflorescence types. These inflorescence types were also noted by Strother (2006b).

Variation in the color of floral ligules, including the intensity of color, and the colors of stigmata and anther tubes was noted within this set of samples. Ligules of florets were bright yellow for one sample from North Carolina and three samples from Iowa (Fig. 5.7a–d) or pink with yellow bases for the majority of samples, both from Iowa and North Carolina (Fig. 5.7e–k). Both colors were mentioned by Strother (2006b), interpreted by him as bluish and yellowish. Occurrence of plants with yellow florets in Iowa corresponds to data of the distribution of this type (see Sect. 5.2.1.3), as Iowa belongs to the area where both types (yellow and pink) can be distributed ("area of sympatry of both phases") (Strother 2006b). In North Carolina, only yellow forms were expected (Strother 2006b); however, we observed pink-tinged florets in most samples from this state. Stigma color of stigma varied from yellow to light purple and pink. The anther tubes were either with anthocyanin coloration (for a majority of samples) or without. The presence or absence of anthocyanin in the anther tube was not correlated to the presence or absence of anthocyanin on ligules. Data from our observations of leaf, inflorescence, and ligule color traits fit the description given by McGregor et al. (1986).

Anthocyanin on involucral bracts was observed in the majority of samples. Darker markings were arrow-shaped, i.e., with pigmentation distributed along the margin of the upper parts and apices of the bracts (Fig. 5.7l–n). Anthocyanin coloration of involucral bracts was lacking in 13 samples from Iowa and 1 sample from

Fig. 5.7 *Lactuca canadensis* L. – variation in ligule pigmentation: light yellow (Iowa 36/05, 37/05, 37/05) (**a**–**c**), yellow (North Carolina 41/06, 41/06) (**d**, **e**), dark yellow (North Carolina 40/06) (**f**), light purple with white base (Iowa 80/08) (**g**), purple with yellow base (Iowa 55/08, 55/08, 60/08) (**h**–**k**); anthocyanin on involucral bracts (Iowa 47/05, 47/05, North Carolina 37/06) (**l**–**n**)

North Carolina. This trait was not noted by McGregor et al. (1986). Absence of anthocyanin in involucral bracts was recorded both on samples with yellow florets and those with pink florets. Plants with potential hybrid phenotypes involving *L. canadensis* and *L. ludoviciana* were observed in Iowa during field trips in 2008. Two samples were morphologically assessed under greenhouse conditions. While the segregation of some morphological traits was observed in one sample, plants within the second sample were morphologically uniform. The hybrid origin of these plants should be verified by molecular analyses.

5.2.2.2.2 Allochthonous *Lactuca* Species in North America

Lactuca saligna
In North America, *L. saligna* var. *saligna* was observed in one location only (Salinas, California) (Lebeda et al. 2012a). Rosette leaves were pinnatisect with acute apices, without anthocyanin coloration. Rosette leaves were not described, and the presence of leaf anthocyanins was not mentioned by Strother (2006b). Stem leaves of plants assessed were narrowly lanceolate with acute apices, conforming to Strother's (2006b) description. However, the stem leaves and even the stem itself lacked trichomes, contrary to Strother (2006b) who mentioned prickly setose midribs on the stem leaves. These plants formed pyramidal panicles of heads; this observation differs slightly from McGregor et al.'s (1986) description of virage (corymbose) panicles. Floral ligules were yellow with anthocyanin coloration on their lower sides. These two traits correspond to the description by Strother (2006b). Our data on leaf morphology and ligula color correspond to the description given by McGregor et al. (1986). Anthocyanin was diffusely distributed on the involucral bracts and present in the anther tubes. These traits were not treated by McGregor et al. (1986).

Lactuca virosa
Six samples of *L. virosa* originated from Washington, California, and Oregon (Lebeda et al. 2012a) were grown in the greenhouse for evaluation. Based on the shape of their stem leaves, they belong to var. *cruenta*. Entire rosette leaves were broadly elliptic with obtuse apices for three samples (one from Oregon, one from Washington, and one from California). Rosette leaves of the remaining three samples from Washington were divided (pinnatifid) with rounded to obtuse apices and strong vertical undulation and blistering on the leaf blades. While three abovementioned samples with entire rosette leaves developed deeply divided stem leaves (pinnatisect) with subacute apices, stem leaves of samples with pinnatifid rosette leaves with obtuse apices were observed on plants with divided rosette leaves. Rosette leaves and divided stem leaves of this species were not described by Strother (2006b). Plants from one sample from Oregon developed corymbose panicles; all other samples formed pyramidal panicles. Corymbose panicles were not mentioned by Strother (2006b) for this species. Floral ligules were bright yellow. Anthocyanin coloration was not recorded in the rosette or stem leaves nor on the ligules or involucral bracts.

Lactuca serriola
L. serriola frequently occurs on the North American continent in both its common forms; f. *serriola* with divided stem leaves and f. *integrifolia* with entire stem leaves were observed often during various field trips (Lebeda et al. 2012a). The occurrence of various leaf forms was mentioned by McGregor et al. (1986) but was not treated taxonomically. Our data on the shape of rosette and stem leaves correspond to the

description given by McGregor et al. (1986). Beyond the description of McGregor et al. (1986) where only the conical panicle was mentioned as the typical inflorescence type, we also observed corymbose panicles in our set of samples.

We recorded broad variation in the expression of morphologic traits (the shape of rosette and stem leaves, shape of leaf apices, distribution and quality of trichomes on leaves and stems, distribution pattern of anthocyanin on leaves, floral ligules and involucral bracts, inflorescence type, and achene size and shape).

An evaluation of morphological traits of 231 plant samples of *L. serriola* (Lebeda et al. 2011, 2012a) was conducted on morphological traits and three developmental stages (the start of bolting, flowering, seed maturity) and was performed following the descriptor list of Doležalová et al. (2002a). Among the 12 morphological traits evaluated, those on rosette and stem leaves illustrate the phenotypic variation present within this species.

Leaf size and shape potentially have large effects on ambient leaf temperature. Because leaf lobing reduces the distance across the lamina, the rate of heat transfer is predicted to be greater in a lobed leaf than in an unlobed leaf with equivalent area (Parkhurst et al. 1968). The morphology of deeply lobed leaves may also reflect direct selection for increased hydraulic efficiency; however, leaf shape is only one among many factors influencing leaf thermal regulation; other factors could include water content, leaf thickness, spectral reflectance, orientation, and plant architecture (Nicotra et al. 2011).

Rosette Leaves

Both basic forms of rosette leaves, entire and divided (Fig. 5.8a–b), were recorded. Among the plants with divided leaves, we observed considerable variation in the incision depth (Fig. 5.9). In samples from the Western USA, nearly 50% of samples didn't develop the leaf rosette; plants without leaf rosettes could be found in all the Western states (Fig. 5.8c). This feature is typical for plants from arid areas with short springs and hot summers (Kitner et al. 2015).

Rosette leaves of samples from Canada and the Western USA were pinnatilobed, pinnatifid, pinnatipart, or pinnatisect. Plants from Midwest developed only pinnatilobed or pinnatifid rosette leaves (Fig. 5.9). Shallow lobes are likely an adaptation to mild climatic conditions and sufficient humidity (Nicotra et al. 2011). The more arid or otherwise more extreme climatic conditions in the Western USA and Canada are reflected by deeply divided rosette leaves. Notably, rosette leaves were not described by Strother (2006b).

Rosette leaves with obtuse apices were predominant in samples from all three regions. In contrast to samples from the Western USA and Canada, subacute apices were not observed in Midwestern populations (Fig. 5.10).

Plants with entire and divided stem leaves were recorded in all three areas; plants with divided stem leaves predominated in all areas (Fig. 5.11). Plants with entire stem leaves were recorded in the province of Québec (Canada) and in all states of the Midwest. Within the West, they were not recorded on plants from Idaho and Nevada. Two samples from the Midwest and two from the West were heterogeneous for this trait (Fig. 5.8d).

Fig. 5.8 *Lactuca serriola* L. – rosette and cauline leaves: irregularly incised divided (Toronto 13/02) (**a**), entire (Minnesota 05/08) (**b**), lacking rosette development (Nevada 62/06) (**c**), mixture of plants with divided and entire leaves (Washington 23/11) (**d**)

The stem leaves were incised to various depths (Fig. 5.11). All four categories of divided stem leaves (pinnatilobed, pinnatifid, pinnatipart, and pinnatisect) were observed in plants from Canada and the Western USA. Plants with the most deeply divided stem leaves (pinnatisect) were not recorded among samples from the

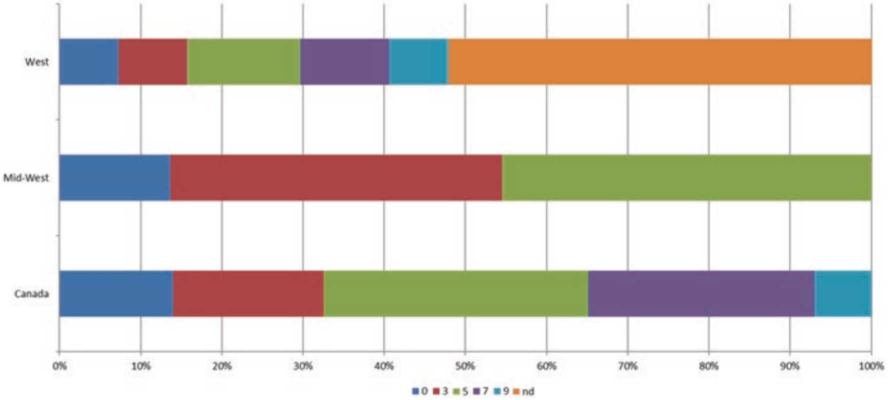

Fig. 5.9 Shape of rosette leaves of 231 samples *Lactuca serriola* L. from the Western USA (165 samples), Midwestern USA (22 samples), and Canada (44 samples): 0, entire; 3, pinnatilobed; 5, pinnatifid; 7, pinnatipart; 9, pinnatisect; nd, rosette not developed. Frequency of occurrence (%) of each category of the shape of rosette leaves is expressed for each geographical area

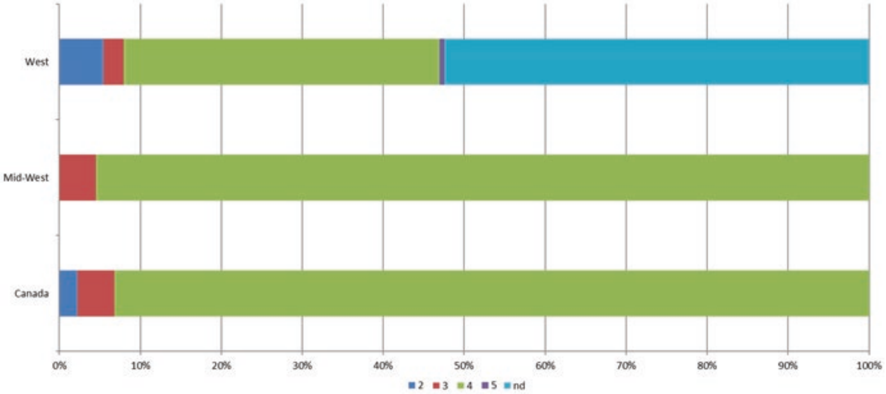

Fig. 5.10 Shape of the apices of rosette leaves of 231 samples *Lactuca serriola* L. from the Western USA (165 samples), Midwestern USA (22 samples), and Canada (44 samples): 2, subacute; 3, rounded; 4, obtuse; 5, mucronate; nd, rosette not developed. Frequency of occurrence (%) of each category of the shape of the apices of rosette leaves is expressed for each geographical area

Midwest. The absence of deeply divided stem leaves in that region can be explained as a morphological adaptation to the relatively mild climate of this region. The apices of stem leaves varied from subacute to rounded, obtuse, and mucronate, with obtuse being most common (Fig. 5.12).

Various patterns of anthocyanin distribution on stem leaves were recorded (Fig. 5.13a, b), as well as various patterns of arrangement and pigmentation of trichomes on the stem leaves (Fig. 5.13c–h). One sample from Arizona and eight from California developed dense trichomes on both sides of their stem leaves and on the upper parts of their inflorescences. These fall within the range of variation of *L. serriola* var. *coriacea* (Feráková 1977) (Fig. 5.13c, f–h). This variety was not

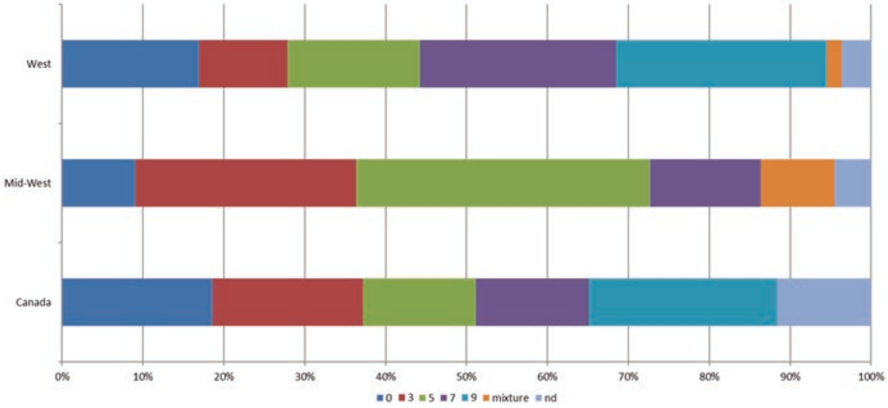

Fig. 5.11 Shape of stem leaves of 231 samples *Lactuca serriola* L. from the Western USA (165 samples), Midwestern USA (22 samples), and Canada (44 samples): 0, entire; 3, pinnatilobed; 5, pinnatifid; 7, pinnatipart; 9, pinnatisect; mixture, plants with both entire and divided stem leaves in sample; nd, not assessed. Frequency of occurrence (%) of each category of the shape of stem leaves is expressed for each geographical area

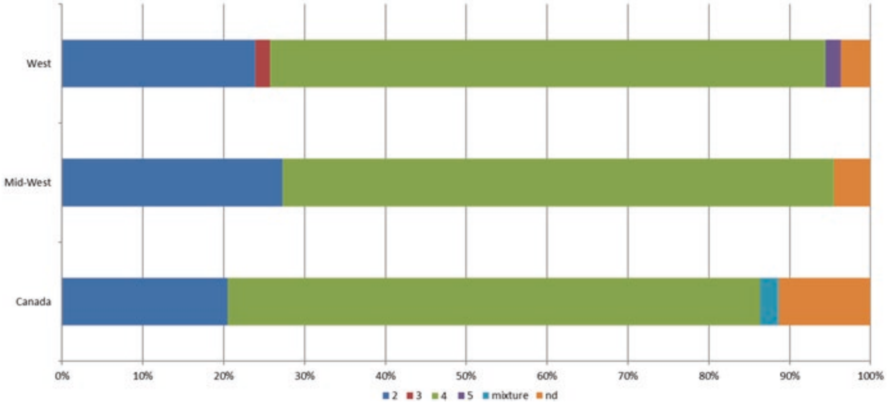

Fig. 5.12 Shape of apices of stem leaves of 231 samples *Lactuca serriola* L. from the Western USA (165 samples), Midwestern USA (22 samples), and Canada (44 samples): 2, subacute; 3, rounded; 4, obtuse; 5, mucronate; mixture, plants with both subacute and obtuse apices in sample; nd, not assessed. Frequency of occurrence (%) of each category of the shape of the apices of stem leaves is expressed for each geographical area

mentioned either by Strother (2006b) or McGregor et al. (1986). The phenotype of these plants, and especially the "xerophytic look" of plants from one location in California (Fig. 5.13h), reflects their adaptation to arid climatic conditions (Peel et al. 2007). Dense trichomes on leaves and stems developed as an adaptation to dry hot climatic conditions and are genetically fixed; these traits persist during cultivation under non-stressful conditions in the greenhouse.

Fig. 5.13 *Lactuca serriola* L. – cauline leaves: anthocyanin distribution along margin (Arizona 71/02) (**a**) and in spots (Montana 122/08) (**b**); sharp, stout trichomes on midrib and leaf blade (California 161/08) (**c**); anthocyanin in thin trichomes on midrib (California 55/06) (**d**); white, thin trichomes on midrib (Colorado 153/08) (**e**); white, smooth trichomes on leaf blade (California 112/04) (**f**); dense trichomes with anthocyanin on the leaf blade (California 88/02) (**g**); dense trichomes on the upper part of the stem and upper leaves (California 96/08) (**h**)

One sample from California with entire leaves that nearly lacked trichomes resembled a cultivated form of *L. sativa*, namely, stalk lettuce (Fig. 5.14a–e). Organoleptic tests of its stem leaves confirmed their limited bitterness. There are several explanations for the origin of these plants: (i) natural mutation, (ii) spontaneous hybridization

Fig. 5.14 *Lactuca serriola* f. *integrifolia* (Gray) S. D. Prince & R. N. Carter (California 87/04): the bolting stage (**a**), the beginning of flowering (**b**), stem lacking trichomes (**c**), concave profile of a cauline leaf (**d**), lower side of the midrib lacking trichomes (**e**)

of *L. serriola* with *L. sativa* and consequent self-pollination, and (iii) escape of *L. sativa* from cultivation and its spontaneous hybridization with *L. serriola*.

Developmental Stages
The number of days after sowing when the first plant within each sample entered the appropriate developmental stage was recorded. The start of bolting was recorded between 42 and 120 days after sowing (das.) for plants from Canada and between 42 and 117 das. for those from the Midwestern and Western USA. Samples from Canada and the Midwestern USA were medium or late bolting. In samples from the

Western USA, 50% of samples were early to bolt (Fig. 5.15). Only 8% of samples from the West were late bolting. Uniformity in this feature was recorded in 89 early bolting (42 and 66 das.) samples from the Western USA. Uniform bolting was recorded for one sample from Canada only (bolted 42 das.), and only one sample from the Midwestern USA was uniform in this trait (bolted 103 das.). Heterogeneity in bolting was recorded in ~90% of samples from Canada and the Midwestern USA but also in samples from the Western USA. The period between the beginning of bolting of the first plant within sample and the last plant varied among samples; in extreme cases, it reached 75 days.

Plants from different regions differed in flowering initiation (Fig. 5.16). Most samples from Canada flowered 151 das. Early-flowering samples were recorded

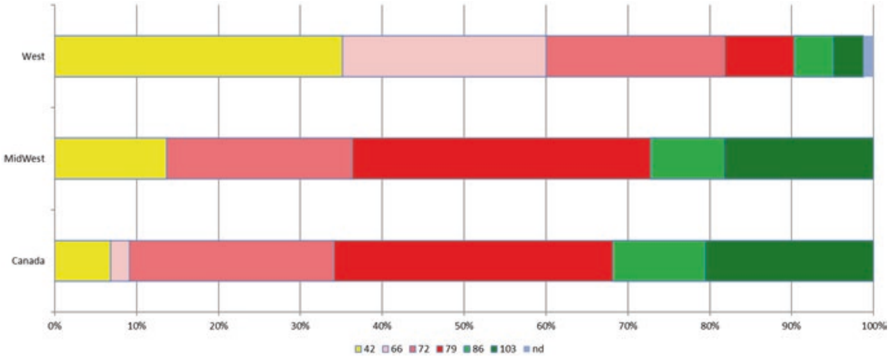

Fig. 5.15 Beginning of bolting (days after sowing (das.)) of 231 samples of *Lactuca serriola* L. from the Western USA (165 samples), Midwestern USA (22 samples), Canada (44 samples): categories, days after sowing; yellow tints, early bolting; red tints, medium bolting; green tint, late bolting. Frequency of occurrence (%) of each category (das.) of beginning of bolting is expressed for each geographical area

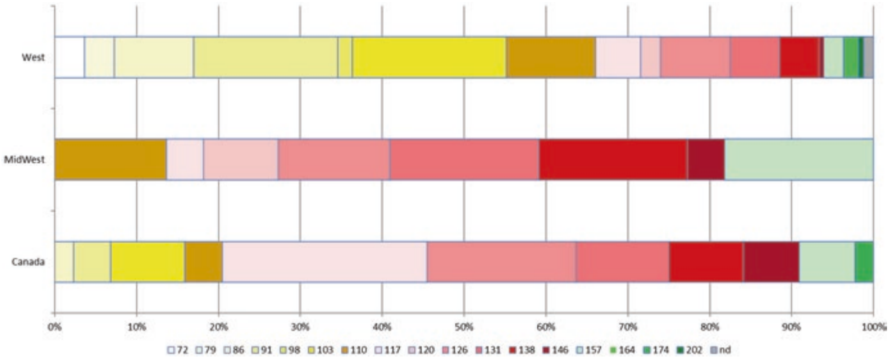

Fig. 5.16 Beginning of flowering (days after sowing (das.)) of 231 samples *Lactuca serriola* L. from the Western USA (165 samples), Midwestern USA (22 samples), and Canada (44 samples): categories, days after sowing; yellow tints, early flowering; red tints, medium flowering; green tint, late flowering. Frequency of occurrence (%) of each category (das.) of beginning of flowering is expressed for each geographical area

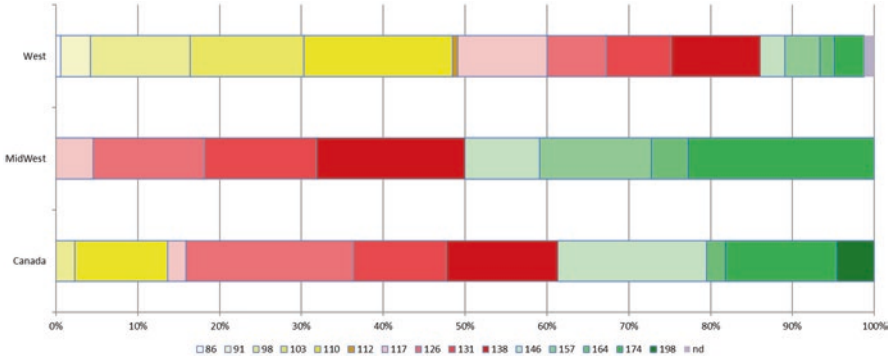

Fig. 5.17 Beginning of seed maturity (days after sowing (das.)) of 231 samples *Lactuca serriola* L. from the Western USA (165 samples), Midwestern USA (22 samples), and Canada (44 samples): categories, days after sowing; yellow tints, early seed maturity; red tints, medium maturity; green tint, late maturity. Frequency of occurrence (%) of each category (das.) of beginning of seed maturity is expressed for each geographical area

only sporadically. Plants from the West flowered 72 das.; most samples were early in this developmental stage, and 20% of samples were medium flowering. Only a few samples started to flower after 151 days (the latest flowered 202 das.). Samples from the Midwest began to flower 103 das., with the majority medium flowering. The last Midwestern sample began to flower at 157 das.

The stage of seed maturity was first reached by samples from the Western USA at 86 das. (Fig. 5.17). Most samples from the West were early or medium in maturity; only 10% of samples were late. Samples from Canada reached seed maturity between 98 and 198 das. Most Canadian samples were of medium maturity. Samples from the Midwest were medium or late.

These results reflect the ecological adaptations of plants to their local climatic conditions. Hot, dry climates in the West, typically with winter rains and summer drought (Peel et al. 2007), select for strategies that allow plants to survive summer stresses and accelerate seed maturity by early bolting, flowering, and maturation. The milder climates of the Midwest (Peel et al. 2007) allow for delays in all three developmental stages. These features are fixed genetically, as they were also expressed under optimal greenhouse conditions.

The phenological timing is important for annual species because they must complete their life cycle during one single growing season. Genetically based clines in phenological traits are common, e.g., earlier flowering time as a response to shorter growing season at high elevations (Alexander 2010). However, plants also respond to environmental variability by phenotypic plasticity (Sultan 2000), a trait that may be under selection in introduced populations (Richards et al. 2006), and so plasticity can be an important component of any phenological response to environmental conditions (Nicotra et al. 2010).

In an analogous experiment with a set of 87 *L. serriola* samples acquired in Europe in 2000, the beginning of bolting varied within the whole set was 72 das. to

111 das., and the flowering stage was recorded 109 das. for the earliest and 268 das. for the latest sample (Křístková et al. 2007). The earliest bolting European samples entered to this developmental stage after 60% of samples from Western USA already had reached this stage (Fig. 5.15); and similar differences were recorded also for the beginning of the flowering. The period between both developmental stages in the whole set was 16–139 days; the shortest mean value of 27 days for this period was recorded for the samples from mountainous regions of the Italian Alps, an area around Grenoble (France) and mountainous areas of the Slovak Republic. Generally, the beginning of bolting of these samples was delayed. On the contrary, the longest mean value (47 days) between beginning of bolting and flowering was recorded for samples from Southern Europe (Po River lowlands (Italy) and Côte d'Azur and Provence (France)), all with an early start to bolting (Křístková et al. 2007). These results indicate that reproductive timing of plants is influenced by the original ecogeographic conditions that persist when plants are cultivated in unified conditions and are fixed genetically.

Populations of *L. serriola* collected along elevation gradients in the Wallowa Mountains (Oregon, USA) and Switzerland were studied for phenotypic plasticity and developmental stages (Alexander 2010). The limit for seed set of 1400 m a.s.l. was the same for native and introduced plants. However, the limit for flowering was 400 m higher for introduced plants due to their faster development. The close correlation between the elevational limits observed in the experiment and in natural populations supports the interpretation of a genetic basis for the difference in elevational limits of *L. serriola* in each region. Introduced plants were characterized by phenotypic plasticity (Alexander 2010). Populations *L. serriola* from the Wallowa Mountains had significantly greater genetic variability than those from Switzerland, potentially resulting from recombination of previously isolated genotypes during their introduction to a new range (Alexander et al. 2009a).

Achenes

We recently evaluated 121 samples of *L. serriola* representing 81 populations from 11 US states (Midwest, South Dakota, Iowa, and Wisconsin; West, Washington, Oregon, Idaho, Wyoming, Nevada, Arizona, Utah, and California) and 44 samples from 4 Canadian populations (Ontario and Québec) for variation in achene morphology (Table 5.3). Seed for this evaluation was acquired on collecting missions to North America and Canada in 2002, 2004, and 2006 (Lebeda et al. 2012a). Each sample was represented by 50 randomly selected achenes produced in a greenhouse during multiplication of samples. Data were treated statistically by nested ANOVA (General Linear Models; GLM) (Hintze 2007).

Achenes from the USA and Canada significantly differed in one parameter only – in the length of the beak. The beak was significantly longer for achenes from the USA (4.33 mm; SD 0.51) than for those from Canada (4.02 mm; SD 0.58). No significant differences by country of origin were detected for the length and width of achene body or the index of both parameters. They were found only for beak length. Achenes from the West (4.39 mm; SD 0.03) had longer beaks than those from the Midwest (4.01 mm; SD 0.07).

Table 5.3 Correlations between morphologic parameters of achenes of 121 samples of *Lactuca serriola* L. from the Western USA, Midwestern USA, and Canada and geographic characteristics of the original locations of seed samples (Spearman correlation, r_s)

	Geographic characteristics of the original locations		
Morphologic trait	Latitude	Longitude	Elevation
Length of achene body (Lab, in mm)	−0.083*	0.065*	0.131*
Width of achene body (Wab, in mm)	−0.024*	0.023*	0.070*
Index Lab/Wab	−0.032*	0.021*	0.014*
Length of beak (Lb, in mm)	−0.301*	0.273*	0.082*

*Statistically significant at the level of $p < 0.05$

However, there were correlations between all achene traits measured and the geographic location of collection sites (Table 5.3). Length and width of achene body were most strongly influenced by elevation; length of beak was most significantly influenced by longitude (Table 5.3).

Achene parameters also differed significantly between leaf forms of *L. serriola* (Table 5.4). Achenes of *L. serriola* f. *integrifolia* are slightly longer and broader than those of *L. serriola* f. *serriola*. The index of achene length to width is slightly lower for f. *integrifolia*; achenes are “more rounded” in comparison with f. *serriola*.

Similar studies on achene morphology in *L. serriola* have been conducted, by examining sets of European samples (Novotná et al. 2011; Křístková et al. 2014). In those studies, latitude had the greatest influence on achene traits with similar results (Novotná et al. 2011; Křístková et al. 2014), and the statistically significant differences were also observed between achenes of f. *serriola* and f. *integrifolia* (Novotná et al. 2011).

5.2.2.3 Genetic Diversity of Wild *Lactuca* Species and *L. sativa*

Species of *Lactuca* are predominantly selfers (Lebeda et al. 2007a; Davey and Anthony 2011), which typically allocate more variation among populations than within them (Nybom et al. 2014). The majority of studies performed on various *Lactuca* species populations reflects the regional variation available for large-scale processes of gene flow and differentiation, rather than the amount of diversity that is available for individual populations to respond to local selective pressures.

Differences in the genetic backgrounds of various *Lactuca* species on a large geographical scale have been identified (D’Andrea et al. 2006; Kitner et al. 2008; Lebeda et al. 2009b, 2011; Jemelková et al. 2015). Large-scale structuring of genetic variation can be ascribed to selection and colonization history (Nybom et al. 2014). In natural populations of three wild *Lactuca* species occurring in the Near East, Kitner et al. (2015) demonstrated that populations were well genetically differentiated from other populations of the same species. While a substantial portion of the total variation of given species was represented by differences among particular

Table 5.4 Mean values for morphologic parameters of achenes of 121 samples of *Lactuca serriola* L. from the Western USA, Midwestern USA, and Canada and differences in these values between *L. serriola* f. *serriola* and *L. serriola* f. *integrifolia* (Gray) S. D. Prince & R. N. Carter (Mann-Whitney U test)

L. serriola	Morphologic trait											
	Length of achene body (Lab, in mm)			Width of achene body (Wab, in mm)			Index Lab/Wab			Length of beak (Lb, in mm)		
	N	$\bar{x}$	SD	*N*	$\bar{x}$	SD	*N*	$\bar{x}$	SD	*N*	$\bar{x}$	SD
f. *serriola*	33,463	3.09*	0.32	33,463	0.96*	0.15	33,463	3.30*	0.55	33,463	4.24	0.54
f. *integrifolia*	6454	3.11*	0.34	6454	0.97*	0.16	6454	3.29*	0.58	6454	4.25	0.55

N number of achenes analyzed, $\bar{x}$ mean, *SD* standard deviation
*Statistically significant at the level $p < 0.05$

populations, notably, different genotypes could often be sampled along relatively short transects (<200 m) within populations (Kitner et al. 2015). Detailed studies considering the genetic diversity of autochthonous North American *Lactuca* species have not been published.

5.2.2.3.1 Wild *Lactuca* spp.

5.2.2.3.1.1 Genetic Variation

Apart from studies where accessions of wild *Lactuca* species (*L. serriola*, *L. saligna*, *L. virosa*) were used as reference/outgroup for studies of *L. sativa* cultivars (Simko and Hu 2008; Simko 2009; see below), there are only four papers analyzing genetic variation of *L. serriola* individuals collected on the North American continent. Riar et al. (2011) explored genetic diversity among a collection of 22 *L. serriola* biotypes collected in Washington State (Fig. 5.18), together with *L. sativa* (cultivar Baja, USA) and *L. perennis* L. (Romania). This study grouped *L. serriola* accessions based on herbicide reaction: cluster I included individuals resistant to ALS (acetolactate synthase/ALS-inhibitor) and 2,4-D (red signs on Fig. 5.15), cluster II included individuals resistant to ALS (in green), and cluster III included individuals lacking herbicide resistances (in blue). However, cluster I included both resistant and susceptible *L. serriola* accessions. Although the authors stated that the clustering pattern corresponded well with geographical distributions (Riar et al. 2011).

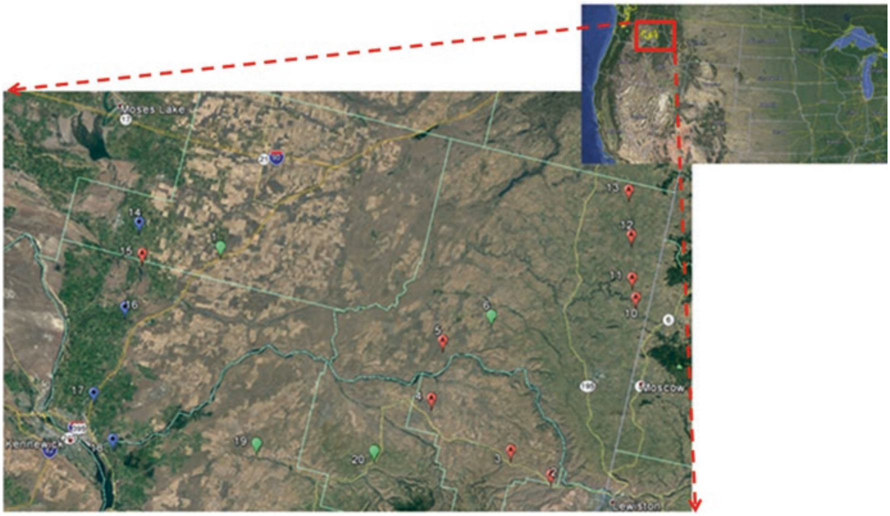

Fig. 5.18 Sampling sites of *L. serriola* L. accessions analyzed by Riar et al. (2011). Coloring corresponds to their resistance to herbicides (red, resistant to ALS and 2,4-D; green, resistant to ALS; blue, lacking resistance to either herbicide)

Fig. 5.19 Distribution of *L. serriola* L. collection sites in the North American continent (red, D1 sub-cluster; yellow, D2 sub-cluster; green and blue color, outlying accessions)

Lebeda et al. (2011) examined a set of 92 *L. serriola* accessions, covering a broad transect of territory in North America between California and Quebec. The majority of accessions formed a large cluster with two sub-clusters, which corresponded to distinct regions. While sub-cluster D1 (in red on Fig. 5.19) represented samples collected exclusively in California, Nevada, Utah, Oregon, and Arizona, samples from the northern part of the USA (Oregon, Wyoming, Wisconsin) and Canada (Quebec, Ontario) were members of sub-cluster D2 (in yellow on Fig. 5.19). Evidently, the Sierra Nevada and other geographic barriers form a natural boundary between *L. serriola* populations (metapopulations) collected along the Pacific coast and in the southwest and those populations sampled northward and eastward (Rocky Mts., Great Plains, and Southeastern Canada). However, we should point out that the bootstrap value supporting the separation of both sub-clusters was rather weak (Lebeda et al. 2011).

Alexander et al. (2009a, b) compared native (Valais, Switzerland) and introduced (Wallowa Mountains, Oregon) *L. serriola* populations and those of *Solidago canadensis* L, identifying a relatively low proportion of genetic variation attributed to differences between areas. However, populations of *L. serriola* were more genetically structured than *S. canadensis*, and this structure was substantially greater in the native than in the introduced area. Populations of *L. serriola* were significantly more diverse in the introduced area (Alexander et al. 2009a, b). The greater variability of *L. serriola* in the introduced area, where it occurs over a greater elevational range, can be explained by increased outcrossing among admixed populations. This suggests that the ecological amplitude of alien species might be enhanced after population admixture in the new range, especially for species with highly structured native populations (Alexander et al. 2009a, b). This was explored further by Alexander (2013) who found that non-native *L. serriola* originated primarily from Europe with low rates of admixture from Asia. It has rapidly refilled its climatic niche in its new ranges, associated with the evolution of flowering phenology to produce clines along climate gradients that mirror its native range (Alexander 2013). Some non-native *L. serriola* plants now grow in climates more extreme than those found in Europe and have evolved new developmental phenologies. This suggests that some rapid-cycling plant populations can adapt quickly to changing climatic conditions that are already within the climatic niche space occupied by the species elsewhere in its range but that evolution to conditions outside of this range may be more difficult (Alexander 2013).

As noted above, except for Alexander et al. (2009a, b), the studies above did not compare actual populations, but assayed pseudopopulations comprised of individual plants collected over large geographical areas. Moreover, none of them found significant clustering of samples by their geographical origins. An AFLP and isozyme study conducted on European *L. serriola* populations showed that accessions originating in various ecogeographical conditions of Europe differ significantly (Lebeda et al. 2009b). This might imply that the spread of *L. serriola* across the North American continent was relatively fast, from a limited number of founding populations originating from Europe (Alexander 2013).

5.2.2.3.1.2 Genome Size and DNA Content Variation

Previous studies made on individual *Lactuca* species showed rather large variation in this genome size (Doležalová et al. 2002b; Koopman 2000; Koopman et al. 2002). All the species of *Lactuca* native to North America (except for *L. tatarica* subsp. *pulchella*) and those of the Old World have substantial differences in their haploid chromosome number (North American n = 17), making them both geographically and genetically isolated (Lebeda et al. 2007a). In the North American species, higher contents of nuclear DNA have been established in comparison with Eurasian taxa (Doležalová et al. 2002b). On the other hand, the small differences in nuclear DNA content were detected in our pilot study of North American *L. serriola* samples (Lebeda et al. 2011).

5.2.2.3.1.3 Frequency of Disease Resistance Based on the RGC2 Resistance Gene Cluster

Kuang et al. (2006) analyzed the frequency and variation of *Dm3* in 1033 samples representing 49 natural populations of *L. serriola*. Inoculation by *Bremia lactucae* carrying the avirulence gene *Avr3* demonstrated that *Dm3* was present only in one of the analyzed samples, which originated in Pavia, Italy. The most recent critical review (Parra et al. 2016) to examine the current state of *Dm* genes confirmed the existence of 51 resistance genes and factors and 15 quantitative trait loci in lettuce and its wild relatives to *B. lactucae*. However, none originated in North America, suggesting that there is untapped potential within North American *Lactuca* species for their exploitation in resistance breeding (Lebeda et al. 2011, 2012a, 2014).

5.2.2.3.2 Genetic Diversity of *Lactuca sativa* Cultivars

The number of registered lettuce cultivars between 2000 and 2010 by US Plant Variety Protection (PVP) and utility patents was 180 (131 PVP cultivars, 56 utility patents, and 7 cultivars dually registered by both PVP and patent (Mikel 2013)). Recent publications on the genetic background of lettuce cultivars consist of a summary of the genealogy of North American varieties (Mikel 2007, 2013) and molecular genotyping of selected sets of lettuce cultivars and related *Lactuca* species (Witsenboer et al. 1997; Hu et al. 2005; Simko and Hu 2008; Simko 2009).

Simko and Hu (2008) used microsatellite markers for analyses of 90 *L. sativa* cultivars, while target region amplification polymorphism (TRAP) markers were applied to 54 cultivars analyzed by Hu et al. (2005) and Simko (2009). There is good agreement between the assessment of population genetic structure and classification into horticultural types (Fig. 5.20; Hu et al. 2005; Simko and Hu 2008; Simko 2009).

Coefficient of parentage (CP) values range from 0 to 1, with 0 an estimate of no relationship (no genetic similarity) and 1 an estimate of maximum relationship (complete genetic similarity), and CP among cultivars of leaf, romaine, and crisphead lettuce types registered from 2000 through 2010 was 0.02, 0.15, and 0.13, respectively (Mikel 2013). Mikel (2013) found more genetic diversity among leaf than crisphead or romaine cultivars, in agreement with earlier studies (Hu et al. 2005; Witsenboer et al. 1997). Mikel (2013) attributed the higher CP values of romaine and crisphead lettuce to the commonly used breeding practice of recycling and the recurrent use of closely related, elite lines and cultivars. For example, the two most important crisphead ancestors, “Vanguard” and “Salinas,” together accounted for 35.9% of genes among modern crisphead cultivars. Simko (2009) also found very limited phenotypic variability and the lowest level of genetic variation within cultivar Iceberg (a crisphead type).

The parentage of ancestral crisphead cultivars “Vanguard” and “Salinas” involves wild *Lactuca* species. “Vanguard” was developed from a series of interspecific crosses with wild progenitors, namely, *L. virosa* (PI 125130) and *L. serriola* (PI 125819, PI 114435, and PI 114512) (Thompson and Ryder 1961; Whitaker 1974). These interspecific crosses first led to the development of breeding line BL 5192 and later to BL 5504 (parent of “Vanguard”) and BL 8830 (parent of “Salinas”). US cultivars and accessions of wild *Lactuca* species were used for the generation of lettuce genetic linkage maps (Truco et al. 2007; McHalle et al. 2009; Stoffel et al. 2012). Truco et al. (2007) combined results from previous studies from interspecific crosses (Kesseli et al. 1994, Witsenboer et al. 1997, Waycott et al. 1999, Johnson et al. 2000, Jeuken et al. 2001) *L. sativa* × *L. saligna*, *L. sativa* × *L. serriola*, or *L.*

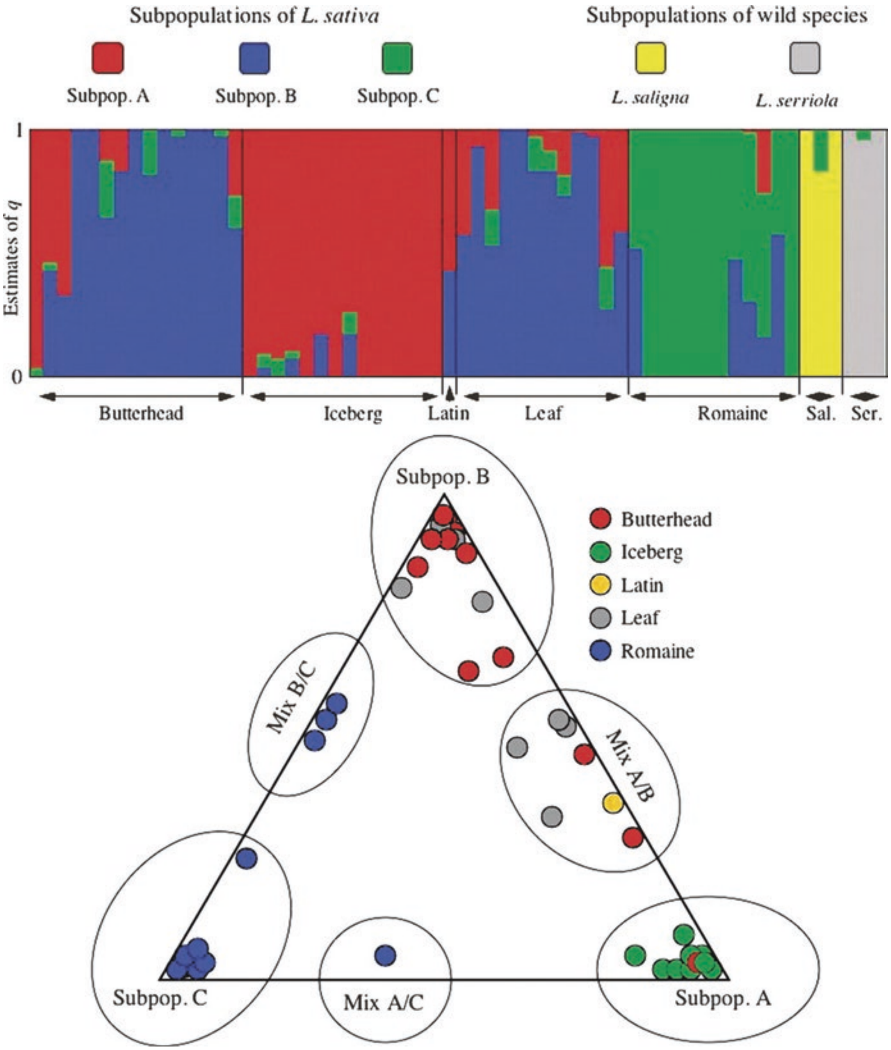

Fig. 5.20 (Top) Bar plot of population structure estimates for 60 *Lactuca sativa* L., *Lactuca saligna* L., and *Lactuca serriola* L. accessions (Simko and Hu 2008). Population structure was assessed with 388 TRAP markers. Each accession is represented by a single vertical bar broken into five colored segments, with lengths proportional to q of the five inferred subpopulations ($K = 5$). The sum of q values for each bar is 1 ($\sum_k q_k = 1$). The horizontal axis shows the five horticultural types (butterhead, iceberg, latin, leaf, romaine) and two wild species (*L. saligna*, *L. serriola*). (Bottom) Triangle plot of population structure estimates for 54 cultivars with 107 TRAP markers that are polymorphic in *L. sativa* (Simko and Hu 2008). A colored point represents each accession, with colors corresponding to the five horticultural types (butterhead, iceberg, latin, leaf, and romaine). The estimated vector for an accession consists of three q values that correspond to the three inferred subpopulations ($K = 3$). The sum of q values for an accession is 1 ($\sum_k q_k = 1$). For an individual accession, the distance to one edge of the triangle gives each of the three q values. Accessions that are in one of the corners are thus assigned completely to the corresponding subpopulation (Simko and Hu 2008)

saligna × *L. sativa* which were analyzed by various methods to develop an integrated map of lettuce.

McHalle et al. (2009) provided a detailed analysis of the genomic architecture of disease resistance in lettuce. Among others, two accessions have been used frequently in these studies – *Lactuca sativa* “Salinas” and *L. serriola* accession UC96US23. These accessions were used together with other *Lactuca* species by Stoffel et al. (2012) to generate a high-resolution genetic map. *Lactuca virosa* and *L. saligna* are sexually incompatible species with *L. sativa* (de Vries 1990), and the data generated by Stoffel et al. (2012) support the findings of Kesseli et al. (1991) that these two species are not progenitors of *L. sativa.*

5.2.2.3.2.1 Genetic Diversity of Lactuca sativa Cultivars: Case Study of cv. Salinas

A draft 2.4-Gb reference sequence assembly is now available for the 2.7-Gb genome of *L. sativa* cv. Salinas along with an ultradense genetic map (http://lgr.genomecenter.ucdavis.edu; S. Reyes-Chin Wo, A. Kozik, D. Lavelle, and R. W. Michelmore, unpublished data). Christopoulou et al. (2015) identified 1134 genes in this lettuce reference genome that are potentially involved in pathogen recognition, of which 385 were predicted to encode nucleotide-binding leucine-rich repeat receptor (NLR) proteins. The NLRs were grouped into 25 multigene families and 17 singletons. Forty-one percent of these NLR-encoding genes belonged to three families, the largest being *RGC16* with 62 genes in cv. Salinas. The majority of NLR-encoding genes are located in five major resistance clusters (MRCs) on chromosomes 1, 2, 3, 4, and 8 and cosegregate with multiple disease-resistance phenotypes. Most MRCs contain primarily members of a single NLR gene family (Christopoulou et al. 2015).

5.3 Wild *Lactuca* Species: Their Exploitation and Utilization

5.3.1 History of Lettuce Breeding and Importance of Wild Lactuca *Relatives*

Lettuce was introduced to the New World shortly after Columbus arrived in 1492, and its cultivation quickly spread being reported in Haiti by 1565 and in Brazil by 1647 (Ryder and Whitaker 1995). The first lettuce cultivars were introduced to North America by European seed companies in the nineteenth century. By the end of the nineteenth century and early part of the twentieth century, improvement of these European cultivars was practiced by US growers and seed companies. Improved cultivars were established in the US market under new names (e.g., “Sans Rivale à Graine Blanche” from Vilmorin-Andrieux became “Unrivalled” from John A. Bruce & J. A. Summers in 1902 and finally “White Boston”) (Tracy 1904; Rodenburg 1960). The cultivar “Iceberg” was named and introduced into the USA in 1894 by W. Atlee Burpee & Co., which stated that the variety was of foreign origin (Tracy 1904). The variety named Iceberg is not an iceberg type but rather a Batavia type. The designation “Iceberg” was used in the lettuce industry for firm crisphead cultivars.

The earliest public breeding program in lettuce began in California in 1923 (Ryder 1999). At first, cultivars were bred for market and home gardens around, and then development of the crisphead lettuce enabled the transport of heads in refrigerated rail cars from the Western USA to major markets in the East and Midwest (Ryder and Whitaker 1995). The cultivar “New York” was one of the most popular early cultivars in the USA, being extensively planted in most parts of the country (Tracy 1904). Unfortunately, it was highly susceptible to a disease called brown blight caused by a soilborne virus.

This cultivar was used in the development of a major group of cultivars (the “Imperial” group) beginning in 1929 (Rodenburg 1960; Ryder and Whitaker 1995; Mikel 2007), which were resistant to brown blight. In 1941, from the cross of “Imperial 152” × “Brittle Ice” × “Imperial 615,” the first cultivars of the “Great Lakes” group appeared, with improved characteristics (Rodenburg 1960).

The “Imperial” and “Great Lakes” cultivars were susceptible to *Bremia lactucae*, which appeared in the USA in 1932, leading to the development of the resistant cultivars “Valverde” (Fig. 5.21a) and “Calmar” (Ryder and Whitaker 1995). In the development of the cultivar “Calmar,” which was released in 1960, wild *L. serriola* (PI 104854) was used for interspecific crossing with cultivated lettuce from the “Imperial” group (Mikel 2007). This cultivar and its derivatives became the dominant group of cultivars in California, until replaced by “Salinas,” released in 1975 (Ryder and Whitaker 1995; Mikel 2007). However, the cultivar “Calmar” contributed to the parentage of “Salinas.” The next most important source in the genetic background of “Salinas” was derived from the interspecific cross of *L. sativa* with *L. virosa* (PI 125130) and *L. serriola* (PI 114512, PI 114535, and PI 125819) (Ryder 1999; Mikel 2007). “Salinas” and similar cultivars became dominant cultivars in

Fig. 5.21 American lettuce cultivars “Valverde” (**a**) and “Vanguard” (**b**). (Author of photos: B. Mou, USDA/ARS, Salinas, USA)

most lettuce production areas in the world (Ryder and Whitaker 1995). *Lactuca virosa* (PI 125130) and *L. serriola* (PI 114512, PI 114535, PI 125819) also were involved in other important hybridization events with *L. sativa*, after initial use in the development of the cultivar "Vanguard" released in 1958 (Mikel 2007). The cultivar "Vanguard" (Fig. 5.21b) was the first derivative of the difficult cross between cultivated lettuce and *L. virosa*. This species evidently contributed genes for the dark green color and excellent leaf texture that characterize "Vanguard," "Salinas," and their derivatives (Ryder and Whitaker 1995). Analysis of the pedigree histories of 146 lettuce cultivars registered in the USA by Plant Variety Protection and/or utility patent between 2000 and 2010 demonstrated that the cultivars "Vanguard" and "Salinas" followed by the "not *L. virosa*" cultivar "Calmar" were the elite parents most frequently used in lettuce breeding (Mikel 2007, 2013). Of the 37 progenitor cultivars, breeders at public institutions and private companies in the USA developed 31 new cultivars in the period 1970–2004, and 10 of these progenitors of today's lettuce cultivars were developed before 1960 (Mikel 2007). The cultivar "Salinas" was frequently crossed with romaine lettuce types, and the romaine parental cultivar "Parris Island Cos" was repeatedly crossed with leaf types contributing to romaine and leaf lettuce genetic diversity (Mikel 2013). *Lactuca saligna* (PI 261653), a source of disease resistance (Lebeda et al. 2014), was crossed to the iceberg type of cultivated lettuce to develop "Salad Crisp," the first lettuce cultivar with genetic material from *L. saligna* (Provvidenti et al. 1980). The cultivar "Salad Bibb" (HXP 3550) is an open-pollinated butterhead-type lettuce with multiple disease resistance, developed through a series of crosses of unspecified accessions of *L. saligna* with several *L. sativa* cultivars (PVPA 8500060) (Mikel 2007; Ryder and McCreight 2014).

Detailed reviews of wild *Lactuca* species used in lettuce breeding are available (Pink and Keane 1993; Lebeda et al. 2007a; Mou 2008; Davey and Anthony 2011; Lebeda et al. 2014). Three wild *Lactuca* species, *L. serriola*, *L. saligna*, and *L. virosa*, were used for crosses with *L. sativa* most frequently until the end of the twentieth century. Recently, the interests of the leading world lettuce breeding programs have expanded to explore the diversity of other wild *Lactuca* species (Lebeda et al. 2014), e.g., *L. aculeata* (Jemelková et al. 2015). However, there is still low genetic diversity related to the fact that only a few germplasm accessions of wild *Lactuca* species have been used in lettuce breeding (Table 5.5). In early breeding, few accessions were successfully incorporated, and most were provided to the US NPGS by European botanic gardens; however, the primary collecting site of these samples remains unclear. From this viewpoint, the enormous phenotypic, phenologic, and genetic variability of wild *Lactuca* species (autochthonous and/or allochthonous) together with the presumed variability in their responses to biotic and abiotic factors represents a great challenge for lettuce breeders.

Currently, ~20 breeding companies and other institutions are developing new lettuce lines and cultivars in the USA. In the public sector, only the University of California in Davis, University of Florida in Gainesville, and the USDA/ARS in Salinas, CA, have active breeding and genetic research programs (Leafy Vegetable Crop Germplasm Committee 2015).

Table 5.5 Origin of germplasm accessions[a] of wild *Lactuca* species used in the early breeding programs of lettuce in the USA

Lactuca spp.	PI number	Year of acquisition	Country of origin	Location	Reference
L. sativa L.	PI 120965	1937	Turkey	Edirne bazaar	Mikel (2013)
L. sativa L. (primitive, oilseed)	PI 251245	1958	Egypt		Ryder (1979)
L. saligna L.	PI 261653	1959	Portugal		Provvidenti et al. (1980)
L. serriola L.	PI 104854	1934	United Kingdom	Botanic garden in Cambridge; Mikel (2013) reports Russia as a country of the origin	Mikel (2013)
L. serriola L.	PI 114512	1936	Sweden	Botanic garden in Göteborg	Mikel (2007, 2013)
L. serriola L.	PI 114535	1936	United Kingdom	Botanic garden in Cambridge	Mikel (2007, 2013)
L. serriola L.	PI 125819	1937	Afghanistan	Khanabad, 366 m altitude	Mikel (2007, 2013)
L. serriola L.	PI 91532	1931	Uzbekistan	Tashkent	Witsenboer et al. (1995), Simko (2013)
L. virosa L.	PI 125130	1937	Sweden	Botanic garden in Stockholm	Mikel (2007, 2013)

[a] Passport data for PI accessions derived from USDA, ARS, National Genetic Resources Program (2016)

5.3.2 Desirable Characters and Their Prospective Uses in Breeding

Horticulturally important traits of lettuce are connected to the size, color, weight, and yield of heads/rosettes, the taste and texture of leaves, and uniformity of maturity. For cultivated lettuce, desirable traits include rapid vegetative development but slow bolting, novel leaf colors and shapes, high nutritional value, low content of latex and reduced bitterness, reduced nitrate accumulation, uniform development and harvest, extension of postharvest shelf life, and broad environmental adaptation (Ryder 1999, 2001; Davey and Anthony 2011; Simko et al. 2014b; Hunter et al. 2017).

One of the main goals of current lettuce breeding is to bring together multiple disease- and pest-resistance traits. Some *Lactuca* accessions have been shown to possess multiple resistances which can be transferred to cultivated lettuce and combined with horticulturally important traits (Lebeda et al. 2014). Tolerance of lettuce cultivars to abiotic stresses can also be derived from wild *Lactuca* species originally adapted to extreme habitats. However, wild *Lactuca* species contain many unfavorable traits including tough leaves and woody stems, often with spines, and the production of latex and bitter compounds with sedative properties (Pink and Keane 1993). Despite this, it is worth noting that wild *Lactuca* species can contribute to lettuce improvement not only via their resistance genes but also by influencing organoleptic traits.

5.3.3 Gaps and Challenges for the Future

The effective conservation and management of wild crop relatives have been addressed (Maxted et al. 2008a, b; Ford-Lloyd et al. 2008). The linking of in situ and ex situ conservation with the use of wild crop relatives is the leading principle of wild plant germplasm conservation and management (Maxted and Kell 2008). Access to wild genetic resources and the possibility for exploiting them depend upon the successful and reasonable protection of wild species in situ (Iriondo and De Hond 2008), upon the complex study of wild species in natural habitats, and upon the possibility for exchanging information and biological material (Azzu and Collette 2008).

Genetic resources of wild *Lactuca* species (Lebeda et al. 2004a, 2007a, 2009a, 2014) are an integral part of our global plant heritage, and they play important roles in recent lettuce breeding (Lebeda et al. 2007a; Mikel 2007; Maggioni et al. 2008; Mou 2008). The most important remaining gaps and challenges related to the effective use of this germplasm are highlighted in the following paragraphs.

The most recent inventory of the International Lactuca Database (ILDB) with passport data for 11,643 *Lactuca* accessions and of the Dutch national *Lactuca* germplasm collection (van Treuren and van Hintum 2009; van Treuren et al. 2011) confirmed previous conclusions (Lebeda et al. 2004a, 2009a) regarding gaps in overall collection structure. Wild *Lactuca* germplasm is not adequately conserved by national or regional genebanks; neither the species spectrum nor the full geographic distribution of the genus is adequately represented in germplasm collections (Lebeda et al. 2004a, 2007a, 2009a). *Lactuca* germplasm originating from North America is very poorly represented in these collections (Lebeda et al. 2011, 2012a; see Sect. 5.4.2 of this chapter).

Because of poor knowledge of the taxonomy and biogeography of the genus (Lebeda et al. 2004b), basic errors in the taxonomic status and duplications of wild *Lactuca* accessions were found during recent studies of germplasm collections (Doležalová et al. 2004; Lebeda et al. 2007a, 2009a; van Hintum and Boukema 1999; Doležalová et al. 2007; Sretenović-Rajičić et al. 2008).

Despite enormous progress in research on wild *Lactuca* germplasm, there are still many important gaps. The following seven points are critical for the future success of wild *Lactuca* germplasm utilization (Lebeda et al. 2009a, 2012a, 2014):

1. Comprehensive research on biosystematic and phylogenetic relationships
2. Detailed floristic, biogeographic, and ecologic delimitation of the distributions of taxa

3. Clarification of interspecific crossability in the genus and the structure of genepools
4. Reconsideration of existing germplasm collections in relation to geographic origin, ecology, diversity, and passport data
5. Organize collecting and exploration field missions, especially to the areas of high species richness and diversity
6. Increase activities focused on characterization and evaluation of traits important for the management of genebank collections and their efficient utilization in breeding
7. Broader international cooperation among diverse public institutions and between public institutions and the private sector

5.4 Conservation Status and Germplasm Collections

5.4.1 In Situ Conservation

North America, as a temperate region, is relatively impoverished with regard to its genepools and potential to provide major crops, in contrast to tropical areas, which exhibit great diversity (Davis et al. 1997b). The conservation of crop wild relatives, including *Lactuca* spp., is expensive and technically complicated (Kramer et al. 2011). Beyond their valuable traits, they possess many unwanted features. Therefore, it cannot simply be introduced into farmers' fields or breeding programs (Dempewolf and Guarino 2015). An initiative for establishing a global network for in situ conservation of crop wild relatives has been recently developed by the FAO, the University in Birmingham (UK), and Biodiversity International (Dulloo 2015). In practice, in situ conservation of crop wild relatives is often planned within existing protected reserves (Maxted et al. 2008a, b, 2014, 2016). However, there has been relatively little progress on the conservation of crop wild relatives outside protected areas (Dulloo 2015).

5.4.1.1 Current Status

An overview of the conservation status of wild, autochthonous *Lactuca* species in the USA and Canada (NatureServe 2016a, b) is presented in Table 5.6. Their assessment is not applicable for the allochthonous species, *L. saligna*, *L. serriola*, and *L. virosa*. Global conservation status of all the autochthonous *Lactuca* species is classified as secure (G5) or apparently secure (G4), and, thus, their species protection is not organized on a global level. On a national level, *L. floridana* and *L. ludoviciana* are classified as imperiled (N2) in Canada. The conservation status of wild *L. biennis*, *L. canadensis*, *L. floridana*, *L. hirsuta*, *L. ludoviciana*, and *L. tatarica* var. *pulchella*, when assessed on the subnational level, indicates that each of these taxa is classified as S1 (critically imperiled) in at least one US state. In addition, *L. ludoviciana*

Table 5.6 The conservation status of wild *Lactuca* species in the USA and Canada (NatureServe 2016a, b)

Lactuca spp.[a]	NatureServe Status Global (USA/Canada)	Number of US states/Canadian provinces with conservation status			
		SX, SH, S1, S2, S3	S4, S5	Not ranked	Not applicable
North American autochthonous species					
L. biennis (Moench) Fernald	G5 (NNR/N5)	4/4	7/8	23/0	1/0
L. canadensis L.	G5 (N5?/N5)	2/1	6/5	39/1	0/1
L. floridana (L.) Gaertn.	G5 (N5?/N2)	5(6)/2	4(5)/0	21/0	0/0
L. graminifolia Michx.	G5? (NNR/nt)	1/nt	0/nt	11/nt	0/nt
L. hirsuta Muhl. ex Nutt.	G5? (N5?/N4N5)	11(12)/3	2(3)/1	14/0	0/0
L. ludoviciana (Nutt.) Riddell	G4G5 (N4N5/N2?)	5/1	1/0	20/1	0/1
L. tatarica var. *pulchella*	G5T5 (N4N5/N5)	3/1	1/4	25/2	0/0
North American allochthonous species					
L. saligna L.	GNR (NNA/NNA)	0/0	0/0	2/0	29/2
L. serriola L.	GNR (NNA/NNA)	0/0	0/0	2/0	48/9
L. virosa L.	GNR (GNR/ NNA)	0/0	0/0	0/0	4/0

[a]Scientific names follow Kartesz (1994)

NatureServe Status for species – global (G/T), national (N), subnational (S):

X	Presumed extinct (not located despite intensive searches and virtually no likelihood of rediscovery)
H	Possibly extinct (known from only historical occurrences but still some hope of rediscovery. There is evidence that the species may be extinct but not enough to state this with certainty)
1	Critically imperiled (at very high risk of extinction due to extreme rarity (often five or fewer populations), very steep declines, or other factors)
2	Imperiled (at high risk of extinction or elimination due to very restricted range, very few populations, steep declines, or other factors)
3	Vulnerable (at moderate risk of extinction or elimination due to a restricted range, relatively few populations, recent and widespread declines, or other factors)
4	Apparently secure (uncommon but not rare; some cause for long-term concern due to declines or other factors)
5	Secure (common, widespread, and abundant)
NR	Not ranked (ongoing process)
NA	Conservation status not applicable (exotic species or because of hybrids without conservation value)
nt	Species not treated

Numbers in parentheses – conservation status ranged between categories S3 and S4

? Inexact numeric rank

and *L. tatarica* var. *pulchella* are critically imperiled (S1) in at least one Canadian province. Subnational status as possibly extirpated (SH) was recorded for *L. floridana* in Minnesota and Manitoba; for *L. hirsuta* in Connecticut, Maryland, and Virginia and in Prince Edward Island; for *L. ludoviciana* in Missouri; and for *L. tatarica* var. *pulchella* in Michigan. *Lactuca hirsuta* is presumed extinct (SX) in the District of Columbia, and *L. ludoviciana* has the same conservation status (SX) in Illinois and Indiana (NatureServe 2016a, b).

So far, the direct economic potential of autochthonous North American *Lactuca* species for the improvement of cultivated lettuce has not been adequately recognized. They form part of the tertiary genepool of *L. sativa*. Although these species undoubtedly occur in many existing protected areas (Lebeda et al. 2012a), they are unlikely to receive targeted conservation management as most national parks and other protected areas conserve CWRs passively (Maxted et al. 2016).

Both autochthonous and allochthonous *Lactuca* species, *L. biennis*, *L. canadensis*, *L. floridana*, *L. pulchella*, *L. saligna*, *L. scariola*, *L. serriola*, *L. tatarica*, and *L. virosa*, are on the list of weeds of the USA and Canada (WSSA 2016). We suspect that the weed status of some of autochthonous species, such as *L. biennis* and *L. floridana*, should be reconsidered. In particular, the allochthonous species truly should be monitored carefully, as they have the potential to disrupt both agricultural production and native plant communities through their uncontrolled spread. For example, in the inventory of California's invasive plants, there were not enough data to assess the ecological impacts of the roadside and agricultural weed, *L. serriola* (Bossard et al. 2006). Prickly lettuce is a good example of the "two sides of one coin": it is considered a source of valuable traits in lettuce breeding, and, thus, its diversity should be conserved, but its spread (especially in agroecosystems) must be controlled by herbicides and should be carefully monitored in fragile natural ecosystems.

5.4.1.2 Needs, Opportunities, and Challenges

Protection of wild plant biodiversity is a generally accepted need which contributes to the stability of ecosystems and crop production. In situ conservation of wild *Lactuca* species needs a species-specific approach based on i) our knowledge of taxonomic status, ii) knowledge of species' distributions and their spatiotemporal changes, and iii) recognition of the direct and indirect impacts of management protocols on lettuce breeding and production and on wildlife and landscape protection and health.

5.4.2 Ex Situ Conservation

5.4.2.1 Genebanks and Other Germplasm Collections and Their Status

In the case of *Lactuca* germplasm, there are eight important lettuce and wild *Lactuca* seed collections around the world (Lebeda et al. 2007a, 2009a). Of these, four are in North America (Table 5.7) and the rest in Europe. However, detailed information about the holdings, maintenance, conditions, availability, evaluation, and documentation of the stored accessions is limited (Lebeda et al. 2007a, 2009a). Lettuce and its wild relatives represent ca 3.4% of total number of conserved vegetable accessions in the USA (ca 87,000).

Table 5.7 Wild *Lactuca* species collections in the USA

Name	Location	Storage conditions
Western Regional Plant Introduction Station	Pullman, WA	Distribution seeds at 4 °C; original seed lots at −18 °C
USDA-ARS *Lactuca* Germplasm Collection	Salinas, CA	−18oC, RH not controlled
Lactuca Genetic Resources Collection, University of California	Davis, CA	5 °C, RH controlled
US National Center for Genetic Resources Preservation	Fort Collins, CO	−18 °C, 5–7% RH

Adapted from Lebeda et al. (2007a); Leafy Vegetable Crop Germplasm Committee (2015)

The Western Regional Plant Introduction Station (WRPIS) in Pullman, Washington, is the primary national repository and distribution center for lettuce genetic resources within the US National Plant Germplasm System (NPGS). There are two major lettuce collections in California. The USDA *Lactuca* Germplasm Collection in Salinas (LGCS) is considered the largest and most diverse collection of defined and characterized accessions in the world, (McGuire et al. 1993; Lebeda and Astley 1999; Lebeda et al. 2004a; Leafy Vegetable Crop Germplasm Committee 2015). The other California repository is the *Lactuca* Genetic Resources Collection at the University of California in Davis (LGRCD) which is a primary holder of lettuce molecular genetic materials and serves as a backup repository for standard genetic resources in California. The US National Laboratory for Genetic Resources Preservation (NLGRP) at Fort Collins also preserves lettuce germplasm (McGuire et al. 1993; Leafy Vegetable Crop Germplasm Committee 2015). Passport information, as well as observations on various morphological and horticultural traits for *Lactuca* germplasm accessions, is freely accessible through the web-based GRIN-Global database (http://www.ars-grin.gov/); this database includes 2938 accessions of the genus *Lactuca*, with 779 of them being of wild *Lactuca* taxa.

Agriculture and Agri-Food Canada's Plant Gene Resources of Canada (PGRC) is an integral part of the Saskatoon Research Centre located at the University of Saskatchewan. The PGRC seed genebank is the main repository for seed. The Canadian web-based database, GRIN-CA, has adopted the information system used in the USA (http://pgrc3.agr.gc.ca/search_grinca-recherche_rirgc_e.html). As for lettuce genetic resources, only six accessions of *L. sativa* are entered in the Canadian web-based database GRIN-CA and no accessions of wild *Lactuca*. All these accessions are available for distribution. Four accessions were donated by the Vavilov Institute of Plant Industry, Saint Petersburg, Russian Federation; one originated in California and the sixth from Ontario, Canada.

Although the genetic resources of wild *Lactuca* taxa represent very important sources for many traits in commercial lettuce breeding (Lebeda et al. 2004a, 2007a, 2009a, 2011, 2012a, 2014; Davey and Antony 2011), currently only 27 (20%) of the known species are available in the world's *Lactuca* germplasm collections (mostly of European origin) (Lebeda et al. 2004a, 2007a). A summary of all the wild *Lactuca* taxa reported in the recent NPGS GRIN-Global database (September 2016) is given in Table 5.8. In total, 20 wild *Lactuca* species representing 779 accessions are con-

Table 5.8 Wild *Lactuca* taxa entered in the US National Plant Germplasm System (NPGS) with numbers of accessions and availability. Source of primary data: GRIN-Global database (http://www.ars-grin.gov/, September 2016)

Taxon[a]	No. of acc./%	No. of acc. available for distribution
L. aculeata Boiss. & Kotschy	5/1	0
L. altaica Fisch & C.A. Mey.	13/2	0
L. biennis (Moench) Fern.	5/1	0
L. canadensis L.	10/1	1
L. dregeana DC.	1	0
L. floridana (L.) Gaertn.	8/1	2
L. georgica Grossh.	18/2	0
L. indica L.	5/1	1
L. inermis Forssk.	2	2
L. ludoviciana (Nutt.) Riddell	2	1
L. orientalis (Boiss.) Boiss.	4/1	0
L. perennis L.	7/1	2
L. quercina L.	10/1	2
L. saligna L.	92/12	9
L. serriola L.	419/54	160
L. tatarica (L.) C.A. Mey.[b]	14/2	1
L. tuberosa Jack.	1	0
L. undulata Ledeb.	2	0
L. viminea (L.) J. & C. Presl	1	0
L. virosa L.	95/12	2
Lactuca not determined	65/8	2
Total	779/100	185

[a] Species classification according to passport data; autochthonous North American species are in bold

[b] There is only one accession of *L. tatarica* subsp. *pulchella* of US origin; the other accessions of *L. tatarica* come from the Old World

served there. However, only 24% (185 acc.) of them are available for distribution, and some of these accessions (8%, 65 acc.) have not yet been taxonomically determined to the species level.

The autochthonous North American species with accessions listed in the GRIN-Global database are *L. biennis*, *L. canadensis*, *L. floridana*, *L. ludoviciana*, and *L. tatarica* subsp. *pulchella*, and they form 25% of listed *Lactuca* species richness. But they are represented by only 26 accessions, 3% of the total number of wild *Lactuca* accessions being conserved. A substantial part of collection (78%, 606 acc.) is represented by three species: *L. serriola* (54%), *L. saligna* (12%), and *L. virosa* (12%). The remaining species are represented by very few accessions (from 1 to 18) (Table 5.8). A summary of wild *Lactuca* represented in the GRIN-Global database organized by continent shows that the majority (96%) of accessions originate from

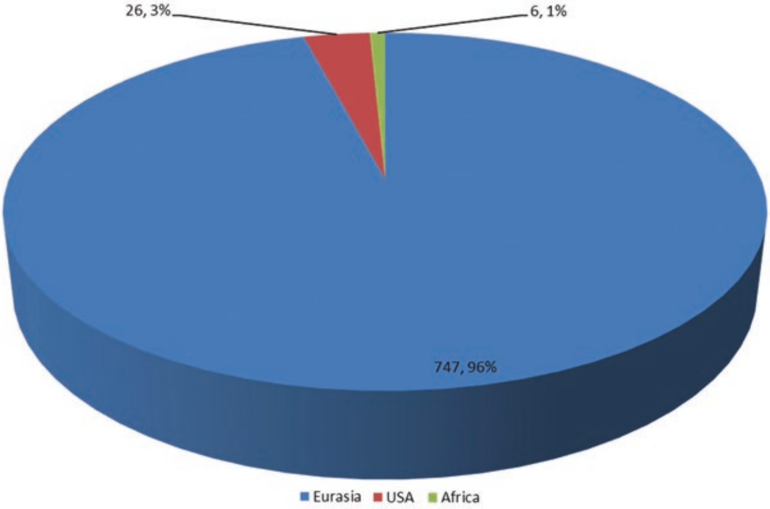

Fig. 5.22 Representation (number of accessions, percentage of total) of wild *Lactuca* spp. in the USDA, ARS National Plant Germplasm System by continent. (Source of primary data: GRIN-Global database (http://www.ars-grin.gov/, September 2016)

Eurasia (Fig. 5.22). Very few accessions (3%) come from North America, and only four North American accessions are available for distribution (Table 5.8).

A detailed search of the GRIN-Global database revealed that some passport data concerning an accession's origin can be misleading. This is most obvious in accessions donated by sources within the USA, where the country of origin does not correspond with the species' natural range, as was found for accessions of the species, *L. aculeata*, *L. altaica*, *L. indica*, and *L. inermis*. This fact has previously been mentioned by Lebeda et al. (2004a), who noted that secondary sources of origin (institutions, botanical gardens, general donor sources) have often been confused with the primary places of origin (natural occurrence). This is misleading from the phytogeographical viewpoint and can be deceptive, especially for novice users, who may overlook basic information about native ranges.

Regarding the representation of *Lactuca* species listed in the NPGS in relation to the primary genepool of *L. sativa* (Koopman et al. 1998, 2001; Koopman 1999), a substantial part of collection (59%) is constituted by accessions of *L. aculeata*, *L. altaica*, *L. dregeana*, *L. georgica*, and *L. serriola* (Fig. 5.23). The secondary genepool is represented by *L. saligna* and *L. virosa* accessions, which form 24% of total number of accessions, and tertiary species, *L. quercina*, *L. tatarica*, and *L. viminea*, forming only 3% of accessions. This emphasis on wild species belonging to the primary genepool is probably due to the fact that only recently have species of the secondary and tertiary genepools been regarded as significant donors of important traits (Lebeda et al. 2004a, 2007a, 2009a).

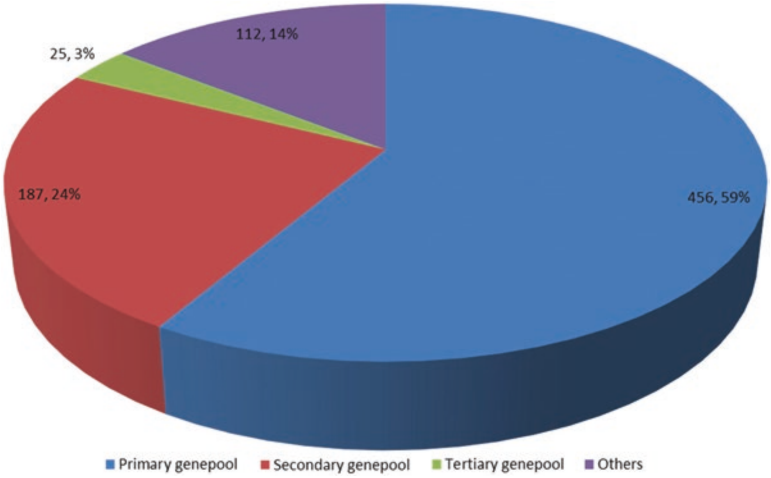

Fig. 5.23 Representation (number of accessions, percentage of total) of wild *Lactuca* spp. in the USDA, ARS National Plant Germplasm System by genepool (sensu Harlan and de Wet (1971), see Sect. 5.2.2.1 of this chapter). (Source of primary data: GRIN-Global database (http://www.ars-grin.gov/, September 2016)

5.4.2.2 Acquisition, Exploitation, and Regeneration

With the adoption of the Convention on Biodiversity (CBD) in 1993 by the United Nations Environment Program, access to genetic resources worldwide began to become more restricted. Article 15 of the CBD provided that countries have national sovereignty over their genetic resources and access to these resources should be on the basis of prior informed consent and mutually agreed terms. The International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA), which came into force in 2004, allows for the exchange of many plant genetic resources without excessive transaction costs, but it does not cover all crops, including the leafy vegetables (Leafy Vegetable Crop Germplasm Committee 2015). Recently, there were 67 new accessions of wild *Lactuca* species added to the WRPIS collection. They were collected in Kyrgyzstan, Uzbekistan, and the Republic of Georgia (Hellier 2014).

Passport information is generally available for leafy vegetable accessions in the GRIN-Global database. A substantial part of the lettuce collection was tested within the germination program of WRPIS for viability, and accessions with a backup sample viability below 80% have been prioritized for regeneration (Hellier 2013, 2014, 2016).

At the WRPIS, seeds of wild *Lactuca* are started in the greenhouse in vermiculite, if germination rates are adequate, or in a germination chamber on blue blotter paper, if low or unknown. Seedlings are transplanted to a soilless growing medium, with a target population of 30 plants per accession. Three- to four-week-old seedlings of *L. virosa* are vernalized at 4 °C for 5 weeks before being moved to the greenhouse. Most wild *Lactuca* species are grown in the greenhouse under long photoperiods, with insect and disease control as needed. When the seedlings reach anthesis, they are covered with plastic mesh bags to facilitate seed collection. Accessions are spatially isolated, with at least one greenhouse bench between each accession (B. Hellier, personal communication, 2016).

Allogamous species that are winter-hardy seedlings are cultivated in field plots with spatial isolation in excess of 1.5 km. The autogamous species, *L. georgica*, is also regenerated in field plots, where seedlings vernalize effectively by being allowed to overwinter, protected by a frost cover (B. Hellier, personal communication, 2016).

McGuire et al. (1993) presented detailed information about the LGCS and the LGRCD. Lettuce and the closely related wild species are self-pollinating, so to maintain stocks, usually 6–12 plants per accession are grown in small plots. For materials that are used in trials, as many as 96 plants in large containers may be grown per season. The LGRCD has been developed both as a part of the lettuce breeding program for the state of California and as a part of the classical and molecular genetic research and teaching program at the University of California – Davis's Genome Center. Seed stocks are efficiently maintained at 5 °C and low relative humidity (Walters 2015).

5.4.2.3 Wild *Lactuca* Descriptors and Germplasm Characterization

The NPGS GRIN-Global database provides only a basic descriptor list for the characterization and evaluation of lettuce accessions, following the format approved by the Leafy Vegetable Crop Germplasm Committee. This lettuce descriptor list has 5 categories (disease, morphology, phenology, subset, and other) and 14 characters complemented by pictures. At the WRPIS, descriptor data are collected on accessions during the regeneration process. Images of rosettes, cauline leaves, flowers, a single plant, and all plants growing for the accession are taken. If an accession is not phenotypically uniform, images representing each phenotype are also taken (B. Hellier, personal communication, 2016). The characterization and evaluation of genetic resources of wild *Lactuca* taxa have, to date, been neglected in North America, with the exception of the LGCS and LGRCD collections. Currently, there is no descriptor list in the NPGS specifically for wild *Lactuca* species.

Representatives of the working group on leafy vegetables of some European genebanks, within the activities of the European Cooperative Program (ECP/GR), developed a basic descriptor list that covers *L. sativa*, *L. serriola*, and related species from the primary genepool (Lebeda and Boukema 2005; Maggioni et al. 2008). In addition, a list of the most important morphological characters of wild *Lactuca* species was created (Doležalová et al. 2003). There have also been national descriptor lists published for the characterization of other major *Lactuca* collections, e.g., those from the Centre for Genetic Resources (CGN, Wageningen, the Netherlands) (Boukema et al. 1990) and the National Programme of Conservation and Utilization of Plant Genetic Resources of the Czech Republic, for both cultivated lettuce (Křístková et al. 2008) and its wild relatives (Doležalová et al. 2002a).

The LGRCD has been evaluated with emphasis on disease resistance (McGuire et al. 1993; Lebeda et al. 2014). Molecular markers are being developed around resistance genes, which should make it easier to screen and introgress them into commercial lettuce cultivars (Simko 2013). Within this research program, a molecular database and genetic maps for *Lactuca* and a few other agriculturally important Asteraceae (such as sunflower) are being developed at the UC-Davis as a part of the Compositae Genome Project (http://compgenomics.ucdavis.edu/compositae_data.php?name=Lactuca+sativa).

5.4.2.4 Needs, Opportunities, and Challenges

Among important topics concerning the conservation status of wild *Lactuca* germplasm that need future attention, the highest priorities should be given to evaluation and acquisition. Efforts should continue to clean up contamination in some accessions and increase the frequency of viability testing. Evaluation of disease and insect resistance, bolting activity, and reaction to environmental stresses are of paramount importance. The most important challenges facing wild *Lactuca* conservation are:

(a) Taxonomic determination of accessions of unknown *Lactuca* taxa
(b) Regeneration of accessions which are unavailable for distribution
(c) Development of more extensive descriptor lists for wild *Lactuca* accessions held in North American genebanks
(d) Characterization and evaluation of wild *Lactuca* genetic resources for traits of value in their management and efficient utilization in lettuce breeding
(e) Additional emphasis on species from the secondary and tertiary genepools
(f) Exploration to collect wild *Lactuca* taxa from North America and other poorly sampled regions, such as Africa, and from under-sampled taxa in regions of high overall *Lactuca* diversity, such as Southwest Asia

5.5 Conclusions and Future Prospects

This chapter is one of the most comprehensive and critical reviews to demonstrate the full range of shortcomings in our understanding of autochthonous and allochthonous wild *Lactuca* germplasm in North America. Currently, we lack much of the basic botanical, ecological, biogeographic, genetic, and plant pathology information on *Lactuca* species in North America, not to mention a reasonable sampling of especially the autochthonous taxa in North American genebanks. Because of gaps in scientific knowledge and the high importance of this information for practical applications (lettuce breeding, weed management, protection and conservation, etc.), this genus needs urgent and efficient actions taken by American academic and research institutions, including genebanks, and the involvement of the private sector (agriculture, horticulture, and breeding), which could ultimately profit from these activities.

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Chapter 6
Pumpkins, Squashes, and Gourds (*Cucurbita* L.) of North America

Heather Rose Kates

Abstract Pumpkins and squash (*Cucurbita* L. spp.) include six independently domesticated crop species and subspecies that are grown worldwide for their edible fruits and seeds and for ornamental interest. Because domesticated pumpkins and squashes can be crossed with each other and with diverse primary genepool relatives, contributions from *Cucurbita* crop wild relatives (CWR) have enabled the development of disease-resistant cultivars and represent a vast pool of untapped genetic variability underlying traits including drought tolerance and disease resistance. Even so, thorough evaluations of these wild species for agronomically important traits are limited. The 12 *Cucurbita* crop wild relatives of North America are more narrowly distributed than they were in the past because of the extinction of megafaunal dispersers and because of habitat loss, and the genetic diversity of wild *Cucurbita* species may be decreasing; one North American wild relative, *C. okeechobeensis* (Small) L. H. Bailey ssp. *okeechobeensis*, is nearly extinct, and some others are rare. Ex situ and in situ conservation of these species that includes phenotypic assessments are needed to better utilize the wealth of genetic resources available for pumpkin and squash crop improvement.

Keywords *Cucurbita* · Ex situ conservation · In situ conservation · Genetic resources

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H. R. Kates (✉)
Florida Museum of Natural History, University of Florida, Gainesville, FL, USA
e-mail: hkates@ufl.edu

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6.1 Introduction

6.1.1 Origin and Historical Use of the Pumpkins, Squashes, and Gourds

Domesticated *Cucurbita* include “vegetables” called pumpkins, summer and winter squash, and gourds and are among the most important vegetable crops native to North America (Small 2014). The incredibly long and rich domestication histories of multiple North American *Cucurbita* species produced pumpkin, squash, and gourd crops that are unrivalled in fruit morphological diversity (Duchesne 1786; Naudin 1856) and wide range of adaptation to cultivation. Three pumpkin and squash crop subspecies are native to North America: the widely cultivated and economically important *Cucurbita pepo* L. ssp. *pepo* (pumpkin, vegetable marrow, cocozelle, zucchini), *C. pepo* ssp. *ovifera* (L.) D. S. Decker (scallop, acorn, crookneck, straightneck), and *C. argyrosperma* C. Huber ssp. *argyrosperma* (silver-seed gourd, green-stripe cushaw, calabaza pipiana), a less widely cultivated crop that is important in traditional Mesoamerican agricultural systems (Montez-Hernandez and Eguiarte 2002). The three pumpkin and squash crop species and subspecies likely domesticated outside of North America are the widely cultivated *C. maxima* Duchesne ssp. *maxima* (giant pumpkin, hubbard squash, buttercup squash, kabocha squash), *C. moschata* Duchesne (butternut squash), and *C. ficifolia* Bouché (figleaf gourd), a *Cucurbita* crop that is relatively unknown in the United States but widely cultivated in Latin America and regionally important in some regions of Asia.

Because fruit and varietal terms including “pumpkin,” “summer squash,” “winter squash,” “gourd,” and “cushaw” have been inconsistently applied to the diverse subspecies and varieties of domesticated *Cucurbita*, it is sometimes difficult to distinguish between accounts of different crop subspecies. For clarity, we will use “pumpkins and squashes” to refer to *Cucurbita* crops generally. To refer to individual crop subspecies, we will use the botanical name or “pepo pumpkin and squash” for *C. pepo* ssp. *pepo*, “ovifera pumpkin and squash” for *C. pepo* ssp. *ovifera*, “cushaw” for *C. argyrosperma* ssp. *argyrosperma*, “giant pumpkin” for *C. maxima* ssp. *maxima*, “figleaf gourd” for *C. ficifolia*, and “butternut squash” for *C. moschata*, although many common and varietal names can be used to refer to these crop subspecies.

The wild ancestors of the *Cucurbita* crops likely appealed to ancient seminomadic native peoples because of their large and conspicuous easily collected fruits (Paris 2016). Wild *Cucurbita* plants are monoecious, multibranched vines that grow along the ground or over trees and other plants or structures (Erwin 1931; Bailey 1943) and bear large (12–15 cm) alternately arranged palmate leaves on long petioles (Paris 2016). Tendrils, flowers, and roots are all borne at the leaf axil. The fruits of wild *Cucurbita* vary somewhat among species but are generally round, 3.5–8.0 cm in diameter, with a green exocarp that may be striped or unstriped and may be yellow or green at maturity (Nee 1990). The rinds of wild *Cucurbita* are hard and lignified (Robinson and Decker-Walters 1997), and their flesh contains cucurbitacins that render them inedible unless repeatedly boiled (Nabhan 1985). Therefore, *Cucurbita* plants were likely initially selected by native North Americans for their edible, high-calorie seeds as well as for the use of their durable rinds as containers; the latter was of utmost importance to seminomadic people prior in the preceramic era (Small 2014). Discovery of rare, non-bitter or less bitter *Cucurbita* fruits likely led to the eventual non-bitter *Cucurbita* crops we know today. Native North Americans also ate the stems and flowers of *Cucurbita* and used the saponin-containing flesh as soap, and archaeological evidence suggests many of the undomesticated wild species were used by humans (Nabhan 1985). All *Cucurbita* domesticates likely moved outside of their initial range of domestication into other areas of the New World before European contact (Fritz 1994; Smith 2001).

The traits that define the domestication syndrome of pumpkins and squashes include more uniform germination, a reduction in size and abundance of trichomes that interfere with harvesting, an increase in the size of fruits and seeds, and a reduction in the bitter taste of the flesh (Lira-Saade and Montez-Hernandez 1994). Some cultivated *Cucurbita* varieties have a bush habit, and most domesticated subspecies exhibit a much wider range of fruit color, shape, and size than their wild relatives. Domesticated species in general have a decreased resistance to drought and disease. Pumpkins and squashes have been important food in Mexico for millennia, where fruits are processed and consumed in a variety of ways. The seeds of pumpkins and squashes are a popular snack food and are also ground into a meal used to make sauces. Pumpkin and squash flowers are eaten stuffed or fried and are used to color and flavor soups and salads (Paris 1989). The origin, current extent of cultivation, most common uses, and cultivar groups for each domesticated species are described below and summarized in Table 6.1.

Cucurbita pepo

The domestication of pepo pumpkin and squash is among the earliest plant domestications in human history (Smith 2006). Archaeological evidence indicates that pepo pumpkin and squash was domesticated from an unidentified wild species in Mexico around ~10,000 years B.P. (Smith 2006). Prior to the 1980s, ancient remains of *C. pepo* from ~5000 years B.P. discovered in eastern North America were thought to represent the spread of domesticated pepo pumpkin and squash from Mexico (Smith 2006). However, there is now strong support for the independent domestication of ovifera pumpkin and squash from a different *C. pepo* subspecies (*C. pepo* ssp. *ovifera*) in what is currently the United States (Decker 1988; Decker-Walters 1990; Decker-Walters et al. 1993). The domestication of *C. pepo* ssp. *ovifera* (which includes cultivated scallop, acorn, crookneck, and straightneck squashes) is one of a small number of domestications that confirms the status of eastern North America as an independent center of plant domestication (Smith 2006).

Domesticated pepo and ovifera pumpkins and squashes were introduced into Europe and Asia Minor in the late 1400s, and secondary diversification of these crops occurred in Asia Minor (Robinson and Decker-Walters 1997). Detailed drawings, paintings, and writings from Europe provide evidence that two ancient lineages of domesticated *C. pepo* were initially brought to Europe from America,

Table 6.1 Cultivated North American pumpkins and squashes

Subspecies	Cultivar groups	Origin	Current cultivation	Most common uses
C. pepo L. ssp. *pepo* (pepo pumpkin and squash)	Pumpkin, vegetable marrow, cocozelle, zucchini, round ornamental gourds[a]	Mexico ~10,000 years B.P.[b]	Worldwide	Fruit (immature, mature, canned)
C. pepo L. ssp. *ovifera* (L.) D. S. Decker var. *ovifera* (L.) Harz (ovifera pumpkin and squash)	Scallop, acorn, crookneck, straightneck, oviform ornamental gourds[a]	Eastern North America ~5000 years B.P.[b]	Worldwide	Fruit (immature, mature, canned)
C. argyrosperma C. Huber ssp. *argyrosperma* (cushaw)	Silver-seed gourd, green-stripe cushaw, calabaza pipiana[c]	Southern Mexico ~7000 years B.P.[b]	Limited. Mexico, USA, Central America	Seeds (snack food, oil, meal); fruit (usually mature)
C. maxima Duchesne ssp. *maxima* (giant pumpkin)	Banana squash, delicious squash, buttercup squash, hubbard squash, show pumpkins, turban squash, kabocha[d]	South America ~4000 years B.P.[b]	Worldwide esp. Africa and Asia	Fruit (immature, mature, canned, decorative)
C. moschata Duchesne (butternut squash)	Cheese, crookneck, bell[e]	Unknown (Mexico, Central America, or South America) >5000 years B.P.[f]	Worldwide esp. Africa and Asia	Fruit (immature, mature, canned)
C. ficifolia Bouché (figleaf gourd)	None commercially recognized. Other names include Malabar melon and shark fin gourd	Unknown (Mexico, Central America, or South America) >3000 years B.P.[g]	Limited. Mexico, Central America, South America, China. High (>1000 m) altitudes	Fruit (immature, mature), as rootstock

[a] Paris et al. (2012)
[b] Smith (2006)
[c] Lira-Saade and Montes-Hernandez (1994)
[d] Decker-Walters and Walters (2000)
[e] Robinson and Decker-Walters (1997)
[f] Cohen (1978)
[g] Towle (1961)

"pumpkin" (*C. pepo* ssp. *pepo* var. *pepo*) and "scallop" (*C. pepo* ssp. *ovifera* var. *clypeata*), and that additional cultivar groups were developed from these lineages in Europe or Asia and were subsequently brought to America (Paris 1989). Among these varieties with probable European origins are the varieties of *C. pepo* that are most economically important today: "zucchini" and "acorn squash" (Paris 1989).

Cucurbita argyrosperma

C. argyrosperma ssp. *argyrosperma* includes cultivated silver-seed gourd, green-stripe cushaw, and Calabaza pipian. The domestication of cushaw apparently occurred in Mexico, and archaeological remains of domesticated cushaw have been dated to as early as ~7000 years B.P. (Smith 2006). In contrast to the other five *Cucurbita* crops, cushaw did not leave its origin of domestication during the Columbian exchange and today is still cultivated primarily in Mexico and Central America with minor cultivation in Asia (Robinson and Decker-Walters 1997). It is unclear why cushaw was not brought to Europe during the Columbian exchange, but the reason for its historical and current lack of cultivation compared with other *Cucurbita* crops is likely due to the inferior quality of its fruit (Lira-Saade and Montez-Hernandez 1994).

Cucurbita maxima

Domesticated *C. maxima* ssp. *maxima* is among the most widely cultivated and morphologically diverse *Cucurbita* crop subspecies (Grubben and Chigumira Ngewerume 2004). *Cucurbita maxima* ssp. *maxima* was domesticated ~4000 years ago from the South American subspecies *C. maxima* ssp. *andreana* that occurs in Argentina and Uruguay and more rarely in Bolivia (Decker-Walters and Walters 2000). *Cucurbita maxima* ssp. *maxima* was brought to the Old World during the Columbian exchange (Decker-Walters and Walters 2000) and is now cultivated all over the world, with a secondary center of diversity in Asia (Ferriol et al. 2004) where extensive breeding and improvement of new varieties have occurred.

Cucurbita moschata

The origin of butternut squash is unclear. As recently as the early 1900s, butternut squash was thought to be of Asian origin (Lira-Saade and Montes-Hernandez 1994) although all wild *Cucurbita* species are native to the New World. Multiple lines of evidence now confirm that *C. moschata* was domesticated somewhere in Mexico, Central America, or South America. The oldest archaeological remains of *C. moschata* were found in the Ocampo caves of Northwestern Mexico and date from ~5000 years B.P. More recent archaeological remains have also been found in northern Belize (2000 B.P.), Guatemala (2000 B.P.), and Peru (3000 B.P.) (Cohen 1978).

Cucurbita moschata moved outside of its area of domestication prior to European contact. For example, the *C. moschata* landrace "Seminole pumpkin" was first grown by indigenous groups of Florida in the United States before Europeans arrived (Lira-Saade and Montes-Hernandez 1994). By the end of the 1800s, *C. moschata* was cultivated in Asia and Africa (Robinson and Decker-Walters 1997).

Cucurbita ficifolia

The origin of figleaf gourd is also unclear, and, like *C. moschata*, the figleaf gourd was thought to have had its origin in Asia (Lira-Saade and Montes-Hernandez 1994). Some authors have suggested Central America or southern Mexico as the site of domestication for figleaf gourd based on etymological evidence (Andres 1990), but archaeological evidence points instead to the Andean region of South America

(Andres 1990). Phylogenetic studies have been unable to support any of these hypotheses as *C. ficifolia* is not closely related to any single wild *Cucurbita* species (e.g., Sanjur et al. 2002; Zheng et al. 2013; Kistler et al. 2015; Kates et al. 2017). Figleaf gourd spread from the New World to Europe and Asia as early as the 1600s, and its cultivation has since spread to many other parts of the world (Andres 1990).

6.1.2 Current Agricultural and Economic Importance of Pumpkins, Squashes, and Gourds

The current agricultural and economic importance of the domesticated lineages of *Cucurbita* differs substantially. Because of the inconsistent and ambiguous nomenclature of cultivated forms, it is impossible to determine the precise contribution of individual subspecies to total *Cucurbita* agricultural production. *Cucurbita moschata*, *C. maxima* ssp. *maxima*, *C. pepo* ssp. *pepo*, and *C. pepo* ssp. *ovifera* are the most economically important, and references to production and consumption of "pumpkins, squashes, and gourds" refer to all of these subspecies. The terms "pumpkin" and "squash" are also used; in this case, pumpkin still refers to all subspecies, but squash is more likely to refer to varieties of *C. pepo* ssp. *pepo* or *C. pepo* ssp. *ovifera.*

China and India are the largest producers of pumpkins, squashes, and gourds today, and in these countries, *C. moschata* and *C. maxima* ssp. *maxima* are the most commonly grown *Cucurbita* crops (Yang and Walters 1992; Sharma and Lal 1998). This contrasts with the relative importance of *Cucurbita* crop subspecies consumed in the United States, where pepo and ovifera pumpkins and squashes are the most popular *Cucurbita* crops. The "pumpkin" types of *Cucurbita* consumed in the United States are mostly produced domestically (Minor and Bond 2017, and in 2014 750 K tons of pumpkins were produced in the United States (Minor and Bond 2017). In contrast, most of the "squash" types of *Cucurbita* consumed in the United States are imported (FAOSTAT 2002), and the United States is the largest importer of squash worldwide.

Cushaw and figleaf gourd are of regional importance rather than worldwide economic importance. Cushaw is rarely grown outside of the Western Hemisphere and is not widely grown outside of its origin of domestication in Mexico (Robinson and Decker-Walters 1997). Figleaf gourd is regionally popular in some areas outside of its likely area of domestication but is still relatively rare outside of Mexico, Central America, and South America (Andres 1990).

There is a wide range of modern uses of pumpkins and squashes that often vary by species and by variety. The commercial uses of pumpkins and squashes include (in order of importance) immature and mature fruit as food (fresh market and processed), seeds for direct consumption, seeds for vegetable oil, mature fruit as animal feed, seeds for meal, and nonedible types for ornamental use. In general, round-fruited types are usually grown for mature fruits or seed (Paris 2016), and the long or flat-fruited types are primarily grown for consumption of immature fruits (Paris 1989). *Cucurbita* fruits are a good source of Vitamin A, with levels comparable to that of avocados, asparagus, musk melon, Brussels sprouts, artichokes, and green olives (Whitaker and Davis 1962), and are an excellent source of starch. The fat and oil content of *Cucurbita* seeds is very high and is comparable to sunflower and soybean oil in its fatty acid profile (Whitaker and Davis 1962). In some countries including the United States, most varieties of "pumpkins" are seasonal crops, and up to 90% of annual consumption occurs between October and January.

Cucurbita pepo

The popularity and importance of edible varieties of pepo and ovifera pumpkins and squashes have increased tremendously since the 1970s (Small 2014). The United States produces a modest amount of pepo and ovifera pumpkins and squashes (less than 900 K tons in 2014 compared with 7 M tons in China and 5 M tons in India) (FAOSTAT 2002) but is the largest importer of pumpkins, squash, and gourds in the world. Ninety-five percent of squash consumed in the United States is grown in Mexico (FAOSTAT 2002). There are four cultivated varieties of edible pepo pumpkins and squash and four cultivated varieties of edible ovifera pumpkin and squash.

Currently, the zucchini variety of pepo pumpkin and squash (*C. pepo* ssp. *pepo* var. *cylindrica*), also known as "summer squash," is the most popular *Cucurbita* crop in the United States (Paris 2008). This pepo pumpkin and squash variety is consumed as a fresh vegetable in its immature state (Robinson and Decker-Walters 1997). Prior to the 1980s, yellow and green "summer squash" consumed in the United States and around the world included immature fruits of nearly all eight edible varieties of pepo and ovifera pumpkin and squash. These diverse varieties of "summer squash" have been replaced with uniform-inbred and highly improved types of *C. pepo* ssp. *pepo* var. *cylindrica*, reflective of a pattern of reduced genetic and morphologic variety in *C. pepo* produced worldwide (Paris 1989). Breeding and cultivation of pepo pumpkin and squash is increasingly dependent on inbreeding, as the importance of virus-resistant transgenic zucchini increases. Approval for production in Mexico is under consideration and is likely to exacerbate this trend (Reyes et al. 2015). The other three varieties of edible pepo pumpkin and squash are "pumpkin" (*C. pepo* ssp. *pepo* var. *pepo*), which includes creeping cultivars that produce round, flat-ended fruits (most famously the Halloween "jack-o-lantern" type); "cocozelle" (*C. pepo* ssp. *pepo* var. *longa*), a variety that produces long, cylindrical fruits eaten in the unripe state; and "vegetable marrow" (*C. pepo* ssp. *pepo* var. *fastigata*), a semi-creeping variety that bears short, cylindrical fruits most commonly eaten when mature.

The four varieties of ovifera pumpkin and squash are the semi-shrubby "scallop" (*C. pepo* ssp. *ovifera* var. *clypeata*), which is eaten in its immature state and is the cultivated ovifera pumpkin and squash variety that most resembles a wild ancestor based on phenotype; "acorn" (*C. pepo* ssp. *ovifera* var. *turbinata*), a variety that can be shrubby or creeping and bears soft-rinded fruit that can be eaten in its mature state; and "crookneck" (*C. pepo* ssp. *ovifera* var. *torticollia*) and "straightneck" (*C. pepo* ssp. *ovifera* var. *recticollis*), two similar varieties that include shrubby plants that produce yellow fruits eaten in their immature state.

Cucurbita argyrosperma

Three varieties of cushaw are grown, primarily in Mexico where they are cultivated near the range of their wild ancestor, *C. argyrosperma* ssp. *sororia*. *Cucurbita argyrosperma* ssp. *argyrosperma* var. *argyrosperma* (silver-seed gourd) likely represents the initial domesticate from which the other cultivated varieties were subsequently developed in different parts of its range of cultivation in Mexico. Limited genetic data reveals a high proportion of wild ancestry for samples of silver-seed gourd (Kates et al., unpublished), but more extensive sampling at the varietal level is needed to determine whether this variety truly represents the initial domesticate of this species. The large seed size of this variety suggests that its seeds, rather than its flesh, were the target of initial domestication (Lira-Saade and Montez-Hernandez 1994). Silver-seed gourd is grown infrequently by home gardeners in the United States as a curiosity (Lira-Saade and Montez-Hernandez 1994). *Cucurbita argyrosperma* ssp. *argyrosperma* var. *callicarpa* (green-stripe and white cushaw; Japanese pie pumpkin) is considered the most recent or specialized variety of cushaw, and the diversity of shapes, colors, and size of the fruits and seeds suggests it was domesticated for its flesh and its seeds (Lira-Saade and Montez-Hernandez 1994).

Outside of Mexico, cushaw is a crop of minor importance in South America and in the United States (Lira-Saade and Montez-Hernandez 1994). A third cultivated variety, *C. argyrosperma* ssp. *argyrosperma* var. *stenosperma* (calabaza pipiana), is another more recently derived variety of cushaw, and although it also has diverse fruit morphology (Lira-Saade and Montez-Hernandez 1994), it is now mostly grown in Mexico and Central America for its seeds (Merrick 1995). A fourth variety of cushaw, *C. argyrosperma* ssp. *argyrosperma* var. *palmeri*, is wild and thought to be a feral escape from cultivation (Lira-Saade and Montez-Hernandez 1994). Genetic data resolve a close relationship between *C. argyrosperma* ssp. *argyrosperma* var. *palmeri* and the cultivated varieties and support its status as a feral rather than a truly wild taxon (Kates et al., unpublished).

Cucurbita maxima

Outside of the Americas, *C. maxima* ssp. *maxima* is one of the two most common *Cucurbita* crops consumed. The many cultivars of *C. maxima* ssp. *maxima*, known generally as "pumpkins" (Sharma and Lal 1998), are very popular in Asia and Africa where their mature fruits are widely used in cooking and as cattle feed. In contrast to the minor nutritional importance of squash and pumpkin consumption in the United States, in Africa and Asia, *C. maxima* ssp. *maxima* pumpkins may serve as a staple food when grain production is limited (Sharma and Lal 1998).

Attempts to classify the diverse *C. maxima* ssp. *maxima* into cultivar groups are inconsistent, but popular named varieties include banana squash, delicious squash, buttercup squash, hubbard squash, show pumpkins, turban squash, and kabocha (Decker-Walters and Walters 2000). Varieties of *C. maxima* ssp. *maxima*, especially the "buttercup" variety, are the most popular type of pumpkins and squashes consumed in Africa. *Cucurbita maxima* ssp. *maxima* also includes all "giant pumpkins," varieties that produce the largest fruits in the world. Giant pumpkins are popular as ornamental pumpkins in the United States for Halloween and are celebrated in many festivals and competitions.

Cucurbita moschata
Cucurbita moschata is one of the two most popular *Cucurbita* species outside of the Americas. Like *C. maxima*, its many regional varieties, which were developed in Central and South America, Africa, and the United States (Lira-Saade and Montes-Hernandez 1994), are often referred to as "pumpkins." Among these, the three cultivar groups commercially recognized in North America are cheese, crookneck, and bell (including the popular "butternut" cultivar) (Robinson and Decker-Walters 1997). In the United States, all canned pumpkin is *C. moschata*, and the most popular variety of canned pumpkin is Libby's Select Dickinson (Geisler 2014).

Cucurbita ficifolia
Figleaf gourd is not common in industrialized countries (Robinson and Decker-Walters 1997) but is used as food and cattle feed in Mexico, Central America, and South America. *Cucurbita ficifolia* is also popular in some regions of China where it is known as "shark fin melon" because of its use in a soup that resembles shark fin soup. *Cucurbita ficifolia* is also used as a rootstock for grafting cucumber (Robinson and Decker-Walters 1997). Research has demonstrated the potential of the proteolytic enzymes in the pulp of *C. ficifolia* fruit to treat wastewater from the industrial processing of foods derived from fish (Illanes et al. 1985), but this use of *C. ficifolia* has never been implemented.

6.1.3 Challenges in Cultivation of Squashes, Pumpkins, and Gourds

Viral, Bacterial, and Fungal Diseases
Disease susceptibility is common in all Cucurbitaceae crops (e.g., *Citrullus* (watermelon) and *Cucumis* (cucumber and melon)) but is comparatively understudied in *Cucurbita*. For example, fewer disease resistance genes have been reported for pumpkins, squashes, and gourds than for the other cucurbit crops (Robinson and Decker-Walters 1997). Insufficient funding is mostly responsible for the relative lack of research to screen germplasm and identify disease resistance in *Cucurbita*, but the large genome size of *Cucurbita* compared to other cucurbits and the fact that certain cucurbit diseases, including downy mildew, are less of a problem in *Cucurbita* than in other cucurbit crops may also play a role.

Diseases attack pumpkins and squash at every stage of development, from germinating seeds to mature fruits (Robinson and Decker-Walters 1997). The major challenge in the cultivation of the North American squashes, pumpkins, and gourds are viral diseases, especially those transmitted by aphids, whiteflies, and other insects (Paris 2016); virus resistance is one of the most important goals of *Cucurbita* breeding. Virus susceptibility in *Cucurbita* is a moving target; the most damaging viruses vary by region and change over time, and newly damaging viruses are reported frequently (Paris 2016). Some of the viruses that infect pumpkins and squashes are the cucumber mosaic virus (CMV), watermelon mosaic virus (WMV), zucchini yellow mosaic virus (ZYMV), and papaya ringspot virus (PRV) (Robinson and Decker-Walters 1997). Among these, ZYMV has been the most destructive since the 1970s (Paris 2016). Because there are no chemical tools to control these viruses, the only way to limit the damage is through breeding resistant crops or management of the insect vectors using pesticides (Molinar et al. 2012).

Fungal and bacterial diseases that are the most damaging to pumpkin and squash crops include powdery mildew (*Erysiphe cichoracearum* DC.), downy mildew (*Pseudoperonospora cubensis* (Berkeley & M. A. Curtis) Rostovzev), gummy stem blight (*Didymella bryoniae* (Fuckel) Rehm), charcoal rot (*Macrophomina phaseolina* (Tassi) Goid), root and fruit rot caused by *Phytophthora capsici* Leonian, *P.* spp. and *Fusarium solani f.* sp. *cucurbitae* (Mart.) Sacc, bacterial wilt (*Erwinia tracheiphila* (Smith) Bergey), and bacterial leaf spot (*Xanthomonas campestris* pv. *cucurbitae* (Pammel) Dowson) (Robinson and Decker-Walters 1997). Fungal and bacterial diseases of squash are controlled by long-term rotation out of cucurbits (4 years or more), the use of clean seed, chemical treatment (Molinar et al. 2012), and generally reducing environmental stress whenever possible.

Susceptibility to diseases varies among domesticated *Cucurbita* species. With a few exceptions (see Walkey and Pink 1984; Lebeda and Křistkova 1996; Křistkova and Lebeda 2000), pepo and ovifera pumpkins and squashes and wild *C. pepo* do not naturally contain resistance to diseases (Paris 2016). Susceptibility of giant pumpkin to major cucurbit diseases is apparently similar to pepo and ovifera pumpkins and squashes (Provvidenti et al. 1978; Keinath 2014), though this observation is based on a small number of studies. Disease resistance in cushaw and wild *C. argyrosperma* has not been as well-studied and also appears to be rare (Provvidenti et al. 1978; Luitel et al. 2016; Wessel-Beaver 1998), but some *C. argyrosperma* germplasm exhibits resistance to downy mildew and offers a potential source for breeding downy mildew-resistant squash and pumpkins (Lebeda et al. 2016). Butternut squash is resistant to a greater number of diseases than other domesticated species (e.g., Provvidenti et al. 1978, ZYMV, PRV, tomato ringspot virus, tobacco ringspot virus, squash curl leaf virus; Chavez et al. 2011, crown rot; Zhou et al. 2010, downy mildew). The prospects and limitations of utilizing pest and disease-resistant crop wild relatives (CWR) for crop enhancement are discussed in Sect. 6.2. To avoid the loss of susceptible crops, farmers apply pesticides to target insect vectors, rotate pumpkin and squash crops, and avoid irrigation practices that excessively wet squash leaves or create standing water (Sharma and Lal 1998). To address the need for disease-resistant *C. pepo* crops, geneticists and breeders in the United States created a transgenic zucchini with virus-resistance genes.

The transgenic variety of zucchini called “Freedom II” was the second transgenic crop to be deregulated for commercial use in the United States in 1995 (Tricoli et al. 1995). There are currently at least six transgenic cultivars of *C. pepo* ssp. *cylindrica* being sold in the United States that are resistant to WMV, ZYMV, and cucumber mosaic virus (Gaba et al. 2004). The impact of transgenic zucchini on worldwide pepo pumpkin and squash production is very limited for several reasons.

Resistance to the three viruses listed above apparently increases the vulnerability of the resistant squash to other viruses and to some insect pests (Sasu et al. 2009). Additionally, the United States is not a major producer of pepo pumpkin and squash; Canada is the only country that allows the import of transgenic pepo pumpkin and squash from the United States (CBAN 2018), and nearly all zucchini sold in the US market is imported from Mexico (FAOSTAT 2002), where transgenic squash has not been deregulated (Cruz-Reyes et al. 2015). The potential deregulation of transgenic pepo pumpkin and squash cultivars in Mexico is discussed in Sect. 6.4.1.

Non-disease Challenges to Cultivation

The severity of some non-disease challenges to cultivation differs among the species and varieties of ovifera and pepo pumpkins and squashes and cushaw due to the phenotypic diversity of the cultivated types. All pumpkin and squash crops are sensitive to very low temperatures and continuous frost (Lira-Saade and Montes-Hernandez 1994; Sharma and Lal 1998) and to heavy precipitation and standing water, which can cause fruit to rot. Cultivation of varieties of pepo and ovifera pumpkins and squashes and of cushaw that are grown for mature fruits (e.g., the acorn variety of ovifera pumpkin and squash, most important cultivars of cushaw) requires high water use. Pumpkins and winter squash are among the highest water-using vegetable crops (Daniello 2003) in contrast to summer squashes (e.g., zucchini, straightneck, crookneck), which have the lowest water requirements. Pumpkins and winter squash also require large amounts of arable land to support their vine or semi-bush habit. The bush habit has been selected for in nearly all summer squash varieties (Paris 2016), but these types require larger applications of fertilizer (Sharma and Lal 1998).

Insect pests that damage pumpkin and squash crops include seed-corn maggot larva (*Delia platura* Meigen), which are associated with high amounts of decaying organic matter in the soil; wireworms (*Limonius* spp. and others); squash bugs (*Anasa tristis* DeGeer); whiteflies (*Bemisia argentifolii* Gennadius and *Trialeurodes vaporariorum* Westwood); aphids (*Aphis gossypii* Glover and *Myzus persicae* Sulzer), which are also disease vectors; cucumber beetles (*Diabrotica undecimpunctata* Mannerheim and *Acalymma trivittatum* Mannerheim); larvae of several species of armyworm (*Spodoptera* spp.); and cabbage looper (*Trichoplusia ni* Hübner) (Molinar et al. 2012; Robinson and Walters 1997). Bitter cucurbitacins present in *Cucurbita* (see Sect. 5.2.3) attract squash bugs, corn rootworm, and cucumber beetle, and wild and domesticated *Cucurbita* species are used as perimeter trap crops in integrated pest management (e.g., Adler and Hazzard 2009; Metcalf et al. 1979).

The Effect of Climate Change on Challenges to Cultivation

Some of the challenges that *Cucurbita* faces in cultivation may intensify under climate change (Chakraborty and Newton 2011). Although the impacts of climate change on cucurbit crops have not been widely modeled and studied, some plant pathogens are expected to spread and infect plants more readily under current climate change scenarios (Pautasso et al. 2012), and environmentally stressed pumpkins and squash are more susceptible to initial infection and subsequent disease development (Robinson and Decker-Walters 1997). Changes in precipitation also pose a threat to *Cucurbita*, especially to winter squash and pumpkin cultivars that require high water input and bear fruits that are vulnerable to rot while they mature. In 2015, unusually heavy summer rains drastically reduced pepo pumpkin and winter squash yield (Kennedy 2015). In the previous year, drought in California reduced yield of *Cucurbita* grown in that state and increased pest damage (CBS News 2014).

There are also characteristics of *Cucurbita* cultivation that may make it resilient to climate change. For example, compared with crops that rely entirely on honey bee pollination, *Cucurbita* crops are also pollinated by native bees (Giannini et al. 2011). Though the potential effects of climate change on pollination of *Cucurbita* crops has not yet been studied, pollination by native bees was found to be a potential buffer against climate change in watermelon (Radar et al. 2013). Pumpkin and squash production as a whole may be less affected by climate change than that of some other crops due to the diversity of cultivated types and the wide range of elevations and temperatures at which they can be grown.

6.2 Crop Wild Relatives of Pumpkins, Squashes, and Gourds

The wild relatives of pumpkins and squashes that occur in North America include six arid-adapted (xerophytic) perennial species and seven non-arid-adapted (mesophytic) annual species, subspecies, or varieties. The greatest species diversity occurs in Mexico (Fig. 6.1), although phylogenetic data suggests the genus likely originated in Central or South America (Schaefer et al. 2009). The wild xerophytic perennial *Cucurbita* species grow in the deserts and dry scrub of Mexico and the Southwestern United States, and wild mesophytic annual species grow in the moist or dry forests and plains of Mexico and the Southern and Central United States. All domesticated *Cucurbita* species and subspecies are derived from the mesophytic annual species group; therefore, all mesophytic annual species are more closely related to cultivated pumpkins and squashes than are any of the xerophytic perennial species. Table 6.2 lists the habitat, distribution, genepool classification, and potential agronomic traits for 13 *Cucurbita* CWRs native to North America. Likely due to the recent divergence of the wild *Cucurbita* species (Zheng et al. 2013), all *Cucurbita* CWR can be crossed with one or more other species in the genus. Introgression of traits from wild to cultivated *Cucurbita* can be made directly from a CWR with desirable traits or using another CWR as a genetic bridge (Yi-Hong Wang et al. 2012).

Because there are multiple domesticated *Cucurbita* species, each *Cucurbita* CWR may be a primary, secondary, and/or tertiary genepool CWR. Below, each CWR is grouped into the genepool rank that denotes its closest relationship to a domesticated *Cucurbita* crop species or subspecies. If a CWR is also in a subsequent genepool group, this is noted.

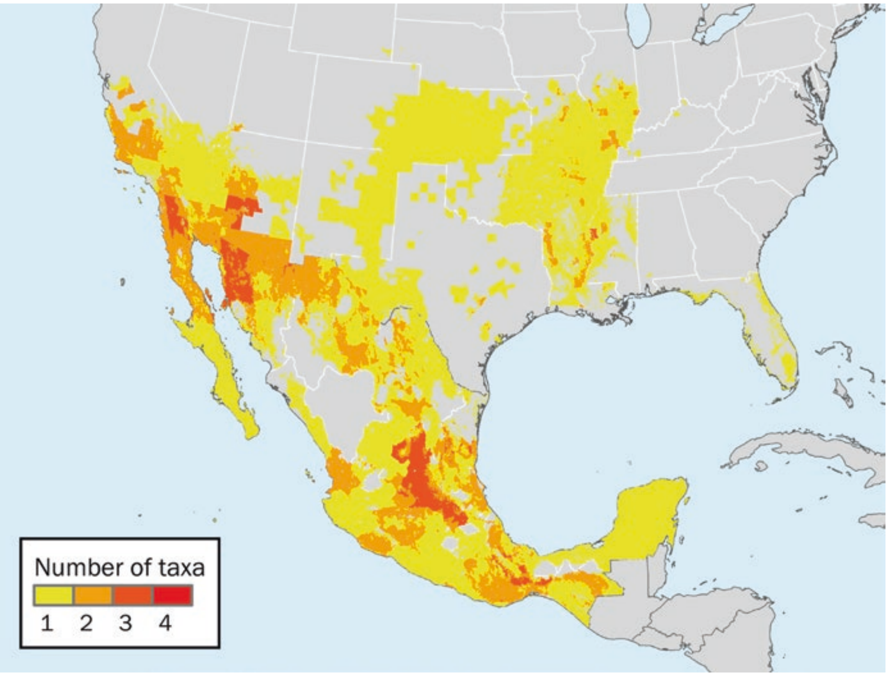

Fig. 6.1 Species richness map of modeled potential distributions of North American *Cucurbita* taxa, based on climatic and edaphic similarities with herbarium and genebank reference localities. Warmer colors indicate areas where greater numbers of taxa potentially occur in the same geographic localities. Full methods for generation of maps and occurrence data providers are given in Appendix 1

6.2.1 Primary Genepool CWR

Cucurbita argyrosperma **ssp.** *sororia* **(L. H. Bailey) L. Merrick & D. M. Bates**
Cucurbita argyrosperma ssp. *sororia* is the putative wild ancestor of cushaw (Merrick 1995), and the two subspecies form fully fertile offspring when hybridized (Merrick 1995). *Cucurbita argyrosperma* ssp. *sororia* is also a secondary genepool CWR of the pepo and ovifera pumpkins and squashes and butternut squash and a tertiary genepool CWR of giant pumpkin and figleaf gourd (Table 6.2). *Cucurbita argyrosperma* ssp. *sororia* is locally widespread and occurs in the lowland thorn-scrub vegetation of the Pacific and, less often, the Gulf of Mexico coasts and from Southern Sonora in Mexico south to Nicaragua (Nee 1990) (Fig. 6.2). Like most *Cucurbita* CWR, *C. argyrosperma* ssp. *sororia* has a weedy growth habit and is most common along roadsides, near agricultural fields, and other disturbed areas (Merrick 1995). It thrives in high-light environments and is often found growing over other plants or manmade structures (Merrick 1995).

Table 6.2 *Cucurbita* CWR

CWR	Genepool (A; B; C; D; E)	Native range	Potential agronomic traits
C. argyrosperma C. Huber ssp. *sororia* (L. H. Bailey) L. Merrick & D. M. Bates	2; 1; 2; 3; 3	Pacific coast from Sonora in Mexico south to Nicaragua	Resistant to BYMV and TmRSV
C. cordata S. Watson	3; 3; 3; 3; 3	Baja California (Mexico)	Drought tolerance, resistant to CMV, TRSV, BYMV
C. digitata A. Gray	3; 3; 3; 3; 3	Southwestern United States and Northwestern Mexico	Drought tolerance; resistant to CMV, TmRSV
C. foetidissima Kunth	3; 3; 3; 3; 3	Southwestern United States and Northern Mexico	Drought tolerance, resistant to CMV, TRSV, BYMB, WMV, and squash vine borer
C. lundelliana L. H. Bailey	2; 3; 2; 2; 2	Southern Mexico (Tabasco to Yucatan) (and Northern Central America)	Resistant to SqLCV, CMV, powdery mildew; used as a genetic bridge for breeding non-interfertile species
Cucurbita okeechobeensis (Small) L. H. Bailey ssp. *martinezii* (L. H. Bailey) T. C. Andres & Nabhan ex T. W. Walters & D. S. Decker	2; 3; 2; 3; 3	Southern Mexico (gulf coast)	Resistant to CMV, BYMV, TRSV, bacterial leaf spot, powdery mildew
C. okeechobeensis (Small) L. H. Bailey ssp. *okeechobeensis*	2; 3; 2; 3; 3	Florida (United States)	Resistant to CMV, BYMV, TRSV, bacterial leaf spot, powdery mildew
C. palmata S. Watson	3; 3; 3; 3; 3	Southwestern United States and Baja California	Drought tolerance; resistant to CMV, TRSV, BYMV, TmRSV
C. pedatifolia L. H. Bailey	3; 3; 3; 3; 2	North-central to Southern Mexico	Drought tolerance; disease resistance unstudied
C. pepo ssp. *pepo* var. *texana*	1; 2; 2; 3; 3	Texas (United States)	Undiscovered
C. pepo ssp. *pepo* var. *ozarkana*	1; 2; 2; 3; 3	Central United States	Undiscovered
C. pepo L. ssp. *fraterna* (L. H. Bailey) Lira et al.	1; 2; 2; 3; 3	Northern Gulf coast of Mexico	Undiscovered
C. radicans Naudin	3; unknown; 2; 3; unknown	North-central to Southern Mexico	Drought tolerance; resistant to CMV, TmRSV, BYMV; production of potato-sized tubers

Genepool relative to A, pepo and ovifera pumpkins and squashes; B, cushaw; C, butternut squash; D, giant pumpkin; E, figleaf gourd. Diseases: cucumber mosaic virus (CMV), watermelon mosaic virus (WMV), tomato ringspot virus (TmRSV), bean yellow mosaic virus (BYMV), tobacco ringspot virus (TRSV), squash leaf curl virus (SqLCV)

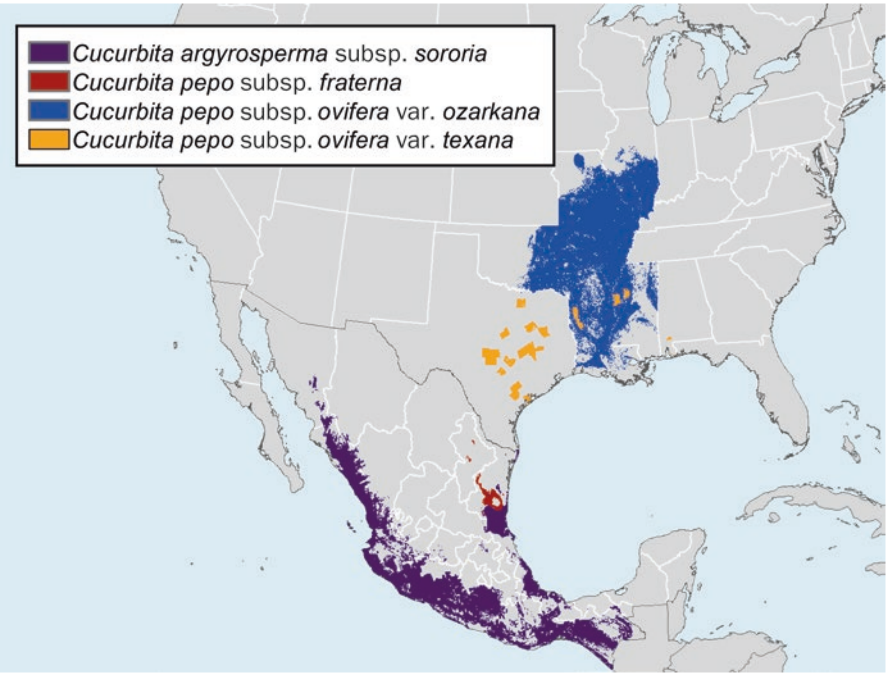

Fig. 6.2 Modeled potential distribution maps of *Cucurbita* primary CWR species (*Cucurbita pepo* L. ssp. *fraterna* (L. H. Bailey) Lira et al., *C. pepo* L. ssp. *ovifera* (L.) D. S. Decker var. *ozarkana* D. S. Decker, *C. pepo* L. ssp. *ovifera* (L.) D. S. Decker var. *texana* (Scheele) Filov, *C. argyrosperma* C. Huber ssp. *sororia* (L. H. Bailey) L. Merrick & D. M. Bates), based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are given in Appendix 1

It is possible to distinguish between *C. argyrosperma* ssp. *sororia* and cultivated cushaw by the wild subspecies' larger and more deeply lobed leaves, later flowering time (Jones 1992), and smaller fruits and seeds. The fruits of *C. argyrosperma* ssp. *sororia* are ovate and relatively small (about 8 cm in diameter) and contain seeds that are around 50–80% smaller by weight than seeds of the cultivated subspecies (Merrick 1995). *Cucurbita argyrosperma* ssp. *sororia* commonly grows near fields of cultivated cushaw in some areas in Mexico, and gene flow between the two subspecies can introduce bitterness into the fruit of the crop (Nabhan 1985; Montes-Hernandez et al. 2005). Gene flow between these two subspecies also introduces characteristics of the crop into wild populations; wild squashes are found with green and white striped rinds, thickened stems, and non-bitter flesh (Nabhan 1985).

Cucurbita argyrosperma ssp. *sororia* is resistant to two viruses: bean yellow mosaic virus (BYMV) and tomato ringspot virus (TmRSV) (Table 6.2). Neither of these viruses is a major threat to *Cucurbita* crop production, and resistance to these viruses is common in *Cucurbita*. Resistance to other viruses including cucumber mosaic virus and watermelon mosaic virus has not been found in *C. argyrosperma* ssp. *sororia* (Provvidenti et al. 1978). There are accounts of wild *C. argyrosperma* ssp. *sororia* being used in rural areas of Mexico medicinally and for its edible seeds (Montes-Hernandez et al. 2005)

Cucurbita pepo **L. (wild)**
Cucurbita pepo ssp. *fraterna* (L. H. Bailey) Lira et al. and the two wild varieties of *C. pepo* ssp. *ovifera* are primary genepool CWR of both ovifera and pepo pumpkin and squash. These three taxa are also secondary genepool CWR of cushaw and butternut squash and tertiary genepool CWR of giant pumpkin and figleaf gourd (Table 6.2). Wild populations of *C. pepo* ssp. *ovifera* that occur in the Midwestern United States are classified as *C. pepo* ssp. *ovifera (L.)* var. *ozarkana* D. S. Decker (Ozark gourd). Those that occur in Texas are classified C. *pepo* ssp. *ovifera* (L.) D. S. Decker var. *texana* (Scheele) Filov (Texas gourd) (Fig. 6.2). Ozark gourd occurs along riverbanks and in other disturbed lowland habitats throughout the Ozark plateau and Greater Mississippi Valley (Smith et al. 2007) and is a persistent weed in agricultural fields (Decker and Wilson 1987), and Texas gourd occurs along riverbanks and in moist thickets in Texas (Erwin 1938). Ozark gourd has been proposed as the wild ancestor of ovifera pumpkin and squash based on isozyme studies (Decker-Walters et al. 1993). Modern molecular phylogenetic analyses have not found support for the separation of Ozark gourd and Texas gourd and thus have not been able to clearly suggest either as the ancestor of ovifera pumpkins and squashes (Kates et al. 2017). However, Ozark gourd and Texas gourd are geographically distinct and can be distinguished from each other based on fruit color and germination time (Decker-Walters et al. 1993, 2002), and the relationships of these two groups of wild *C. pepo* to ovifera pumpkin and squash should be studied further.

Cucurbita pepo ssp. *fraterna* is known from a small number of populations in the upland, seasonally dry thornscrub in Northeastern Mexico (Nee 1990) (Fig. 6.2). Although *C. pepo* ssp. *fraterna* was initially considered as a possible wild ancestor of *C. pepo* ssp. *pepo*, multiple phylogenetic studies of *Cucurbita* do not support that hypothesis (Sanjur et al. 2002; Zheng et al. 2013; Kates et al. 2017). Phylogenetic analysis indicates that *C. pepo* ssp. *fraterna* is highly diverged from the rest of wild *C. pepo* (Kates et al. 2017).

Few cases of disease resistance have been documented in wild *C. pepo* (Paris 2016). To introduce virus resistance into cultivated pepo and ovifera pumpkins and squashes, virus resistance has been introgressed from other less closely related CWR and cultivated *Cucurbita* subspecies (Paris 2016), but these hybridizations are challenging for breeders.

6.2.2 Secondary Genepool CWR

Cucurbita lundelliana **L. H. Bailey**
Cucurbita lundelliana is a secondary genepool CWR of both ovifera and pepo pumpkin and squash and of butternut squash, giant pumpkin, and figleaf gourd and a tertiary genepool CWR of cushaw. *Cucurbita lundelliana* is a mesophytic annual species that is native to Southern Mexico and to parts of Central America where it occurs at low elevations in tropical deciduous forests and as a weed in agricultural fields (Lira et al. 2009) (Fig. 6.3). Before the multiple independent domestications

Fig. 6.3 Modeled potential distribution maps of *Cucurbita* secondary CWR species (*Cucurbita lundelliana* L. H. Bailey, *C. okeechobeensis* (Small) L. H. Bailey ssp. *okeechobeensis*, *C. okeechobeensis* (Small) L. H. Bailey ssp. *martinezii* (L. H. Bailey) T. C. Andres & Nabhan ex T. W. Walters & D. S. Decker, *C. radicans* Naudin, *C. pedatifolia* L. H. Bailey), based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are given in Appendix 1

in *Cucurbita* were hypothesized, *C. lundelliana* was considered as a possible ancestor of all domesticated *Cucurbita* because it is interfertile with all the cultivated *Cucurbita* species other than *C. pepo* (Nee 1990). The ability of *C. lundelliana* to hybridize with many wild and domesticated *Cucurbita* species has led to its use as a bridge to transfer genes between species that are difficult to cross (Whitaker and Robinson 1986). *Cucurbita lundelliana* exhibits resistance to squash leaf curl virus, cucumber mosaic virus, and powdery mildew (Grubben and Chigumira Ngwerume 2004) (Table 6.2). Resistance to squash leaf curl virus has been transferred from *C. lundelliana* to the cultivated species *C. moschata* (butternut squash), but not to the North American crop subspecies. In addition to its importance as a genetic bridge species and as a source of virus resistance, *C. lundelliana* produces fruit that are sometimes used locally as a soap substitute and as a container (Lira et al. 2009).

Cucurbita okeechobeensis **(Small) L. H. Bailey**

Cucurbita okeechobeensis (Okeechobee gourd) includes two geographically disjunct subspecies. These subspecies are secondary genepool CWR of pepo and ovifera pumpkins and squash and of butternut squash, and they are tertiary genepool

CWR of cushaw, giant pumpkin, and figleaf gourd. *Cucurbita okeechobeensis* ssp. *martinezii* (L. H. Bailey) T. C. Andres & Nabhan ex T. W. Walters & D. S. Decker is native to Mexico where it grows at a wide range of elevations from sea level to the mountain cloud forest and is a weed in coffee plantations and agricultural fields (Lira et al. 2009) (Fig. 6.3). *Cucurbita okeechobeensis* (Small) L. H. Bailey ssp. *okeechobeensis* occurs in only two locations in Central Florida in the United States where it grows in the permanently wet soil of riverbanks or lakeshores (Fig. 6.3) (Walters and Decker-Walters 1993). The Okeechobee gourd is one of only two federally listed endangered species native to the United States that were identified as high priority for their value as genetic resources for important food crops (Khoury et al. 2013). The conservation status of the Okeechobee gourd is discussed in Sect. 6.4.1. Both subspecies of *C. okeechobeensis* are resistant to CMV, BYMV, TRSV, powdery mildew (Lira et al. 2009; Jahn et al. 2002; Formisano et al. 2010), and bacterial leaf spot (Robinson and Decker-Walters 1997) (Table 6.2). Resistance to powdery mildew has been introgressed from wild *C. okeechobeensis* to *C. pepo*, and the resistant offspring are commercially produced (Jahn et al. 2002; Formisano et al. 2010).

Cucurbita pedatifolia **L. H. Bailey and** *C. radicans* **Naudin**

Cucurbita pedatifolia and *C. radicans* are secondary genepool CWR to figleaf gourd and butternut squash, respectively, and tertiary genepool CWR to all other *Cucurbita* crops. Of the six xerophytic perennial *Cucurbita* species, the closely related and interfertile xerophytic perennial species *C. pedatifolia* and *C. radicans* (along with tertiary genepool CWR *C. foetidissima*) are the most closely related to the cultivated pumpkins and squashes (Kates et al. 2017). *Cucurbita pedatifolia* and *C. radicans* occur in dry forests of Mexico from Zacatecas at the northern end of their range south to Chiapas (Fig. 6.3). Collections of *C. radicans* suggest that it occurs between and to the west of disjunct northern and southern distributions of *C. pedatifolia* (Fig. 6.3), but the morphological, ecological, and genetic differences of these two species are not documented, and additional work is needed to clarify whether they are truly different species.

Because of their closer relationship to the mesophytic species and because they are sometimes referred to as semixerophytic (though it is unclear how their adaptation to aridity differs from the other xerophytic species), it has been proposed that any of *C. pedatifolia* or *C. radicans* could be used as a possible genetic bridge between the xerophytic and perennial species (Bemis and Whitaker 1969). However, crosses between these species and mesophytic species have been unsuccessful (Robinson and Decker-Walters 1997).

The development of multiple potato-size tuberous roots by *C. pedatifolia* rather than the huge taproots produced by other xerophytic species is a trait that may be beneficial for the development of a drought-tolerant *Cucurbita* starch crop (Andres 1987) (Table 6.2). *Cucurbita radicans* is resistant to CMV, TRSV, and BYMV, but it is susceptible to WMV (Provvidenti et al. 1978) (Table 6.2). *Cucurbita pedatifolia* has not been screened for virus resistance, but considering its very close relationship to *C. radicans*, it may harbor similar traits.

6.2.3 Tertiary Genepool CWR

The four xerophytic perennial *Cucurbita* species that are tertiary genepool CWR for all *Cucurbita* crops occur in the hottest and driest regions in North America: the deserts of Northwestern Mexico and the Southwestern United States (Bemis and Whitaker 1969) (Fig. 6.4). Previously it was thought that the xerophytic species of *Cucurbita* were derived from non-xerophytic species and had subsequently evolved an adaptation to hot, dry climates. However, recent studies suggest that wild squashes tolerant to prolonged drought and extreme temperatures represent the ancestral state of pumpkins and squashes and that domesticated pumpkins, squashes, and gourds and their non-arid-adapted CWR are derived from a drought-tolerant ancestor (Zheng et al. 2013; Kates et al. 2017).

The xerophytic *Cucurbita* CWR species grow at low elevations (generally less than 1300 m) in coarse, dry, sandy soils. They are most common along roadsides and washes where water accumulates during rare periods of precipitation. Compared with the wild species of *Cucurbita* that grow in temperate to tropical grasslands and forests, the species of pumpkins and squashes that grow wild in the deserts and dry forests of North America are conspicuous, and some are quite frequent throughout

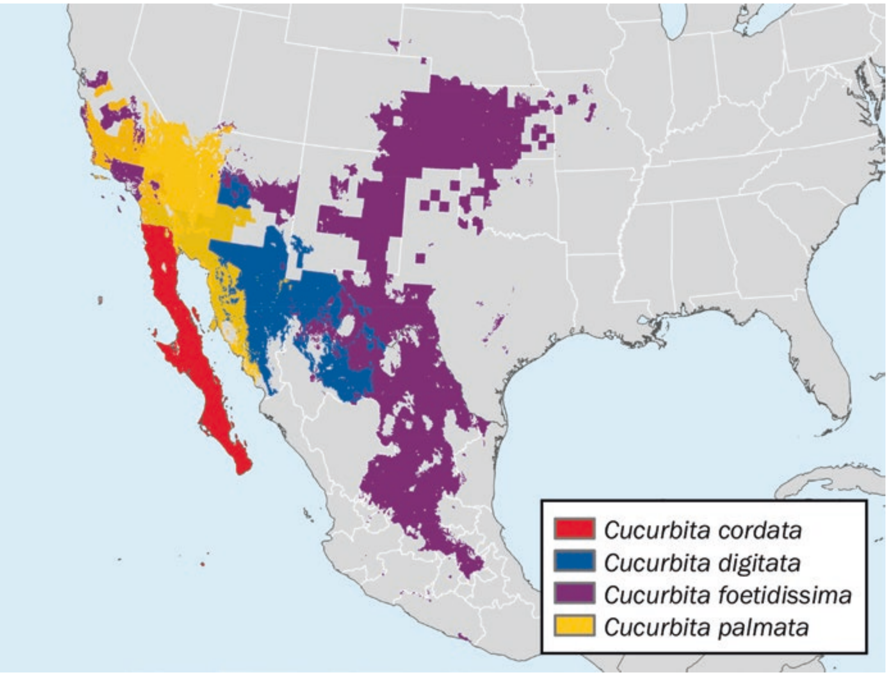

Fig. 6.4 Modeled potential distribution maps of *Cucurbita* tertiary CWR species (*Cucurbita foetidissima* Kunth, *C. palmata* S. Watson, *C. digitata* A. Gray, *C. cordata* S. Watson) based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are given in Appendix 1

their native ranges due to the lack of competition from other plant species. The xerophytic *Cucurbita* CWR can be divided into two groups, one of which is more closely related to cultivated pumpkins and squashes, though more research is needed to understand the relationships among the xerophytic *Cucurbita* CWR. The Spanish or English common names chichicoyota, calabaza de coyote, calabacilla, and coyote melon/gourd may refer to any wild, arid-adapted *Cucurbita* (and rarely to non-arid-adapted wild *Cucurbita*), so here we only use common names that refer to a single species.

Cucurbita foetidissima **Kunth**

Among the xerophytic *Cucurbita* CWR, *C. foetidissima* (buffalo gourd) may be the most well-known due to its weedy, common occurrence, conspicuous folded leaves, and typically abundant, round fruit that is golden yellow at maturity (DeVeaux and Shultz 1985). Buffalo gourd is native to the deserts of the Southwestern United States and Northern Mexico (Bailey 1943) (Fig. 6.4) and grows as a weed, producing dense groundcover on disturbed soils (Deveaux and Schultz 1985). "Fetid gourd" is another common name for buffalo gourd and refers to the unpleasant smell of its leaves and flesh (Nabhan 1985). Like other xerophytic *Cucurbita* CWR, buffalo gourd reproduces primarily asexually (Deveaux and Schultz 1985); although its vines may bear many fruits, both germination and survival of young seedlings are uncommon. Like other xerophytic perennial species, buffalo gourd has low water requirements (Deveaux and Schultz 1985). It is also highly resistant to many insects and diseases that threaten cultivated pumpkins and squashes (Curtis 1946; Shahani et al. 1951; Paur 1952) (Table 6.2), though it is susceptible to squash mosaic virus (Rosemeyer et al. 1982). Buffalo gourd is resistant to some insect pests, including squash vine borer, but cucumber beetles are attracted to the high level of cucurbitacins found in its fruit, roots, and cotyledons (Deveaux and Schultz 1985) (Table 6.2).

Cucurbita palmata **S. Watson,** *C. digitata* **A. Gray, and** *C. cordata* **S. Watson**

This group of tertiary genepool CWR includes the three wild *Cucurbita* species commonly known as "coyote gourd" or "coyote melon," which are the most distantly related to cultivated pumpkins and squashes (Kates et al. 2017). Although there are morphological differences among these interfertile and partly sympatric species, at some point they were reclassified as three subspecies of *C. digitata* (Scheerens et al. 1991). It does not appear that this taxonomy was ever adopted. All three species are native to the lowland deserts of the Southwestern United States and Western Mexico and typically occur in disturbed, gravelly soils (Shcheerens et al. 1991). *Cucurbita cordata* is narrowly distributed in Baja California in Mexico (Fig. 6.4). The distribution of *Cucurbita palmata* extends from Northeastern Baja California through California into the San Joaquin Valley and the southern part of the Salinas Valley and east to near the Colorado River (Bemis and Whitaker 1969) (Fig. 6.4). The southern end of the distribution of *C. digitata* ranges from Northern Sonora, Mexico, to Southern Arizona and New Mexico (Fig. 6.4). *Cucurbita palmata* occurs between the disjunct ranges of *C. digitata* in Southern Arizona and Northern Baja California, and interspecific hybridization is common where the two species are sympatric at the periphery of their ranges (Bemis and Whitaker 1969).

Species in this group of xerophytic perennials exhibit extreme drought tolerance and resistance to many of the viruses that infect cultivated *Cucurbita* (Table 6.2), but because of the distant relationships between the xerophytic perennials and the domesticated *Cucurbita*, introgression of these resistances into the cultivated *Cucurbita* has not been possible (Provvidenti 1990). Although desirable traits from these species may not be directly introgressed into cultivated pumpkins and squashes, modern studies of the genetics underlying these traits could aid in the identification of genes important for conferring disease resistance and drought tolerance in the cultivated species and subspecies.

6.3 Wild Utilized Species

Nearly all *Cucurbita* CWR are utilized in some way by rural people who live within the native ranges of the CWR. The diverse uses for wild pumpkins and squash are based on the bitter chemicals in their flesh, nutritious seeds, and hard rinds, which are the same traits that initially attracted hunter-gatherers to wild pumpkins and squashes. There are accounts of rural desert-dwelling people in the Southwestern United States and Mexico using the undried fruit of coyote melon (*C. digitata*, *C. palmata*, *C. cordata*) for soap due to its saponin-rich flesh (Nabhan 1985). The dried roots of buffalo gourd (*C. foetidissima*) are sold in medicinal herb markets in the Southwestern United States (Nabhan 1985). The non-xerophytic subspecies *C. argyrosperma* ssp. *sororia* is also utilized by rural Mexicans who eat the seeds and sometimes sell them in markets (Merrick 1995). Rural farmers and their families report using the bitter flesh (which contains saponins and cucurbitacins) to treat intestinal worms and as a biocide to purify water (Merrick 1995). Oil from cultivated *Cucurbita* subspecies has recently been shown to have pharmacological properties (Bardaa et al. 2016) that are likely also present and exploitable in the wild *Cucurbita* species and subspecies. Although there are many potential uses for *Cucurbita* CWR, the only wild *Cucurbita* species that was developed for commercial production is buffalo gourd (*C. foetidissima*).

Interest in domestication of buffalo gourd as a dryland oilseed crop emerged following the vegetable oil shortages during the Second World War (DeVeaux and Shultz 1985). Buffalo gourd was considered as a potential oilseed crop as early as 1946, and in the decades that followed, it was the subject of several studies (e.g., Bolley et al. 1950; Shahani et al. 1951) and preliminary cultivation and domestication efforts (Paur 1952; Curtis and Rebeiz 1974; Havener 1974). During the late 1970s and early 1980s, scientists worked to rapidly domesticate the wild species as a dryland oilseed and starch crop (Gathman and Bemis 1990). Researchers determined that the buffalo gourd required 150 mm of water annually if grown for its root and 250 mm annually if grown for seed (DeVeaux and Shultz 1985) and that it could yield up to 3000 kg/ha of seed (Bemis et al. 1978). The oil of seeds produced by buffalo gourd is similar to sunflower oil (DeVeaux and Shultz 1985), and the oil yield was predicted to be up to two times that of sunflower at 91 gal/acre (DeVeaux and Shultz 1985). Root starch from cultivated buffalo gourd was considered as a potential source of ethanol; researchers estimated alcohol yield from buffalo gourd root starch was superior to corn or grain sorghum at around 400 gal/a (DeVeax and Shultz 1985).

Despite the promise of buffalo gourd as an oilseed and ethanol crop for arid lands, interest in the development of the crop waned by 1990 (Small 2014). Commercialization of buffalo gourd failed, apparently due to its lack of unique qualities needed for breeders and farmers to shift their current practices. However, in the decades since interest buffalo gourd declined, reduced supplies of water and arable land that will only grow scarcer are increasing the demand for drought-tolerant crops and biofuel production, and interest in buffalo gourd may be renewed.

6.4 Conservation Status of CWR and WUS

6.4.1 In Situ

The Okeechobee gourd (*C. okeechobeensis* ssp. *okeechobeensis*) is one of only two federally endangered plants native to the United States that have been determined as high priority as genetic resources of important food crops (Khoury et al. 2013), and it faces a continued threat of extinction due to development, competition from invasive species, and climate change. The Okeechobee gourd was historically more widespread in Florida, but by 1930 95% of its habitat was destroyed when pond apple (*Annona glabra* L.) forests were cleared in attempts to develop the Everglades and other regions of Florida for agricultural fields (Ward and Minno 2002). The Okeechobee gourd now only occurs along the shore of Lake Okeechobee and a short stretch of riverbank along the St. Johns River in Central Florida. The St. Johns River populations are somewhat protected as they occur on State Parks Land, but the Lake Okeechobee populations face imminent threat by development, recreation, and water management practices. Furthermore, the populations of Okeechobee gourd that do exist are not robust. Two other CWR, the native vine *Vitis rotundifolia* Michx. and the invasive exotic *Dioscorea bulbifera* L., both appear to outcompete the Okeechobee gourd along the St. Johns River. Some plants surveyed in 2015 by the author did not reemerge in 2016, and though the vines of the Okeechobee gourd plants are extensive, they produced very little, if any, fruit, suggesting a possible lack of suitable pollinators or limitation by other environmental factors.

There are currently no active in situ Okeechobee gourd conservation projects, though multiple grant proposals have been submitted to various public and private organizations (Minno pers. comm.). Public awareness of this nearly extinct CWR is also lacking. Displays throughout the state parks where it occurs warn visitors of the threat of invasive plant and animal species and provide information about the parks' resident federally listed mammal species, the Florida manatee, but do not mention the Okeechobee gourd. Local landowners and park rangers are also currently unaware that a federally listed endangered plant occurs in this area. Local accounts that the vine is regarded by some as a weed suggests some populations may be at risk of removal.

Although the Okeechobee gourd is the only listed endangered *Cucurbita* CWR, many *Cucurbita* CWR are geographically restricted. The current distributions of *Cucurbita* CWR are likely more restricted than they were in the past (Kistler et al. 2015). Disjunct species distributions in *C. okeechobeensis*, *C. digitata*, *C. pedatifolia*, and *C. pepo* and low genetic divergence between geographically distant occurrences of some species (Kates et al. 2017) suggest that the areas where *Cucurbita* CWR occur today represent only a fraction of the areas where they were historically distributed. The narrow present-day distribution of *Cucurbita* CWR may be due to ecological shifts and the extinctions of megafauna that consumed the bitter *Cucurbita* fruit and dispersed *Cucurbita* seeds (Kistler et al. 2015). Although this ancient shift cannot be reversed, the hypothesis that the extinction of large herbivores led to drastic decline in *Cucurbita* CWR populations highlights the importance of dispersal in maintaining the genetic diversity of extant CWR. Commonly, *Cucurbita* CWR are regarded as an agricultural nuisance in Mexico and Central America (Nabhan 1985) and appear regionally vigorous, so in situ conservation efforts are not pursued.

The seeds of *Cucurbita* CWR are now most commonly dispersed by water (Nabhan 1985). After the fruits of *Cucurbita* CWR mature, the flesh inside dries out, and the seeds are preserved inside the lignified rind (Nabhan 1985). These dried fruits may stay in the same place for months but will eventually be carried by flash-floods (Nabhan 1985). As the buoyant *Cucurbita* CWR fruits are carried by fast-moving water, they hit against rocks and banks, and their dry rinds break open allowing the seeds to be scarified and then scattered in a new area. Because of the importance of seasonal flooding for the dispersal of *Cucurbita* CWR, unusually prolonged periods of drought in the deserts of the Southwestern United States and Mexico inhibit the dispersal of *Cucurbita* CWR. Dispersal by water is also important for non-xerophytic *Cucurbita* CWR that occur along rivers and lakes (*C. okeechobeensis* ssp. *okeechobeensis*; wild *C. pepo* ssp. *ovifera*), and lower water levels due to drought and water management practices could negatively impact the dispersal of these *Cucurbita* CWR.

Studies modeling the effect of future climate change on the distribution of *Cucurbita* CWR show that the distributions of all *Cucurbita* CWR are expected to decrease substantially in the next 60 years (Lira et al. 2009). The specialized pollinator of *Cucurbita* CWR, *Peponapis* spp., the squash bee, also faces threats due to climate change and the widespread use of agricultural pesticides (Watanabe 2013). More research is needed on these pollinator species. Because of the large vine habit of *Cucurbita* CWR, populations of *Cucurbita* CWR that grow as weeds in or near agricultural fields are removed to prevent the introduction of undesirable traits into *Cucurbita* crops or to limit their competition with non-*Cucurbita* crops (Nabhan 1985). Similarly, populations of *Cucurbita* CWR that grow on private, nonagricultural lands are also often removed because they are local weeds.

The deregulation of transgenic zucchini (*C. pepo* ssp. *pepo* var. *cylindrica*) in Mexico is currently under consideration (Cruz-Reyes et al. 2015) and has been the subject of numerous studies to examine the potential for transgenes to escape (see Cruz-Reyes et al. 2015; Sasu et al. 2009; Arriaga et al. 2006). Gene flow between populations of wild *Cucurbita* and cultivated *Cucurbita* is well-documented in multiple species, including *C. pepo* (Wessel-Beaver 2000; Wilson et al. 1994; Montes-Hernandez and Eguiarte 2002). The viability of F_1 seed has been experimentally confirmed for some crosses (Cruz-Reyes et al. 2015). Experimental crosses of transgenic squash lines to wild squash have been made to assess the relative competitiveness of the hybrids compared with the parents (Cruz-Reyes et al. 2015). Although transgenic x wild hybrids thus far do not appear to have a competitive advantage compared with wild *Cucurbita*, additional studies are needed (Cruz-Reyes et al. 2015; Arriaga et al. 2006). The need to preserve the genetic variation in wild *Cucurbita* in Mexico is especially high, as these populations likely represent the ancestors of pepo pumpkin and squash and still harbor the genetic diversity lost in the crops during their domestication.

6.4.2 Ex Situ

Maintenance and regeneration of genetically diverse *Cucurbita* CWR germplasm resources is critical for identifying the genes that underlie agronomically important traits in *Cucurbita* CWR. Large collections of *Cucurbita* CWR are held in seedbanks all over the world (e.g., the United States, Mexico, Costa Rica, Russia, Italy, Brazil, Colombia, Bolivia, Czech Republic, Spain, Turkey, and Portugal) (Clark et al. 1991; Nuez et al. 2000; Diez et al. 2002; Lebeda et al. 2007; Ferriol and Pico 2008; Karlova 2008). Collections of *Cucurbita* are particularly common in seedbanks in Mexico, such as the 25 community seedbanks, established in 2005 to preserve in situ conservation (Vera Sanchez et al. 2015), and in the country's largest wild plant seedbank at the Faculty of Higher Studies of Iztacala, UNAM (FESI-UNAM seedbank) (Rodríguez-Arévalo et al. 2017). However, a comprehensive understanding of genebank coverage and gaps for *Cucurbita* CWR in Mexico and other countries is lacking in part due to insufficient collaboration among seedbanks around the world that each have unique systems of cataloguing and distributing germplasm.

Collections of *Cucurbita* CWR from throughout their native ranges are the first step in conserving and increasing ex situ collections of *Cucurbita* CWR. In over 100 years of the USDA plant exploration program, there has been only one exploration for wild *Cucurbita* in the United States that has resulted in deposition of accessions into the National Plant Germplasm System. Collection of North American *Cucurbita* CWR germplasm from outside the United States for deposition into the USDA National Plant Germplasm System is limited due to the phytosanitary and political issues described below. American researchers and botanists made many collections of *Cucurbita* CWR in Mexico in the decades prior to strict regulation; although some of these collections were deposited in the National Plant Germplasm

System in the late 1980s and early 1990s and greatly increased the holdings of *Cucurbita* CWR from Mexico, many of these collections were never deposited (Robinson 1995), and seeds from these collections are unlikely to be viable.

Concerns regarding access and benefit sharing, phytosanitary issues, and a lack of funding limit or prevent sharing of germplasm resources among seedbanks and distributing germplasm to geneticists and breeders internationally. *Cucurbita* is not currently listed in Annex 1 under the Multilateral System of Access and Benefit Sharing of the International Treaty on Plant Genetic Resources for Food and Agriculture (FAO 2017) and thus does not benefit from prearranged facilitated access negotiations. Distribution of germplasm outside of the country where it is held can be critical to ex situ conservation of genetic resources, because *Cucurbita* CWR collected in a climate that differs from its storage location may not flower or fruit in the conditions of its seedbank location (Jarret pers. comm.). For seedbanks in the United States, this can be a problem for *Cucurbita* CWR that are adapted to tropical or subtropical climates. Although this issue certainly affects the ex situ conservation of other CWR, it may be especially problematic for *Cucurbita*. In contrast to the most economically important crops like corn and rice, the infrastructure required to grow and pollinate the large, monoecious *Cucurbita* plants is not in place (Paris 2016), and investing these resources is risky when the regeneration efforts are not likely to succeed.

Limited funding for seedbank activities can restrict the regeneration efforts needed to make collections available for distribution to geneticists and breeders (Jarret pers. comm.). A high proportion of *Cucurbita* CWR held in the US National Plant Germplasm System is unavailable for distribution (Fig. 6.5). Seedbanks respond to user requests. Hence, limited resources may be diverted to maintenance of collections that are more widely used by researchers. Greater demand for

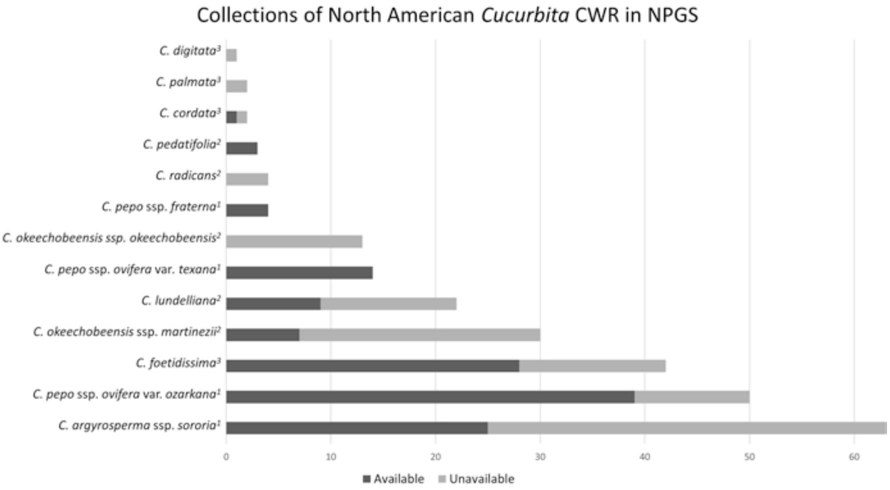

Fig. 6.5 Number of *Cucurbita* CWR accessions in the National Plant Germplasm System (NPGS). Dark gray bars indicate accessions available for distribution; light gray bars indicate accessions currently unavailable. Superscripts denote genepool designations for CWR based on most closely related domesticate

collections of modern cultivars (or specific crops) may limit the resources available for collections of *Cucurbita* CWR, although these species likely harbor some of the most useful traits for crop enhancement (Robinson 1995). Only a few studies have attempted a thorough investigation of potentially valuable agronomic traits of *Cucurbita* CWR (e.g., Provvidenti et al. 1978; Scheerens et al. 1991). The xerophytic perennial species are especially understudied even though they are known to be resistant to drought and to many of the viral diseases that pose a threat to cultivated pumpkin and squash yields. Increased research interest in *Cucurbita* CWR is needed to promote the conservation of genetically diverse CWR in genebanks and to create drought-tolerant, disease-resistant crops that can meet the present and future challenges to food security.

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Chapter 7
Wild Chile Pepper (*Capsicum* L.) of North America

Derek W. Barchenger and Paul W. Bosland

Abstract Chile pepper (*Capsicum* L. sp.) is an increasingly important crop worldwide because of its various culinary and medicinal uses. Despite a diverse primary gene pool, sources of resistance or tolerance to many chile pepper pests and diseases are rare. Novel sources of resistance exist within the broader *Capsicum* wild relative gene pool. Although widely distributed as a group, the wild relatives native to North America (*C. annuum* var. *glabriusculum* (Dunal) Heiser and Pickersgill, *C. frutescens* (L.), and *C. rhomboideum* (Dunal) Kuntze) are not well studied. Their overall lack of phenotypic characterization is likely the largest contributor to the underutilization of these important sources of genetic variability, followed by limited access to plant material, pre- or post-zygotic barriers to fertilization, and linkage drag. Both in situ and ex situ conservation efforts of these species are limited, and one species, *C. lanceolatum* (Greenm.) C. V. Morton and Standl., is now extinct in North America as a result. Increased awareness, financial support and policy changes to enable greater collection and storage would facilitate better characterization and evaluation of these species and increase the potential for their incorporation into modern breeding programs.

Keywords *Capsicum* · Ex situ conservation · In situ conservation · Genetic resources

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D. W. Barchenger
The World Vegetable Center, Shanhua, Tainan, Taiwan, Republic of China
e-mail: derek.barchenger@worldveg.org

P. W. Bosland (✉)
Plant and Environmental Sciences, New Mexico State University, Las Cruces, NM, USA

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7.1 Introduction

7.1.1 Origin and Brief Use History

The genus *Capsicum* L. originated in the arid regions of the Andes Mountains, in what is now Peru and Bolivia, and then migrated to the tropical lowland regions of the Americas (Carrizo et al. 2016). It is estimated that there are currently about 35 wild species within the genus *Capsicum*, all native to the Americas (Bosland and Votava 2012). The majority of cultivated chile peppers belong to the species *C. annuum* L., which includes, bell, chile, and paprika peppers. Its wild progenitor is thought to be *C. annuum* var. *glabriusculum* (Dunal) Heiser and Pickersgill, which has small, erect, round, red, hot fruits. Capsaicinoids are responsible for the pungency of hot peppers and are concentrated in the placenta of the fruit. Wild peppers are primarily dispersed by birds (Tewksbury et al. 1999). Birds lack the transient receptor potential cation channel subfamily V member 1 (TrpV1) and therefore cannot sense capsaicinoids, while mammals can (Jordt and Julius 2002). Additionally, chile pepper seeds cannot survive passage through the mammalian gut, but germination can be increased after passage through the avian gut (Carlo and Tewksbury 2014; Tewksbury and Nabhan 2001).

Chile pepper is an increasingly important crop due to its use as a vegetable, colorant, spice, and medicinal value. There is a remarkable amount of diversity within the genus *Capsicum*, especially for traits such as fruit type, color, shape, taste, size, and capsaicinoid content. Furthermore, preferences for particular traits are regionally specific and can vary greatly within a country or region. According to the Food and Agriculture Organization of the United Nations, the vast majority of chile pepper production (64%) occurs in Asia, while production in the Americas makes up only 13% of global chile pepper production. Consumer demand for chile pepper in North America has substantially increased over the last 30 years (Rehrig et al. 2014) due to the increasing influence of diverse immigrant populations and changing consumer tastes (Gandonou and Waliczek 2013). However, chile pepper has been an important component of the human diet for millennia (Smith 1967). Domestication of chile pepper, one of the oldest New World crops, began approximately 8,000–10,000 years ago (Davenport 1970; Heiser 1969; Pickersgill 1966) and resulted in five domesticated species, *C. annuum* L., *C. baccatum* L., *C. chinense* Jacq., *C. frutescens* L., and *C. pubescens* Ruiz and Pav.. Each species arose from human selection and geographical separation throughout the Americas (Bosland and Votava 2012).

7.1.2 Cultivation

7.1.2.1 Agronomic Practices

Chile pepper production is practiced across a broad range of agroecological conditions, including the humid tropics, dry deserts, and cool temperate climates. Chile pepper can be grown as an annual or a perennial crop. The ability of chile pepper to grow and produce quality fruits in such a wide range of climates has made it a common crop worldwide. Because of its broad climatic tolerance, it is impossible to list a single production method for chile pepper production. One can generalize production as occurring either in the field or in climate-controlled environment, e.g., greenhouse or shadehouse. Although exceptions are common, in most of northern Mexico and the southern United States, chile pepper production occurs mostly in the field. Shadehouse production predominates in hot humid climates, such as Mexico and Thailand. Greenhouse production, on a global scale, typically occurs near population centers and in places with less than optimal environmental conditions. Diseases and pests are serious constraints to chile pepper production in the field and vary by production region (Bosland and Votava 2012). A greenhouse provides a more stable environment for chile pepper production. It protects the plants from adverse climate and pests and provides an optimum temperature year-round. The grower can control temperature, humidity, and even day-length. However, greenhouse production requires relatively high inputs of nutrients and energy for optimal control of growth and product quality.

7.1.2.2 Pests, Diseases, and Climatic Limitations

No matter the production system, growers will almost certainly face some production challenges associated with abiotic and biotic stresses. Pests and pathogens are among the most common causes of reduced productivity in chile pepper. Chile peppers are susceptible to plant pathogenic bacteria, fungi, oomycetes, phytoplasma, and viruses as well as insect and other invertebrate pests. Not every pathogen or pest is present in every production region. Although management strategies are common for many chile pepper pathogens and pests, few are completely effective. Additionally, improper pesticide applications can have negative environmental impacts and be costly to growers. Plant breeders are continuously developing cultivars with resistance to pests and pathogens; however, sources of resistance can often be scarce in the primary gene pool.

The most serious bacterial disease in humid environments is bacterial spot, caused by *Xanthomonas campestris* pv. *vesicatoria*, which has developed resistance to copper compounds and streptomycin, making management challenging. Additionally, at least ten races of *X. campestris* have been identified, making breeding for resistance arduous. Bacterial canker, caused by *Corynebacterium michiganense*, is a major issue for greenhouse production and where chile pepper is grown under cover. In more humid environments, the bacteria *Erwinia carotovora* pv. *carotovora* cause soft rot in chile pepper pods and are a serious postharvest issue. Bacterial wilt caused by *Pseudomonas solanacearum* is a devastating pathogen in humid and tropical environments and causes significant losses to chile pepper production.

Several fungal pathogens are detrimental to chile pepper production. Anthracnose, caused by several species of *Colletotrichum*, is devastating to marketable chile pepper yield as it causes disease on the fruits. The fungus *Alternaria solani* causes the disease early blight and infects both leaves and fruits. Chile pepper stems and fruit can be susceptible to frogeye disease (*Cercospora capsici*) in humid environments.

Powdery mildew (*Leveillula taurica*) causes chlorotic blotches and spots and eventual defoliation toward the end of the season, especially in warm environments. Similarly, Stemphylium leaf spot (*Stemphylium botryosum* f. sp. *capsicum*) can cause defoliation in nearly all production environments. Favored by cool, damp environments, rhizoctonia root rot, caused by *Rhizoctonia solani*, can infect chile peppers from the seedling to mature stages. Southern blight (*Sclerotium rolfsii*) causes wilting and eventual plant death sporadically throughout chile pepper fields. A common temperate climate pathogen, *Verticillium dahliae* causes verticillium wilt with symptoms including yellowing of the leaves, stunting, and death.

There are two major pathogenic oomycetes of chile pepper. Oomycetes are exceptionally challenging because they reproduce both asexually and sexually. Sexual reproduction results in genetic recombination and the rapid accumulation of new virulence factors as well as widespread fungicide insensitivity. *Phytophthora capsici* is an extremely devastating oomycete pathogen that causes significant losses worldwide. Depending on the point of infection, *P. capsici* can cause disease on virtually every part of the plant (fruit rot, leaf blight, stem blight, and root rot), each of which requires a different resistance mechanism. Causing similar symptoms to phytophthora root rot, damping-off (*Pythium aphanidermatum*) is a serious problem for greenhouse production where frequent overhead watering and high humidity are common.

There are three major phytoplasma diseases of chile pepper that are transmitted into the phloem tissue by vectors. Resistance to phytoplasma disease in chile pepper is rare; however, resistance to the vector is more promising. Stolbur causes limp and yellow leaves and eventual defoliation. Brote grande symptoms include a bushy appearance similar to witches-broom and lack of fruit set (Randall et al. 2009). Pepper little leaf also results in witches-broom-like symptoms but is caused by a different phytoplasma than Brote grande.

In tropical regions, viruses are the most serious disease problem faced by chile pepper producers. Nevertheless, viral diseases are also common throughout more temperate production regions. It has been reported that half of the 45 viruses known to infect chile pepper are transmitted by aphids (Green and Kim 1991). Other vectors include nematodes, thrips, leafhoppers, whitefly, beetles, and fungi. The most common viral symptoms include mottling, mosaic, veinbanding, ringspots, necrosis, leaf discoloration, deformation, blistering, and stunting of the plant. Fortunately, resistant cultivars have been developed for many of the virus pathogens in chile pepper.

Insect and other invertebrate pests can be a serious problem for chile pepper production, and pest species differ in each region. Herbivory often results in plant decline and even death due to the reduction of photosynthetic or transport tissue. Additionally, herbivory can open the plant canopy exposing the pods to sunscald, making them unmarketable. Insect and invertebrate pests are harmful because their feeding can stress the plants, making them more vulnerable to attack by other pathogens and pests. Furthermore, invertebrate pests can be vectors of bacterial and viral diseases that can quickly spread throughout a chile pepper field. Breeding for pest resistance is extremely challenging because insects and other pests possess behavioral choice. Emerging evidence suggests that one important aspect in breeding for insect resistance is selection for deterrents such as trichome type and density and volatile phytochemicals (Rakha et al. 2017). However, these physical deterrents have the potential to result in unmarketable or unsafe yield.

Chile pepper does best with a long, frost-free season to produce high good-quality yields. Chile pepper is highly susceptible to frost and grows poorly at temperatures below 15 °C. Rapid germination and emergence is important to ensure a good stand and adequate yields. If seeds are planted early in the season when soil temperatures are too cool, germination rate is slowed, effecting emergence and growth of the seedlings. Slow growth can prolong seedling exposure to insects, diseases, salt, or soil crusting, any of which can kill the seedlings. Higher yields result when daily air temperature ranges between 18 °C and 32 °C during fruit set. The base growing-degree-days temperature is 18 °C, and temperatures below 18 °C result in negligible growth to chile pepper plants (Sanders et al. 1980).

Chile peppers have a high tendency to abort reproductive organs (buds, flowers, and young fruits), and cyclical fluctuations occur in fruit set. Stages susceptible to abortion are very young buds (< 2.5 mm), buds close to anthesis, and flowers and fruits up to 14 d after anthesis. Higher CO_2 concentrations, elevated light, and decreased planting density increase the availability of assimilates within each plant and decrease the likelihood of fruit abortion. The cyclical pattern in fruit set is caused by changes in demand for assimilates (Wubs et al. 2009). Due to competition for assimilates, flower abortion occurs when rapidly growing fruit are present (Bosland and Votava 2012). Fruit set increases when fast growing fruit are almost mature and have a low assimilate demand. Water deficit stress and low nutrient supply also increase abortion levels (Wubs et al. 2009). Low-night and high-day temperatures hamper pollen development, causing low seed set, which can result in fruit abortion.

Soil salinity is also an important consideration in chile pepper cultivation. Saline irrigation water is common in some of the important chile pepper production regions in North America such as the states of Arizona, California, New Mexico, and Texas in the United States and the states of Chihuahua and Sonora in Mexico. High soil salinity often results in poor stand establishment, reduced plant growth, and reduced yield. Chile peppers have a 50% yield loss at electrical conductivity (EC) of 5.8 dSm^{-1} and an additional 13% reduction in yield for every additional unit increase in EC (Bosland and Votava 2012).

7.2 Crop Wild Relatives (CWR) and Wild Utilized Species (WUS) of the Crop

7.2.1 Relationship to Crop

In North America, there are three extant wild relatives of chile peppers. The species *C. annuum* var. *glabriusculum* (2n = 24), commonly called chiltepin or chile piquin (Bosland and Votava 2012; Kraft et al. 2014), grows wild from northern Peru and

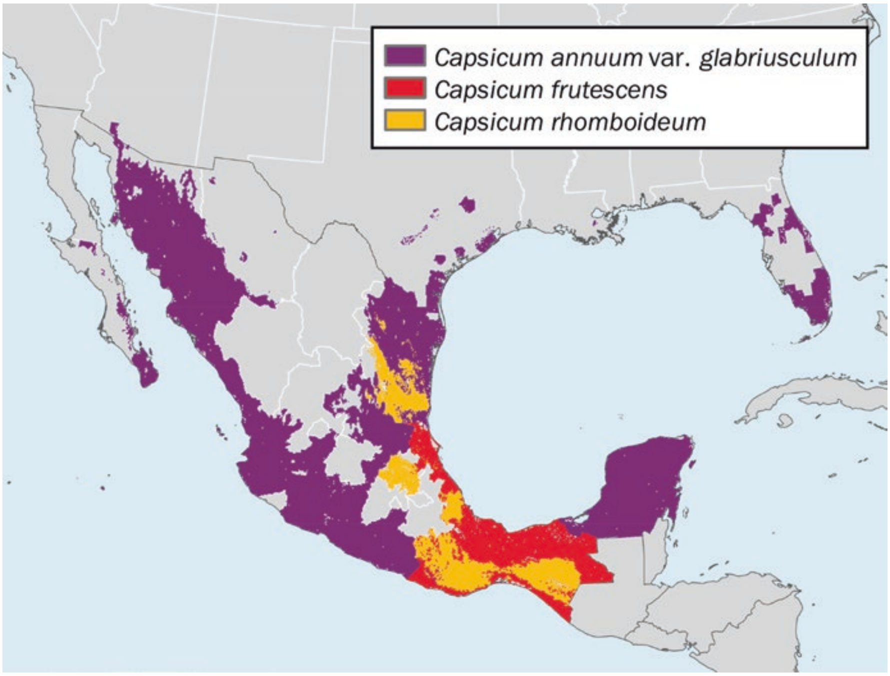

Fig. 7.1 Potential distribution maps for wild native and potentially feral ranges of North American *Capsicum* species, based on reference sightings and germplasm collecting locations. Full methods for generation of maps and occurrence data providers are given in Appendix 1

Colombia up through Central America and Mexico to Arizona and Texas (Fig. 7.1) (Hayano-Kanashiro et al. 2016). Today, chiltepins are harvested from both cultivated and natural populations throughout their growing region and are significant sources of revenue for smallholder farmers, especially in Mexico (Perramond 2005).

Although *C. frutescens* ($2n = 24$) is the second most widely grown North American cultivated chile species, the distribution of wild *C. frutescens* in North America is relatively narrow, limited to the Yucatan peninsula and most southern portions of Mexico (Fig. 7.1). However, the origin of *C. frutescens* is still in question and wild populations in North America might be feral (Gloria Barboza, unpublished data). The wild species *C. rhomboideum* (Dunal) Kuntze, previously known as *C. ciliatum* (Kunth) Kuntze, grows from Peru through Mexico (Fig. 7.1) (Carrizo et al. 2016; Samuels 2015) and has yellow flowers, nonpungent fruits, and a base chromosome number of 13 ($2n = 26$). There was likely a fourth *Capsicum* species, *C. lanceolatum* (Greenm.) C.V. Morton and Standl. ($2n = 26$) native to North and Central America, which was distributed throughout the cloud forests of Guatemala, Honduras, and southern Mexico (Breedlove 1986; Gentry and Standley 1974; Molina Rosito 1975; Standley and Steyermark 1940). However, due to deforestation, *C. lanceolatum* is now only found in Guatemala (Bosland and Gonzalez 2000).

These wild relatives have the potential to be important resources for genetic diversity in modern chile pepper breeding programs.

The *Capsicum* gene pool is extensive compared to other crops. The primary gene pool includes members of the same species or closely related species that can be directly hybridized with the species of interest to produce vigorous and fertile progeny. The secondary gene pool includes plants that belong to related species, but the progeny are often sterile or not vigorous. The tertiary gene pool includes species that can be hybridized with the species of interest, but the progeny must go through embryo rescue to be viable. In chile pepper, there are three primary gene pool complexes, the annuum, baccatum, and pubescens complexes that can be accessed for each of the five domesticated species (Fig. 7.2). These complexes are based on the degree of genetic proximity and reproductive compatibility. For *C. annuum*, the primary gene pool consists of breeding lines, cultivars, and landraces within the species as well as the wild progenitor chiltepin. The secondary gene pool includes *C. baccatum*, *C. chacoense* (Hunz.), *C. chinense*, *C. frutescens*, and *C. galapagoense* (Hunz), while the tertiary gene pool consists of *C. cardenasii* (Heiser and P. G. Sm.), *C. eximium* (Hunz), *C. lanceolatum* (Greenm.) C. V. Morton and Standl., *C. praetermissum* (Heiser and P. G. Sm.), *C. pubescens* (Ruiz and Pav.), *C. rhomboideum*, and *C. tovarii* (Eshbaugh et al.) (Fig. 7.2).

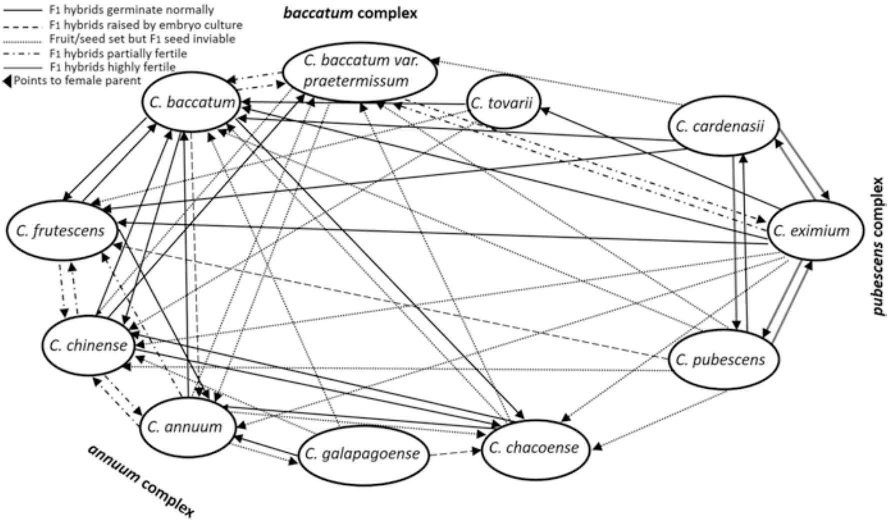

Fig. 7.2 Crossability polygon for some members of the genus *Capsicum*, adapted from Emboden (1961), Eshbaugh (1970), Heiser and Smith (1948), Pickersgill (1971, 1980), and Tong and Bosland (1999). In the annuum complex, *Capsicum annuum* L. var. *glabriusculum* (Dunal) Heiser & Pickersgill is grouped in with *C. annuum* L., and *C. frutescens* L. contains both wild and domesticated accessions. With 13 chromosomes, *C. rhomboideum* does not readily hybridize with any of the domesticated species and is not shown

7.2.2 Utilization

The North American wild relatives of chile pepper are often used as vegetables and spice in cooking as well as in traditional medicine (Pagán et al. 2010). Chiltepins are considered a significant component of the identity and culture of Mexico (Bañuelos et al. 2008). The indigenous Papago and Pima people, from the Sonoran desert regions of the United States and Mexico, have traditionally made annual pilgrimages to harvest chiltepins (Nabhan et al. 1990). During the 1980s, harvesting chiltepins became an important economic activity in the rural areas of northern and central Mexico (Bañuelos et al. 2008; González-Jara et al. 2011). Harvesting chiltepins has traditionally been done by the women, children, and elderly people (Bañuelos et al. 2008) and has been found to significantly increase family income and socioeconomic mobility (Montes 2010). Chiltepins are harvested both from natural populations and cultivated fields (Pagán et al. 2010), and it has been estimated that ~50 tons are harvested each year (González-Jara et al. 2011; Votava et al. 2002) and exports to the United States are ~6 tons per year (Montes 2010). Excessive harvesting has resulted in extinction of some wild chiltepin populations (González-Jara et al. 2011; Nabhan 1990). Although reports are limited, it is likely that wild and potentially adventive populations of *C. frutescens* (Kraft et al. 2013) and *C. rhomboideum* are also harvested and consumed by people in Mexico, but they are far less economically important than chiltepins.

7.2.2.1 Breeding History and Use

In Solanaceae, introgression breeding has been extensively used in tomato (*Solanum lycopersicum* L.) (Lin et al. 2014) and potato (*S. tuberosum* L.) (Hirsch et al. 2013). Conversely, chile pepper breeding programs have made limited use of related wild species (Mongkolporn and Taylor 2011). A major constraint to utilizing this genetic diversity is the lack of access to germplasm. Publically available germplasm collections have few or no accessions of the North American wild *Capsicum* species. Other constraints include pre-zygotic barriers such as pollen-pistil incompatibilities that prevent fertilization and post-zygotic barriers such as embryo or endosperm abortion, weak hybrids, and sterility (Kamvorn et al. 2014; Yoon et al. 2004). These barriers exist largely when hybridizing *C. annuum* to the other North American wild species *C. frutescens* and *C. rhomboideum*. Additionally, the primary and secondary gene pools of domesticated species of chile pepper possess tremendous diversity, limiting the need for wide crosses to make immediate progress. Furthermore, random mutations that result in phenotypic changes are very common in chile pepper. The high level of mutation in chile pepper is likely the result of retro-transposition, as 81% of the *C. annuum* genome is made up of transposable elements (Qin et al. 2014). Despite these limitations, the use of wild relatives for improvement of domesticated chile pepper still has a place in modern breeding programs, for introgression of novel traits, increasing diversity within the current gene pool.

One important aspect of chile pepper breeding is the development of hybrid cultivars. To more efficiently produce hybrids, the use of cytoplasmic male sterile (CMS) lines are required. Interspecific hybridization between *C. annuum* and *C. frutescens* followed by several generations of backcrossing has resulted in male sterility (Csillary 1983). Interestingly, the plasma type of this interspecific hybrid was found to be identical to the original source of CMS in chile pepper identified from an accession collected in India by Peterson (1958) (Shifriss 1997). This is evidence that the most widely used CMS source in chile pepper breeding programs is likely the result of an interspecific hybridization between species of North America. Another source of cytoplasmic male sterility is the *C. chacoense* by *C. annuum* hybridization. Using *C. chacoense* as the female parent, all progeny are male sterile (Pickersgill 1997).

As expected, resistance to the many diseases and pests that attack chile pepper has been the focal point of most interspecific breeding programs. One important example of this is the virus resistance in most modern bell pepper (*C. annuum*) cultivars that was introgressed from the more tropical *C. chinense*. Chiltepins have been used as sources of disease-resistant genes (Gonzalez and Bosland 1991) and have been identified as potential sources of resistance to curly top virus (Bosland 2000). However, there are still many diseases to which sources of stable resistance have not yet been identified or widely incorporated. The oomycete *P. capsici* is one of the most devastating pathogens for chile pepper production worldwide. Criollo de Morelos (CM334), a *C. annuum* landrace from Mexico, has been found as the most widely applicable resistance source to *P. capsici*. However, relying on a single resistance source can lead to the rapid breakdown of resistance on a wide scale. The center of origin of *P. capsici* is hypothesized to be in Mexico. Therefore, it is possible that a chile pepper wild relative native to Mexico might serve as a novel source of resistance to *P. capsici*. In fact, the wild chiltepin has been found to have more resistance genes (2,042) as compared to the domesticated cultivar Zunla-1 (1,665) (Wei et al. 2016). In tomato, the source of broad-spectrum resistance to powdery mildew was identified in a closely related wild relative of tomato (Bai et al. 2008). An alternative concept is introgressing nonhost resistance from wild relatives that have not yet been exposed to a particular disease. Using nonhost resistance could be possible with the wild relatives that are native to more tropical climates as sources of resistance to temperate diseases, such as *V. dahliae*.

An important consideration when using wild relatives as sources of disease resistance is that resistance is often heavily influenced by habitat. Pagán et al. (2012) found that in chiltepin, disease incidence and risk of infection increased as human management increased. Management or cultivation is associated with decreased genetic diversity and habitat species diversity. In fact, they report that species diversity of the habitat was the primary predictor of disease and infection risk, indicating that disease resistance in chiltepin might be associated more with escape and avoidance than resistance genes.

Often, crop wild relatives produce volatile phytochemicals or are highly pubescent, which are generally not part of the domestication syndrome. Evolutionarily, plant trichomes and volatile secondary metabolites play a role in plant defense, especially in regard to phytophagous insects. There has recently been an increased interest in moving these traits from wild relatives into breeding material for insect and other invertebrate resistance (Rakha et al. 2017). *Capsicum rhomboideum* is densely covered in trichomes, making it a possible source for insect resistance. One important consideration when moving volatile compounds into domesticated species is their effect on human health. In other solanaceous crops, the toxic glycoalkaloid solanine can be present in the plant leaves, fruits, and tubers; however, this not the case for domesticated chile pepper. Introducing novel volatiles into chile pepper should therefore be undertaken with careful attention toward such alkaloids.

Members of the genus *Capsicum* also accumulate phytochemicals that play important roles in human health and nutrition (Guzman et al. 2010). The most common colors in mature chile pepper fruits are red, orange, and yellow, which are the result of carotenoid metabolism and accumulation. For the plant, carotenoids act as light-harvesting pigments that absorb light at different wavelengths than chlorophyll (Deli et al. 2001), and they also protect the photosynthetic centers from photooxidative damage (Guzman et al. 2010). For humans, carotenoids are the precursors of vitamin A, and they have high radical scavenging (antioxidant) capacity. Vitamin A deficiency is an important deficiency worldwide (World Health Organization 2009). Another group of important chemical compounds in chile pepper are the capsaicinoid alkaloids, which cause the burning sensation when consumed and are unique to the genus *Capsicum*. Not only are capsaicinoids the reason for the widespread incorporation of chile pepper into global cuisine, they also have antimicrobial effects for food preservation and are widely used as an analgesic. Capsaicinoids have been used to treat arthritis, headaches, and neuropathic pain (Guzman et al. 2010). While capsaicin and dihydrocapsaicin are the major two capsaicinoids normally found in *C. annuum*, there are 20 known other capsaicinoids found in other *Capsicum* species (Bosland and Votava 2012). Capsiate, an analog of capsaicin that does not elicit a heat sensation, has been found to promote energy metabolism and suppress body fat accumulation (Ohnuki et al. 2001). Unlike capsaicin, capsiate can be consumed in large quantities, increasing metabolic activity. Interestingly, the fruit of *C. rhomboideum* and *C. lanceolatum* are not hot and could be a novel source of capsiate or other carotenoids.

Other areas of interest are volatile aroma or flavor compounds. While little is known about the consumer preference for particular aroma compounds in chile pepper, there are clear preference differences among cultivars. In Mexico, certain flavors associated with chiltepins are highly sought after and consumers are willing to pay premiums for more flavorful pods (Villalon-Mendoza et al. 2014). The wild relatives within *Capsicum* could serve as sources for unique and novel flavor compounds that could increase or at least alter consumer demand for chile peppers.

Abiotic stress is another major limitation to chile pepper production. Fruit and flower abortion is sensitive to environmental conditions such as high temperature and low light, which is associated with capacity to uptake assimilates (Aloni et al. 1997). Similarly, photosynthetic ability is strongly negatively affected by NaCl salinity (Bethke and Drew 1992). There is some evidence that chiltepins might be more tolerant to salinity than domesticated chile peppers (López-Aguilar et al. 2012). The other wild relatives of chile pepper might serve as a source of tolerance to the environmental stresses that negatively impact photosynthesis.

7.2.2.2 Challenges to Increased Use

There is tremendous potential for the wild relatives of chile pepper to be more widely used as sources of novel traits. However, the primary limitation to greater use is the overall lack of characterization data of these wild relatives. To date, there have been few efforts directed at identifying the potential value of the wild relatives to modern breeding programs. The genetic diversity and variation within wild populations of *C. annuum* from Mexico has been widely studied (Aguilar-Melendez et al. 2009; Cheng et al. 2016; Loaiza-Figueroa et al. 1989; Oyama et al. 2006; Votava et al. 2002), and the genomic sequence of the wild chiltepin is publically available (Qin et al. 2014). However, publically available phenotypic data for wild species of *Capsicum* of North America is still very limited. One reason for this is that in situ and ex situ populations have been found to be genetically heterogeneous and thus difficult to characterize based upon a manageable number of plants (Votava et al. 2002).

Other limitations to increased use of wild species in modern breeding programs include pre- and post-zygotic incompatibilities. *Capsicum frutescens* and *C. annuum* var. *glabriusculum* are in the white-flowered and yellow-seeded annuum complex and can be more easily hybridized with cultivated *C. annuum*, *C. chinense*, and *C. frutescens* (Fig. 7.1). However, neither *C. rhomboideum* nor *C. lanceolatum* are in the annuum complex and would require the use of bridge crosses, embryo rescue, and chemically induced nondisjunction. Furthermore, *C. lanceolatum* and *C. rhomboideum* have 13 chromosomes ($2n = 26$), while all the cultivated species have 12 ($2n = 24$).

In many crops, the undesirable effects of linkage drag have been a major limitation to efficient exploitation of wild relatives in modern breeding programs (Feuillet et al. 2008). In chile pepper, the wild relatives typically have smaller, hot fruit that readily abscises from the plant, which are dispersal mechanisms that have been lost through domestication (Pickersgill 2007). Wild *Capsicum* species also have a tendency require cross-pollination (Paran and van der Knaap 2007), a mechanism to increase genetic variability that has been lost in the domesticated species and inhibits progress in breeding programs. The wild relatives also often have uneven or reduced germination (Almanza-Enríquez 1998). Reduced or sporadic germination in chile pepper has been found to be associated with a hard seed coat (Eshbaugh 1980; González-Cortés et al. 2015), presence of germination inhibitors (Barchenger and Bosland 2016; Bewley 1997; Prado-Urbina et al. 2015), and rapid degradation in storage (Sandoval-Rangel 2011). In their native habitat of northern Mexico, chiltepins are often found growing in association with nurse plants such as feather bush (*Lysiloma watsonii* Rose) and velvet mesquite (*Prosopis velutina* Wooten) that provide a beneficial microclimate and improve seed germination as well as plant growth and development (Bañuelos et al. 2008; Miranda-Zarazúa et al. 2007). This environment greatly differs from typical chile pepper cultivation.

The lack of available germplasm is also a contributor to the narrow use of the North American wild *Capsicum* species in modern breeding programs. Publically available germplasm collections of the wild *Capsicum* relatives are limited (Kraft et al. 2013). There are ~35 wild species within the genus *Capsicum*, and in general, the public germplasm repositories possess only a small number of these species. Additionally, they usually contain only one or a few accessions within the limited number of wild species. The wild species of *Capsicum* are both genotypically and phenotypically plastic (González-Jara et al. 2011), and to harness the complete genetic variability contained within these wild species, many more accessions from diverse geographic collections sites are required.

7.3 Conservation Status of CWR and Wild Utilized Species (WUS)

7.3.1 In Situ

Although some efforts have been made to collect and conserve wild *Capsicum* species ex situ, little has been done to protect the natural habitats and the native populations of these species (Tewksbury et al. 1999). One example of this is *C. lanceolatum* as described by Bosland and Gonzalez (2000). *Capsicum lanceolatum* was likely once present in the cloud forests of southern Mexico and Central America, but due to deforestation in parts of that region, it is now only present in the Mario D'Arcy Avila Biotopo el Quetzal nature reserve in Guatemala. Bosland and Gonzalez (2000) were not able to identify *C. lanceolatum* in any of the previous localities because agriculture had replaced the forests. Additionally, *C. lanceolatum* was not found in any of the farms or markets they visited. Unfortunately, the cloud forests of Guatemala are also becoming rare, and *C. lanceolatum* has not been identified in any of the regenerated forests. The quickly diminishing populations of *C. lanceolatum* illustrate the importance of preserving the natural habitats of these species, exacerbated by the species being very recalcitrant to ex situ storage. Seed viability is less than 1 year even in temperature- and humidity-controlled storage.

Unlike *C. lanceolatum*, wild populations of chiltepin, *C. frutescens*, and *C. rhomboideum* are still widely distributed throughout Mexico or parts of the United States. Recently, Kraft et al. (2013) identified and collected 347 accessions of *C. annuum* var. *glabriusculum* in the states of Arizona, Baja California, Chiapas, Jalisco, Oaxaca, Queretaro, Sinaloa, Sonora, Tamaulipas, Texas, and Yucatan. Additionally, they found 38 accessions of *C. frutescens* in the state of Veracruz. These species have been recorded from ecologically diverse locations including roadsides, within nature preserves, and cultivated in high agricultural production regions from sea level up to ~2000 m. There are several possible reasons for the overall success of these wild (or in the case of *C. frutescens*, potentially feral) populations. Firstly, chiltepin has some weedy characteristics and can survive in both xeric and more humid environments (Nabhan et al. 1990). Similarly, *C. rhomboideum* can have weedy tendencies and can be found growing on the roadside and in fence rows along crop production roadside (Dennis E. Breedlove, unpublished data). Additionally, the species have economic importance, potentially increasing conscious maintenance of populations (Bañuelos et al. 2008; Pagán et al. 2010). However, overexploitation has resulted in the extinction of some populations (González-Jara et al. 2011; Nabhan 1990). Measures to conserve wild and managed populations of the wild *Capsicum* relatives of North America should be implemented to maintain the source and the architecture of genetic variation (González-Jara et al. 2011).

7.3.1.1 Status (Threatened\Endangered)

There are currently no wild North American *Capsicum* species listed as vulnerable, threatened, or endangered by the US Endangered Species Act, or other regional conservation listings. However, this is likely inaccurate considering the status of *C. lanceolatum* in North America. The conservation status of *C. annuum* var. *glabriusculum* in the United States is listed as demonstrably secure, while neither *C. frutescens* nor *C. rhomboideum* are listed (NatureServe 2017).

7.3.2 Ex Situ

7.3.2.1 Genebank Coverage and Gaps

Genebank repositories around the world house relatively large collections of the domesticated species of chile pepper; however, wild relatives are not well represented in publically accessible collections. As of 2017, the US National Germplasm Resources Information Network (GRIN) system previously housed one *C. lanceolatum* accession (PI 641026), but this accession is no longer in the collection; 3 *C. rhomboideum* accessions (PI 501530, PI 645680, and PI 673044); 67 *C. annuum* var. *glabriusculum* accessions that range from wild plants to selections and cultivars, and all but two are available for distribution; and 282 *C. frutescens* accessions, with 277 available for public distribution, only 10 of which are listed as wild material.

The World Vegetable Center Genetic Resources and Seed Unit houses 6,192 accessions within *Capsicum*, including 490 wild and domesticated *C. frutescens* accessions. The Plant Genetic Resources of Canada houses two accessions of *C. frutescens*, and The Tropical Agricultural Research and Higher Education Center (CATIE) Germplasm Database houses 884 *Capsicum* accessions with 274 *C. frutescens* accessions; however, these collections do not contain any of the other wild species of North America. The French National Institute for Agriculture Research (INRA) germplasm collections includes 27 accessions of *C. annuum* var. *glabriusculum* and 51 accessions of *C. frutescens*.

The public germplasm repositories distribute plant material for research, education, training, and developmental purposes. Availability of seed is dependent upon quantity in the collection and national or international regulation of movement of plant material. Furthermore, concerns regarding phytosanitary issues limit or completely prevent germplasm distribution among international germplasm repositories and to plant breeders and other scientists internationally. A comprehensive understanding of genebank coverage and gaps for *Capsicum* is lacking in part due to insufficient collaboration among public germplasm repositories.

7.3.2.2 Outlook

As tropical rainforest is giving way to agriculture and other forms of habitat modification, wild *Capsicum* germplasm is being lost. Additionally, pre-domestication human management of *C. annuum* var. *glabriusculum* has been shown to result in a significant reduction in genetic diversity (González-Jara et al. 2011). It would be prudent to collect and place in ex situ collections a diverse set of populations of the wild *Capsicum* species. However, the recalcitrant nature of *C. lanceolatum* begets the point of how to effectively store wild species. Research on the cause of the loss of viability would be beneficial, including exploring alternative options to conventional cold storage. Ensuring that national and international policies and regulations are aligned so that these unique resources are able to be collected, conserved, and openly distributed is critical to the overall success of ex situ conservation (Perramond 2005). Germplasm conservation may best be promoted through better characterization and evaluation of current collections, both phenotypically and genotypically, and through building information systems that facilitate access to these data. Finally, greater awareness of the value and threats to these wild resources are needed in order to generate the momentum to better conserve them in situ and ex situ.

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Chapter 8
Crop Wild Relatives of Root Vegetables in North America

Justin E. Anderson, Alexandra Campbell, and Michael B. Kantar

Abstract Root and tuber crops are staples in diets across the world. They are favored due to a large yield associated with the small acreage needed to grow. Generally, they tend to be fairly robust to insect and disease pests and have historically been used as starvation food. Some root and tuber crops, such as potato, sweet potato, or cassava, are the primary source of daily calories for many cultures worldwide. Some tuber crops are only partially domesticated, facilitating the use of crop wild relatives (CWR). Many different cultures have their favorite root crops, but culinary preparation techniques often allow for different tubers to be used, making the acceptance of these crops fairly rapid. Here, we explore the origins and uses of eight tuber and root crops that are important to world diets and have many related wild species in North America.

Keywords Tubers · Species richness · Germplasm · Plant breeding

8.1 Introduction

Root vegetables are an important source of calories in many parts of the world. The favored root vegetable, as well as the preparation, varies depending on country or culture. Many root vegetables have been transported across the world, becoming naturalized in different areas. It is difficult to make many generalizations about root crops due to the large number of species and vegetative organs that are classified under this broad definition (Table 8.1). Here we explore the CWR of carrot

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J. E. Anderson
Department of Molecular Genetics and Physiology of Plants, Ruhr University Bochum, Bochum, Germany

A. Campbell · M. B. Kantar (✉)
Tropical Plant and Soil Science, University of Hawaii at Manoa,
Honolulu, HI, USA
e-mail: colferab@hawaii.edu; kant0063@umn.edu

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Table 8.1 Tuber crop production by country over the most recent 5 years available in FAOStat (FAO 2014)

Country	Crop	Total yield each year (Hg/Ha)				
		2009	2010	2011	2012	2013
Canada	Carrots and turnips	429,415	497,517	506,502	474,370	449,091
	Potatoes	313,126	316,055	295,863	310,155	325,123
	Sugar beet	603,394	495,575	640,496	592,772	672,697
Mexico	Carrots and turnips	260,679	246,947	269,620	264,475	271,622
	Cassava	143,440	131,579	127,352	122,330	146,398
	Potatoes	277,374	277,578	262,734	268,098	267,752
	Roots and tubers, nes[a]	282,617	274,131	266,843	260,069	261,937
	Sugar beet	NA	NA	250,000	180,000	140,000
	Sweet potato	190,454	206,653	201,465	175,168	183,965
	Yautia (cocoyam)	340,000	393,725	421,176	460,502	493,286
United States of America	Carrots and turnips	397,254	421,786	383,489	400,226	384,494
	Potatoes	464,446	452,767	447,140	458,242	463,577
	Sugar beet	581,309	621,142	533,929	655,763	636,939
	Sweet potato	225,200	228,628	233,019	234,472	245,411

[a] *Roots and tubers, nes:* "Including inter alia: arracacha (*Arracacia xanthorrhiza* Bancr.); arrowroot (*Maranta arundinacea* L.); chufa (*Cyperus esculentus* L.); sago palm (*Metroxylon spp*.); oca and ullucu (*Oxalis tuberosa* Molina and *Ullucus tuberosus* Caldas); yam bean, jicama (*Pachyrhizus erosus* (L.) Urb., *P. angulatus* DC.); mashua (*Tropaeolum tuberosum* Ruíz and Pavón); Jerusalem artichoke, topinambur (*Helianthus tuberosus* L.). Because of their limited local importance, some countries report roots and tubers under this commodity heading that are classified individually by FAO" (FAO Stat 2014)

(*Daucus carota* L. *subsp. sativus* (Hoffm.) Schübl. & G. Martens), sweet potato (*Ipomoea batatas* L.), potato (*Solanum tuberosum* L.), Jerusalem artichoke (*Helianthus tuberosus* L.), jicama (*Pachyrhizus erosus* L.), cocoyam (*Xanthosoma sagittifolium* L.), cassava (*Manihot esculenta (L.) Lam.*), and beet (*Beta vulgaris* L.); these eight common root vegetables are known for their economic importance and occurrence of wild relatives in North America.

The concept of gene pools in plant breeding dates back to Harlan and De Wet in the 1970s (Harlan and de Wet 1971). This concept defines boundaries between crops and the often numerous related species remaining in the wild. Experts working to define these pools for all major crop species in the Germplasm Resources Information Network (USDA, ARS 2017) of the US National Plant Germplasm System (NPGS) and the Harlan and De Wet Inventory (http://www.cwrdiversity.org/checklist; Dempewolf et al. 2017) of the Global Crop Diversity Trust have collaborated to create online resources making this valuable plant breeding information readily accessible. These combined databases were used as the basis for the gene pools defined in this review. Through ongoing plant breeding, many of the CWR belonging to these gene pools have contributed valuable traits important to modern crop production. Crop wild relatives are known to harbor many valuable traits, including resistance to biotic stresses, such as plant diseases or herbivores; tolerance to abiotic stresses, such as drought or frost; and even breeding and agronomic traits like yield and male sterility. These valuable traits are considered "potential breeding uses" when witnessed in the CWR and "confirmed breeding uses" when the trait has been crossed into the domesticated crop (Dempewolf et al. 2017). Crop wild relative exploration continues to suggest great potential in these and many other crop traits.

8.2 Carrot (*Daucus carota* L. subsp. *sativus* (Hoffm.) Schübl. & G. Martens)

8.2.1 Introduction

Carrot (*Daucus carota* subsp. *sativus)*, $2n = 2x = 18$, is an important vegetable from the *Apiaceae* family, known for its high nutritional content (provitamin carotenoids). Breeding efforts have significantly increased carotenoid concentration and recently unlocked the underlying mechanism (Iorizzo et al. 2016). There are several other important crops within the *Apiaceae* family, including celery, parsley, fennel, dill, coriander, aniseed, cumin, and caraway. In addition to food uses, many different carrot species have traditionally been used for medicinal purposes (Grzebelus et al. 2011). Carrot, generally grown as a biennial, was domesticated in Central Asia around 1,100 years ago (Iorizzo et al. 2013). Originally yellow or purple, the iconic orange carrot wasn't reported until the 1600s in Europe (Simon 2000).

8.2.2 Crop Wild Relatives and Wild Use

Domestic carrot has widely hybridized with wild carrots from North America and Europe, even suggesting that the origin of the only North American CWR, *Daucus pusillus* Michx., might actually have been an introduction of wild carrot from European settlers (Iorizzo et al. 2013). Current commercial materials are hybrid cultivars, developed using a cytoplasmic male sterility (CMS) system, a trait discovered in CWR (Alessandro et al. 2013). While we focus on North American wild relatives here, carrot has many non-North American relatives (31) that have a long history of breeding use. Carrots respond well to nitrogen applications and irrigation, but there is a need for advancing tolerances to abiotic stresses as the cultivated area increases. Major pests include carrot root fly, hoverflies, and leaf blight (Grzebelus et al. 2011). In carrot breeding, CWR have been an important source of resistance to these pests and helpful in overcoming other breeding limitations (Table 8.2). Ongoing characterization of genetic resources will continue to increase accessibility for breeders.

Table 8.2 Carrot crop wild relatives, genepool classification, and breeding use

Gene pool	Taxon	Native N.A. countries[a]	Breeding use	Number of accessions conserved in NPGS[b]	Number of accessions conserved in PGRC[c]	Number of accessions conserved in BGCI[d]	Number of accessions conserved in GENESYS[e]	Ex situ conservation status[f]	Reference
Tertiary	*Daucus pusillus* Michx.	C, M, U	Gene transfer, sandy soil tolerance, soil salinity tolerance	37	NA	13	46	Well conserved	Camadro et al. (2007, 2008)

[a] Canada (C), Mexico (M), USA (U), according to USDA, ARS (2017)
[b] USDA, ARS (2017)
[c] AAFC (2017)
[d] BGCI (2017)
[e] Global Crop Diversity Trust (2014) GENESYS
[f] Based on occurrence points relative to distribution maps and published literature

8.2.3 Conservation Status

Wild carrot species have long been a popular species for collection and utilization, both for food and medicinal purposes, in both North America and Europe (Banga 1957). The wild carrot species in North America is well conserved in ex situ germplasm collections. The most recent collecting trip by the USDA-ARS in 2010 resulted in the addition of 21 accessions of *D. pusillus* to the NPGS collection. This species has a large distribution and is represented across the southern and western United States, as well as western Canada; due to its broad presence, there are no specific concerns about its conservation status or current efforts to conserve it in situ.

8.3 Sweet Potato (*Ipomoea batatas* (L.) Lam.)

8.3.1 Introduction

Sweet potato (*Ipomoea batatas (L.) Lam.*) is one of the most important root crops in the world with 104 million metric tons produced in 2014 (FAO Stat 2014). Sweet potato is thought to have long been a staple in the human diet with archeological remains dating back 4,000 years (Solis et al. 2001). The crop also is highly nutritious and popular, being grown in over 100 countries (Khoury et al. 2015). The major constraints on production are viruses (SPVD) and insects (*Cylus* spp.), which can decrease yield between 60% and 100% (Khoury et al. 2015). Many of the close relatives of sweet potato show resistance to both biotic and abiotic stress (Table 8.3). Crossing relationships within *Ipomoea* are not well characterized; additionally, utilization is complicated by ploidy differences within and between species (Nimmakayala et al. 2011).

8.3.2 Crop Wild Relatives and Wild Use

The genus *Ipomoea* contains ~500 species, and taxonomic relationships within *Ipomoea* remain unresolved, which is in part due to the large amount of interspecific hybridization. This implies that as new data are generated, the exact relationships of wild relatives to *Ipomoea* are likely to change. The CWR species present in North America include *I. lacunosa* L., *I. leucantha* Jacq., *I. tenuissima* Choisy, *I. cordatotriloba* Dennst., *I. tiliacea* (Willd.) Choisy, *I. splendor-sylvae* House, and *I. trifida* (Kunth) G.Don (Table 8.3; Fig. 8.1). These species occupy ecological niches that may provide adaptation to diverse biotic and abiotic stresses (Table 8.3). There has been a history of eating many of the different wild sweet potato species, as well as using them for medicinal purposes (Austin and Huáman 1996; Pío-León et al. 2017).

Table 8.3 Sweet potato's crop wild relatives, genepool classification, and breeding use

Gene pool	Taxon	Native N.A. countries[a]	Breeding use	Number of accessions conserved in NPGS[b]	Number of accessions conserved in PGRC[c]	Number of accessions conserved in BGCI[d]	Number of accessions conserved in GENESYS[e]	Ex situ conservation status[f]	Reference
Secondary	*Ipomoea batatas* (L.) Lam. var. *apiculata* (Martens & Galeotti) McDonald & Austin	M	Drought tolerance	NA	NA	NA	NA	Poorly conserved	McDonald and Austin (1990)
Secondary	*Ipomoea batatas* (L.) Lam.	M	Drought tolerance; heat tolerance; waterlogging tolerance	NA	NA	NA	NA	Poorly conserved	Khoury et al. (2015)
Secondary	*Ipomoea littoralis* Blume	U	Drought tolerance; heat tolerance; sandy soil tolerance; waterlogging tolerance; dry matter yield; yield improvement; black rot resistance; scab resistance; weevil resistance	2	NA	1	2	Poorly conserved	Iwanaga (1988); Khoury et al. (2015)
Secondary	*Ipomoea tabascana* McDonald & Austin	M	Heat tolerance; waterlogging tolerance	1	NA	1	1	Poorly conserved	Khoury et al. (2015)

Secondary	*Ipomoea trifida* (H.B.K.) G.Don.	M	Drought tolerance; heat tolerance; waterlogging tolerance; dry matter yield; yield improvement; black rot resistance; root knot nematode resistance; root lesion nematode resistance; scab resistance; weevil resistance; high starch content; protein content	46	NA	1	137	Moderately conserved	Sakamoto (1976); Iwanaga (1988); Shiotani et al. (1991); Lebot (2010); Khoury et al. (2015)
Tertiary	*Ipomoea cordatotriloba* Dennst. var. *cordatotriloba*	U	Cold tolerance; sandy soil tolerance	NA	NA	1	NA	Poorly conserved	Khoury et al. (2015)
Tertiary	*Ipomoea cordatotriloba* Dennst. var. *torreyana* (A. Gray) D. F. Austin	M, U	NA	NA	NA	NA	NA	Poorly conserved	NA
Tertiary	*Ipomoea cordatotriloba* Dennst.	M, U	NA	5	NA	6	34	Moderately conserved	NA
Tertiary	*Ipomoea lacunosa* L.	U	Cold tolerance; drought tolerance; gene transfer	7	NA	3	8	Poorly conserved	Khoury et al. (2015); Austin (1978)

(continued)

Table 8.3 (continued)

Gene pool	Taxon	Native N.A. countries[a]	Breeding use	Number of accessions conserved in NPGS[b]	Number of accessions conserved in PGRC[c]	Number of accessions conserved in BGCI[d]	Number of accessions conserved in GENESYS[e]	Ex situ conservation status[f]	Reference
Tertiary	*Ipomoea leucantha* Jacquin	M, U	Drought tolerance; heat tolerance; sandy soil tolerance; gene transfer	NA	NA	NA	NA	Poorly conserved	Khoury et al. (2015); Austin (1978)
Tertiary	*Ipomoea ramosissima* (Poiret) Choisy	M	Cold tolerance; waterlogging tolerance	4	NA	1	1	Poorly conserved	Khoury et al. (2015)
Tertiary	*Ipomoea splendor-sylvae* House	M	Drought tolerance; heat tolerance; waterlogging tolerance	1	NA	1	1	Poorly conserved	Khoury et al. (2015)
Tertiary	*Ipomoea tenuissima* Choisy	U	Cold tolerance; heat tolerance; sandy soil tolerance	1	NA	1	1	Poorly conserved	Khoury et al. (2015)
Tertiary	*Ipomoea tiliacea* (Willdenow) Choisy in D.C.	M	Heat tolerance; waterlogging tolerance	15	NA	2	16	Poorly conserved	Khoury et al. (2015)
Tertiary	*Ipomoea triloba* L.	M	Drought tolerance; heat tolerance; soluble sugar	36	NA	5	67	Moderately conserved	Khoury et al. (2015); Yang et al. (2009)

[a] Canada (C), Mexico (M), USA (U), according to USDA, ARS (2017)
[b] USDA, ARS (2017)
[c] AAFC (2017)
[d] BGCI (2017)
[e] Global Crop Diversity Trust (2014) GENESYS
[f] Based on occurrence points relative to distribution maps and published literature

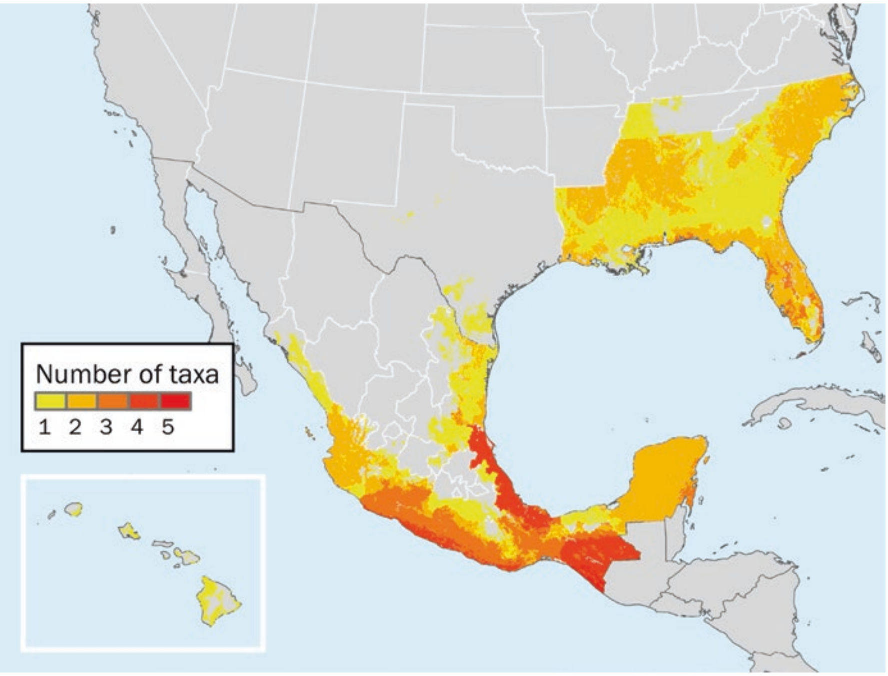

Fig. 8.1 Species richness map of modeled potential distributions of North American *Ipomoea* taxa, based on climatic and edaphic similarities with herbarium and genebank reference localities. Warmer colors indicate areas where greater numbers of taxa potentially occur in the same geographic localities. Full methods for generation of maps and data providers are given in Appendix 1

8.3.3 Conservation Status

The major challenge to using the CWR is the limited number of accessions available in ex situ collections. Recent work has identified that 70% of the CWR of sweet potato have only limited numbers of individuals currently preserved in ex situ collections and therefore are in great need of further collection (Khoury et al. 2015). Currently, there are only 749 germplasm accessions available in germplasm banks (Khoury et al. 2015). Increasing the number of accessions available and the creation of genetic stocks that contain introgressions from wild relatives at the correct ploidy level could prove valuable to ongoing breeding efforts. Due to the difficulty and expense in conservation, the CWR of sweet potato have lagged behind those of other crops in availability.

There is a great need to conserve the wild relatives, especially as the specialty markets of sweet potato increase in value. Several members of the *Ipomoea* genus are listed by NatureServe as vulnerable (*I. tenuissima* Choisy, *I. thurberi* A. Gray, *I. plummerae var. cuneifolia* (Gray) MacBride) or imperiled (*I. tuboides* O. Deg. & van Ooststr., *I. shumardiana* (Torr.) Shinners, *I. microdactyla* Griseb.) in their native ranges across North America (www.natureserve.org; NatureServe 2017); however of these, only *I. tenuissima* has a known breeding use.

8.4 Potato (*Solanum tuberosum* L.)

8.4.1 Introduction

Potato (*Solanum tuberosum* L.) is the fourth most widely produced crop in the world by yield and the most widely produced tuber (Ramsay and Bryan 2011). In 2014, 385 million metric tons were produced (FAO Stat 2014). Potato underwent a single domestication event in the Andean mountain range in Peru from the *Solanum bukasovii* Juz. species complex around 8,000 years ago (Spooner et al. 2005; Ramsay and Bryan 2011). There are a multitude of CWR in potato (Table 8.4), many of which have valuable resistance to the limiting factors to modern potato production, including diseases (e.g., blight, bacterial wilt, verticillium wilt), pests (potato beetle), and abiotic stress (Srivastava et al. 2016). These diverse CWR have been extensively used in potato improvement (Table 8.4), despite limitations of ploidy differences and different endosperm balance numbers. There is a long history of many different wild potato species being consumed, with many different species having specific uses (Ladio 2001).

8.4.2 Crop Wild Relatives and Wild Use

A recent examination of accessions of *Solanum* wild relatives in germplasm repositories found many species are in high need of further collection, including four native to North America: *S. clarum* Correll, *S. hintonii* Correll, *S. hjertingii* Hawkes, and *S. hougasii* Correll (Castañeda-Álvarez et al. 2015). Several species were further identified as having a moderate need for collection, including the North American species: *S. iopetalum* (Bitter) Hawkes, *S. lesteri* Hawkes & Hjert, *S. morelliforme* Bitter & Muench, *S. oxycarpum* Schiede, *S. polyadenium* Greenmam, *S. schenckii* Bitter, *S. tarnii* Hawkes & Hjert, and *S. verrucosum* Schltdl (Castañeda-Álvarez et al. 2015). Unfortunately, several of these same CWR are threatened by habitat destruction and climate change (Fig. 8.2). It is becoming increasingly important to conserve the species underrepresented in genebanks that are being impacted in their native habitats. Despite potato's economic importance and long history of CWR use, many of the CWR have not been evaluated for beneficial traits. Advances in pre-breeding, improved cisgenic techniques, and new genotyping and phenotyping methods will help to continue to unlock the agronomic potential found within these wild relatives, making their conservation ex situ more useful and efficient (Castañeda-Álvarez et al. 2015).

8.4.3 Conservation Status

The coverage of wild potato in ex situ collections is uneven, and better characterization of the many different potato species is needed. There have been extensive efforts to collect *Solanum* species in the United States; these collection efforts were

Table 8.4 Potato's crop wild relatives, genepool classification, and use in potato breeding

Gene pool	Taxon	Native N.A. countries[a]	Breeding use	Number of accessions conserved in NPGS[b]	Number of accessions conserved in PGRC[c]	Number of accessions conserved in BGCI[d]	Number of accessions conserved in GENESYS[e]	Ex situ conservation status[f]	Reference
Secondary	*Solanum agrimonifolium* Rydb.	M	NA	NA	NA	NA	NA	Poorly conserved	
Secondary	*Solanum clarum* Correll	M	NA	14	NA	1	18	Poorly conserved	
Secondary	*Solanum demissum* Lindl.	M	Blackleg and soft rot resistance, potato leaf roll virus resistance, late blight resistance, Colorado potato beetle resistance, cyst nematode resistance, frost tolerance, potato virus Y resistance, wart resistance	164	NA	2	665	Well conserved	Jansky (2000); Bradshaw et al. (2006); Hajjar and Hodgkin (2007); Jansky et al. (2013); Srivastava et al. (2016)
Secondary	*Solanum guerreroense* Correll	M	Spindle tuber viroid resistance	2	NA	1	14	Well conserved	Srivastava et al. (2016)
Secondary	*Solanum hintonii* Correll	M	NA	1	NA	1	2	Poorly conserved	
Secondary	*Solanum hjertingii* Hawkes	M	Blackleg and soft rot resistance, root knot nematode resistance, spindle tuber viroid resistance	13	NA	1	6	Poorly conserved	Jansky (2000); Srivastava et al. (2016)

(continued)

Table 8.4 (continued)

Gene pool	Taxon	Native N.A. countries[a]	Breeding use	Number of accessions conserved in NPGS[b]	Number of accessions conserved in PGRC[c]	Number of accessions conserved in BGCI[d]	Number of accessions conserved in GENESYS[e]	Ex situ conservation status[f]	Reference
Secondary	*Solanum hougasii* Correll	M	Root knot nematode resistance, potato virus Y resistance, late blight resistance	10	NA	1	116	Poorly conserved	Spooner and Bamberg (1994); Jansky (2000); Inglis et al. (2007)
Secondary	*Solanum iopetalum* (Bitter) Hawkes	M	Late blight resistance	60	NA	1	NA	Moderately conserved	Jansky (2000)
Secondary	*Solanum lesteri* Hawkes & Hjert.	M	NA	3	NA	2	NA	Moderately conserved	
Secondary	*Solanum morelliforme* Bitter & Munch	M	NA	20	NA	1	6	Moderately conserved	
Secondary	*Solanum oxycarpum* Schiede	M	NA	20	NA	1	NA	Moderately conserved	
Secondary	*Solanum polyadenium* Greenmam	M	Colorado potato beetle resistance, Late blight resistance	18	4	3	6	Moderately conserved	Srivastava et al. (2016)
Secondary	*Solanum schenckii* Bitter	M	NA	15	NA	1	2	Moderately conserved	

Secondary	*Solanum stoloniferum* Schltdl. & Bouche	M, U	Late blight resistance, potato virus Y resistance, aphid resistance, drought tolerance, heat tolerance, potato leaf roll virus resistance	485	1	3	2	Well conserved	Ross (1979); Bradshaw et al. (2006); Hajjar and Hodgkin (2007); Jansky et al. (2013); Srivastava et al. (2016)
Secondary	*Solanum verrucosum* Schltdl.	M	Late blight resistance	46	NA	2	4	Moderately conserved	Liu and Halterman (2009); Srivastava et al. (2016)
Tertiary	*Solanum bulbocastanum* Dunal	M	Blackleg and soft rot resistance, late blight resistance, root knot nematode resistance, aphid resistance, cyst nematode resistance, drought tolerance, early blight resistance, heat tolerance	56	NA	1	161	Well conserved	Jansky (2000); Hodgkin and Hajjar (2008); Suszkiw (2009); Srivastava et al. (2016)
Tertiary	*Solanum cardiophyllum* Lindl.	M	Late blight resistance, root knot nematode resistance, cyst nematode resistance	11	NA	2	78	Moderately conserved	Srivastava et al. (2016)
Tertiary	*Solanum ehrenbergii* (Bitter) Rydb.	M	NA	28	NA	1	38		

(continued)

Table 8.4 (continued)

Gene pool	Taxon	Native N.A. countries[a]	Breeding use	Number of accessions conserved in NPGS[b]	Number of accessions conserved in PGRC[c]	Number of accessions conserved in BGCI[d]	Number of accessions conserved in GENESYS[e]	Ex situ conservation status[f]	Reference
Tertiary	*Solanum jamesii* Torr.	M, U	Colorado potato beetle resistance, common scab resistance	165	NA	1	82	Well conserved	Srivastava et al. (2016)
Tertiary	*Solanum pinnatisectum* Dunal	M	Blackleg and soft rot resistance, chip making from cold, Colorado potato beetle resistance, drought tolerance, heat tolerance, late blight resistance	19	NA	1	NA	Moderately conserved	Srivastava et al. (2016)
Tertiary	*Solanum stenophyllidium* Bitter	M	Frost tolerance	25	NA	2	4	Moderately conserved	Srivastava et al. (2016)
Tertiary	*Solanum tarnii* Hawkes & Hjert.	M	Colorado potato beetle resistance, late blight resistance, potato virus X resistance	11	NA	1	2	Poorly conserved	Thieme et al. (2008)
Tertiary	*Solanum trifidum* Correll	M	NA	14	NA	1	24	Moderately conserved	

[a] Canada (C), Mexico (M), USA (U), according to USDA, ARS (2017)

[b] USDA, ARS (2017)

[c] AAFC (2017)

[d] BGCI (2017)

[e] Global Crop Diversity Trust (2014) GENESYS

[f] Based on occurrence points relative to distribution maps and published literature

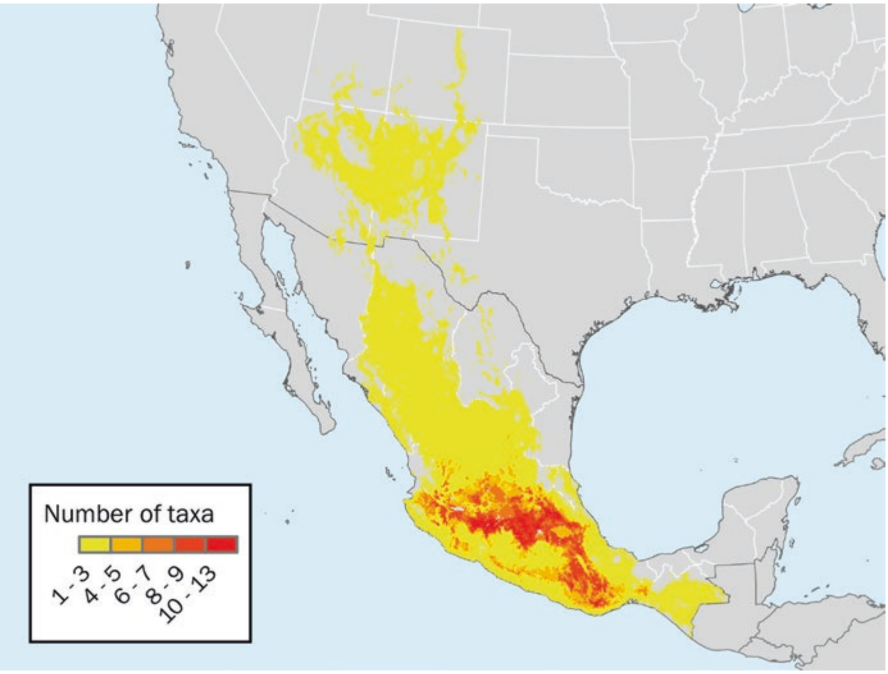

Fig. 8.2 Species richness map of modeled potential distributions of North American *Solanum* taxa, based on climatic and edaphic similarities with herbarium and genebank reference localities. Warmer colors indicate areas where greater numbers of taxa potentially occur in the same geographic localities. Full methods for generation of maps and data providers are given in Appendix 1

led by the USDA-ARS and have focused on *Solanum jamesii* (jam) and *S. fendleri* (fen) (Bamberg et al. 2016). There is only one member of the genus that is listed as of in situ conservation concern by NatureServe; *S. jamesii* is ranked as vulnerable (www.natureserve.org; NatureServe 2017).

8.5 Jerusalem Artichoke (*Helianthus tuberosus* L.)

8.5.1 Introduction

Jerusalem artichoke, the domesticated form of *Helianthus tuberosus* L., shows reduced tuber number and increased individual tuber size relative to wild collected individuals. *Helianthus tuberosus* is native to central North America (Kays and Nottingham 2008; Rogers et al. 1982) and was domesticated in the eastern United States. *Helianthus tuberosus* is an autoallohexaploid whose progenitors are likely the autotetraploid *H. hirsutus* Raf. (an autotetraploid of *H. divaricatus* L.) and the diploid *H. grosseserratus* Martens (Bock et al. 2014). Wild sunflowers have been collected for medicinal and food purposes since prehistory; the most common species to collect and eat are wild *H. tuberosus* and wild *H. annuus* L. (Kays and Nottingham 2008). Little is known about the extent of cultivation in North America prior to European contact due to a limited fossil record. The crop was introduced to the royal court of France in the seventeenth century and soon became a favorite of the European aristocracy (Kays and Nottingham 2008). Cultivation guides were published as early as the mid-eighteenth century (Brookes 1763), and production continued to increase until the potato largely replaced *Helianthus tuberosus* in diets. The crop is grown as a winter or summer annual. There has been little intentional interspecific introgression into domesticated *H. tuberosus*.

Helianthus tuberosus is widely resistant to both insect pathogens and diseases and has often been used as a donor species in *Helianthus annuus* (sunflower) breeding (Kantar et al. 2014). *Helianthus tuberosus* is also salt and drought tolerant and easily grown in coastal arid and semiarid areas (Ma et al. 2011) and has been used to improve soil and water conservation in desertified areas (Cheng et al. 2009). The native range of *Helianthus tuberosus* is quite large, ranging from the Mississippi River to the Atlantic Ocean and from the Gulf of Mexico to the Hudson Bay (Kantar et al. 2015). The large range provides many opportunities to find populations that are adapted to diverse climatic and biological stresses. When cultivated, *H. tuberosus* is planted using tuber parts and replanted every 3 years (Kays and Nottingham, 2008). A major limitation to production is that the species can become a volunteer weed in subsequent crops.

8.5.2 Crop Wild Relatives and Wild Use

Crop wild relatives within *Helianthus* have generally been defined with respect to *Helianthus annuus*, rather than *Helianthus tuberosus*, and are found throughout North America (Fig. 8.3). Despite this, the large species range of *Helianthus tuberosus*, the large number of species in the genus, and the large amount of hybridization within the genus make half of the species in the genus available for hybridization (Table 8.5). The major difficulty with the utilization of other *Helianthus* species is the difference in ploidy; this causes extra generations to be necessary in order to generate useful breeding material. The crop has excellent nutritional properties (Kays and Nottingham 2008), industrial applications (rubber; Seiler et al. 1991a, b, biofuel; Seiler and Campbell 2006), medicinal uses (diabetes treatment; Kays and Nottingham 2008), and forage potential (Seiler and Campbell 2004).

8.5.3 Conservation Status

Conservation priorities differ across the genus, with ~75% of the species needing further collection for ex situ conservation (Kantar et al. 2015). There are several species that are at risk including *Helianthus paradoxus* Heiser, which is ranked

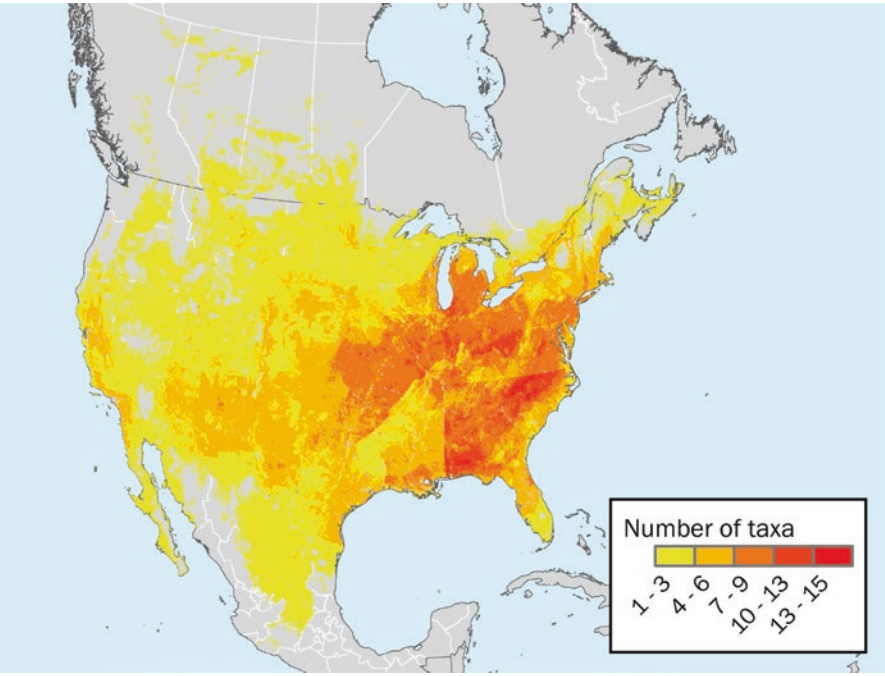

Fig. 8.3 Species richness map of modeled potential distributions of North American *Helianthus* taxa, based on climatic and edaphic similarities with herbarium and genebank reference localities. Warmer colors indicate areas where greater numbers of taxa potentially occur in the same geographic localities. Full methods for generation of maps and data providers are given in Appendix 1

threatened by the US Fish and Wildlife Service (ECOS 2016) and imperiled by NatureServe (www.natureserve.org; NatureServe 2017). *Helianthus neglectus* Heiser is ranked imperiled, and *Helianthus winteri* Stebbins is ranked critically imperiled by NatureServe (2017; www.natureserve.org). There are several species that are ranked vulnerable by NatureServe, including *H. anomalus* Blake, *H. debilis* spp. *tardiflorus* Heiser, and *H. debilis* subsp. *vestitus* Heiser (www.natureserve.org; NatureServe 2017).

8.6 Jicama (*Pachyrhizus erosus* (L.) Urb.)

8.6.1 Introduction

Jicama (*Pachyrhizus erosus* (L.) Urb.) is a tropical short day legume that is grown mostly in warm humid environments with intermediate levels of rainfall (Lim 2016). Indigenous to Mexico and Central America, jicama is now broadly grown across the tropics and neotropics (Reddy 2015). Other crops in the *Pachyrhizus*

Table 8.5 Crop wild relatives of *H. tuberosus* L. and potential breeding uses (the potential breeding uses of CWR are not well defined due to the high level of diversity both in ecological niche and biotic stress that is already present in *H. tuberosus*)

Gene pool	Taxon	Native N.A. countries[a]	Breeding use	Number of accessions conserved in NPGS[b]	Number of accessions conserved in PGRC[c]	Number of accessions conserved in BGCI[d]	Number of accessions conserved in GENESYS[e]	Ex situ conservation status[f]	Reference
Secondary	*H. annuus L.*	C, M, U	Pest, disease resistance, salt tolerance, drought tolerance, herbicide tolerance	3656	655	96	8539	Well conserved	Qi et al. (2012); Miller and Gulya (1988); Jyoti and Brewer (1999); Kane and Rieseberg (2007); Al-Khatib and Miller (2000); Miller and Al-Khatib (2002)
Secondary	*H. anomalus Blake*	U	NA	16	NA	3	12	Poorly conserved	NA
Secondary	*H. argophyllus Torr. & Gray*	U	Downy mildew resistance, disease resistance, salt tolerance, drought tolerance	79	NA	9	94	Moderately conserved	Seiler (1991a); Miller and Gulya (1988); Jan et al. (2004); Hulke et al. (2010); Seiler (1994)
Tertiary	*H. arizonensis Jackson*	U	NA	2	NA	1	5	Moderately conserved	NA
Tertiary	*H. atrorubens* L.	U	NA	12	NA	17	19	Moderately conserved	NA
Secondary	*H. bolanderi* A. Gray	U	NA	14	NA	4	20	Poorly conserved	NA

Secondary	*H. debilis* subsp. *cucmerifolius (Torrey & A. Gray*	U	NA	14	NA	NA	11	Poorly conserved	NA
Secondary	*H. debilis* subsp. *debilis Nutt.*	U	Powdery mildew resistance	13	NA	NA	12	Moderately conserved	Jan and Chandler (1988); Seiler (1991a)
Secondary	*H. debilis* subsp. *silvestris Heiser*	U	NA	22	NA	NA	24	Moderately conserved	NA
Secondary	*H. debilis* subsp. *tardiflorus Heiser*	U	Resistance to broomrape	13	NA	NA	9	Well conserved	Velasco et al. (2012)
Secondary	*H. debilis* subsp. *vestitus Heiser*	U	NA	11	NA	NA	3	Well conserved	NA
Secondary	*H. deserticola Heiser*	U	Downy mildew resistance	24	NA	1	24	Poorly conserved	Seiler (1991b)
Primary	*H. divaricatus* L.	C, U	Broomrape resistance	21	NA	30	50	Poorly conserved	Jan et al. (2002)
Secondary	*H. exilis* A. Gray	U	NA	30	NA	1	41	Moderately conserved	NA
Tertiary	*H. giganteus* L.	C, U	NA	26	NA	33	42	Poorly conserved	NA
Primary	*H. grosseserratus Martens*	U	Broomrape resistance	46	NA	21	69	Moderately conserved	Jan et al. (2002)
Primary	*H. hirsutus* Raf.	C, M, U	NA	14	NA	18	26	Poorly conserved	NA
Tertiary	*H. maximiliani* Schrader	C, U	Broomrape resistance	68	3	27	84	Moderately conserved	Whelan and Dedio (1980); Jan et al. (2002)
Secondary	*H. neglectus* Heiser	U	NA	40	NA	1	41	Well conserved	NA

(continued)

Table 8.5 (continued)

Gene pool	Taxon	Native N.A. countries[a]	Breeding use	Number of accessions conserved in NPGS[b]	Number of accessions conserved in PGRC[c]	Number of accessions conserved in BGCI[d]	Number of accessions conserved in GENESYS[e]	Ex situ conservation status[f]	Reference
Secondary	*H. niveus* subsp. *canescens* A. Gray	M, U	NA	20	NA	NA	22	Poorly conserved	NA
Secondary	*H. niveus* subsp. *niveus* Benth.	M	NA	1	NA	5	14	Poorly conserved	NA
Secondary	*H. niveus* subsp. *tephrodes Heiser*	M, U	NA	11	NA	NA	11	Poorly conserved	NA
Secondary	*H. paradoxus* Heiser	U	Salt tolerance	13	NA	3	20	Well conserved	Seiler (1991a); Lexer et al. (2003); Lexer et al. (2004); Miller and Seiler (2003)
Tertiary	*H. pauciflorus* subsp. *pauciflorus* Nutt	C, U	Sclerotinia resistance	21	NA	NA	21	Poorly conserved	Miller and Gulya (1999); Jan et al. (2006)
Tertiary	*H. pauciflorus* subsp. *subrhomboideus* Nutt	C, U	NA	17	NA	NA	18	Poorly conserved	NA
Secondary	*H. petiolaris* subsp. *fallax* Heiser	U	NA	61	NA	NA	31	Poorly conserved	NA
Secondary	*H. petiolaris* subsp. *petiolaris* Nutt.	C, U	Verticillium resistance; disease resistance; sunflower moth resistance	126	NA	NA	107	Well conserved	Hoes et al. (1973); Rogers et al. (1984); Prescott-Allen and Prescott-Allen (1986); Seiler (1991a); Jan et al. (2004)

Secondary	*H. praecox* subsp. *hirtus* Heiser	U	NA	7	NA	NA	8	Well conserved	NA
Secondary	*H. praecox* subsp. *praecox* A. Gray	U	Downy mildew, rust, verticillium wilt and broomrape resistance; downy mildew resistance	8	NA	NA	10	Well conserved	Seiler et al. (1991a, b)
Secondary	*H. praecox* subsp. *runyonii* Heiser	U	NA	26	NA	NA	27	Well conserved	NA
Secondary	*H. resinosus*	U	NA	23	NA	5	34	Moderately conserved	NA
Tertiary	*H. salicifolius A. Dietr*	U	NA	19	NA	52	27	Moderately conserved	NA
Tertiary	*H. silphioides* Nutt.	U	NA	15	NA	2	16	Well conserved	NA
Tertiary	*H. strumosus* L.	C, U	NA	29	NA	33	46	Poorly conserved	NA
Secondary	*H. winteri* Stebbins	U	NA	NA	NA	NA	NA	Poorly conserved	NA
Primary	*H. tuberosus (wild)*	C, U	Broomrape resistance; sunflower moth resistance	91	7	106	331	Moderately conserved	Rogers et al. (1984); Seiler (2000)

[a] Canada (C), Mexico (M), USA (U), according to USDA, ARS (2017)
[b] USDA, ARS (2017)
[c] AAFC (2017)
[d] BGCI (2017)
[e] Global Crop Diversity Trust (2014) GENESYS
[f] Based on occurrence points relative to distribution maps and published literature

genus include ahipa (*Pachyrhizus ahipa* (Wedd.) Parodi) and Amazonian yam bean (*Pachyrhizus tuberosus* (Lam.) Spreng.) (USDA, ARS 2017). Worldwide, jicama is a minor crop, but locally it is favored as part of many different types of cuisine. Generally, the plant takes approximately 6 months from planting to tuber harvest (Reddy 2015). Tubers can be eaten raw or cooked, having similar food value to potatoes; the immature seedpods can also be eaten, but the mature seeds are not consumed (Lim 2016). There are many different pests that impact crop production, including leafhopper, whiteflies, mealy bug, thrips, termites, coffee bean weevil, and pod borer (Reddy 2015). The most damaging diseases are rust and sincama mosaic virus (Reddy 2015). For acreage to increase, improved agronomic traits and pest tolerance are needed.

8.6.2 Crop Wild Relatives and Wild Use

There is very limited data on CWR breeding uses due to the semidomesticated nature of the crop (Table 8.6). This lack of knowledge has led to lagging conservation efforts for the important wild relatives. However, since antiquity wild jicama has been collected and used as a crop (Bronson 1966), and recently it has increased in use as a specialty crop.

8.6.3 Conservation Status

In general, there is a need to increase the conservation of wild relatives of this species. Only one of the wild relatives is even moderately well conserved in ex situ germplasm collections, with the other species being poorly conserved (Table 8.6). These species have not been well explored for in situ vulnerability.

8.7 Cocoyam, Tannia, Yautia (*Xanthosoma sagittifolium (L.) Schott)*

8.7.1 Introduction

Cocoyam, tannia, and yautia are a few of the many synonymous names for the edible aroid crop *Xanthosoma sagittifolium* (L.) Schott grown in many tropical regions (Reddy 2015). Originating in the northern Amazon Basin in South America, this crop is now widely cultivated around the tropics (Quero-Garcia et al. 2010). Brought to Europe and Africa multiple times during the sixteenth and seventeenth centuries, it eventually was transported to Asia and Oceania by the nineteenth century

Table 8.6 Jicama/yam bean crop wild relatives, genepool classification and breeding uses

Gene Pool	Taxon	Native N.A. countries[a]	Breeding use	Number of accessions conserved in NPGS[b]	Number of accessions conserved in PGRC[c]	Number of accessions conserved in BGCI[d]	Number of accessions conserved in GENESYS[e]	Ex situ conservation status[f]	Reference
Primary	*Pachyrhizus erosus* (L.) Urb.	M	NA	7	NA	16	84	Moderately conserved	NA
Secondary	*Pachyrhizus ferrugineus* (Piper) M. Sorensen	M	NA	NA	NA	NA	1	Poorly conserved	NA
Secondary	*Pachyrhizus sp.*	M	NA	3	NA	NA	23	Poorly conserved	NA

[a] Canada (C), Mexico (M), USA (U), according to USDA, ARS (2017)

[b] USDA, ARS (2017)

[c] AAFC (2017)

[d] BGCI (2017)

[e] Global Crop Diversity Trust (2014) GENESYS

[f] Based on occurrence points relative to distribution maps and published literature

(Quero-Garcia et al. 2010). Cocoyam is often used as food when other sources of calories are unavailable. The traits important for cultivars include corm shape, plant architecture, plant size, corm color, and leaf color. Most of the cultivars are local heirloom types. One major limitation to production is cocoyam root rot disease; identifying resistance to this pathogen is the primary breeding objective (Reddy 2015). Currently there are a limited number of breeding programs, and breeding efforts have yet to see much success, possibly due to ploidy differences. In Cameroon, where cocoyam improvements were initiated, few viable seeds were produced (Tambong et al. 1997; Onokpise et al. 1999). DNA markers have been used to study cocoyam diversity; however, the genetic dissimilarity between the accessions was low, and the existing ex situ collection was deemed of limited value as a genetic resource (Quero-Garcia et al. 2010).

8.7.2 Crop Wild Relatives and Wild Use

Current understanding of the cocoyam genepool is limited to knowledge of species within the *Xanthosoma* genus (Table 8.7). Phenotypic characterization of current and newly collected accessions could prove most helpful for ongoing plant breeding. While cocoyam is an old crop (Bronson 1966), it is not frequently grown on a large scale; this has led to extensive wild crafting and use of different species interchangeably.

8.7.3 Conservation Status

Xanthosoma requires extensive collection; this group of species is very understudied despite a wide distribution across Mexico (Fig. 8.4). It is necessary to define many of the basic species relationships as well as how they can be used to improve cultivars. *Xanthosoma* species are either not well explored or secure in situ.

8.8 Cassava (*Manihot esculenta* Crantz)

8.8.1 Introduction

Cassava (*Manihot esculenta* Crantz) is widely cultivated in the tropics, currently providing the third highest number of calories after maize and rice (FAO Stat 2014). Cassava contains many valuable introgressions from wild relatives as there are few crossing barriers within the *Manihot* genus (Table 8.8). Cassava was domesticated ~5000 years ago in the American Tropics (Piperno and Holst 1998). There still remains

Table 8.7 Cocoyam, tannia, or yautia (*Xanthosoma sagittifolium* (L.) Schott) crop wild relatives, genepool classification, and breeding use

Gene pool	Taxon	Native N.A. countries[a]	Breeding use	Number of accessions conserved in NPGS[b]	Number of accessions conserved in PGRC[c]	Number of accessions conserved in BGCI[d]	Number of accessions conserved in GENESYS[e]	Ex situ conservation status[f]	Reference
Undefined	*Xanthosoma mexicanum* Liebm.	M	NA	NA	NA	4	1	Poorly conserved	NA
Undefined	*Xanthosoma narinoense* Bogner & L. P. Hannon	M	NA	NA	NA	NA	NA	Poorly conserved	NA
Undefined	*Xanthosoma obtusilobum* Engl.	M	NA	NA	NA	NA	NA	Poorly conserved	NA
Undefined	*Xanthosoma robustum* Schott	M	NA	NA	NA	21	5	Poorly conserved	NA
Undefined	*Xanthosoma wendlandii* (Schott) Standl.	M	NA	NA	NA	2	NA	Poorly conserved	NA
Undefined	*Xanthosoma yucatanense* Engl.	M	NA	NA	NA	NA	NA	Poorly conserved	NA

[a] Canada (C), Mexico (M), USA (U), according to USDA, ARS (2017)

[b] USDA, ARS (2017)

[c] AAFC (2017)

[d] BGCI (2017)

[e] Global Crop Diversity Trust (2014) GENESYS

[f] Based on occurrence points relative to distribution maps and published literature

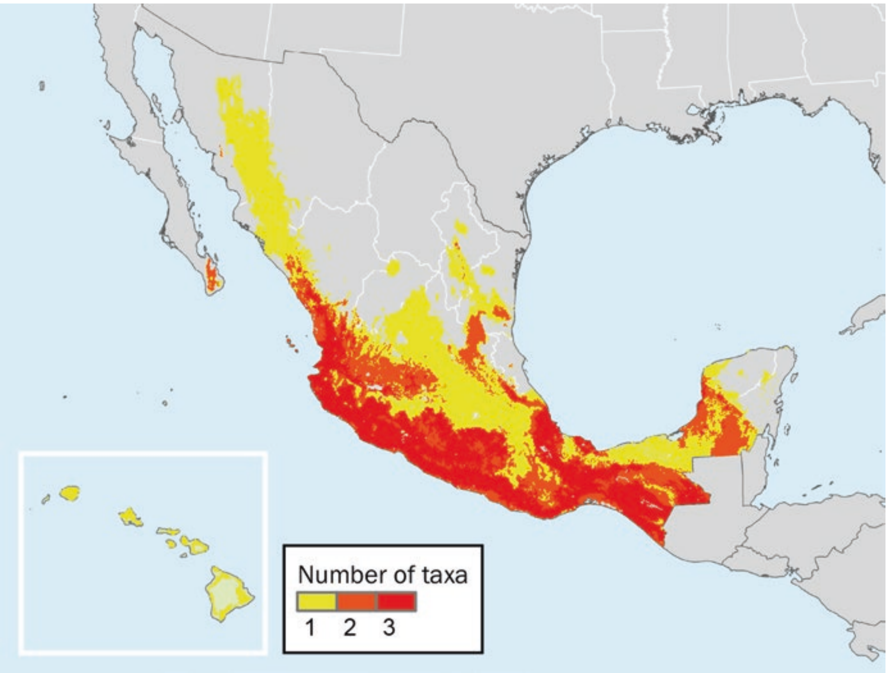

Fig. 8.4 Species richness map of modeled potential distributions of North American *Xanthosoma* taxa, based on climatic and edaphic similarities with herbarium and genebank reference localities. Warmer colors indicate areas where greater numbers of taxa potentially occur in the same geographic localities. Full methods for generation of maps and data providers are given in Appendix 1

debate over the precise geographic origin and if there was a single or multiple domestications (Bradbury et al. 2013; Olsen and Schaal. 1999). The oldest archeological evidence of cassava cultivation dates to 7000 years ago in the Andean and Caribbean regions (Piperno et al. 2000). Cassava was brought to Europe in the sixteenth century and made its way to Asia and Africa by the eighteenth century (Onwueme 2002). Although it is known for its good general drought tolerance and growth in low-nutrient environments, there are many problems that can decrease yields, including cassava mosaic virus, bacterial blight, and brown streak disease (Narina et al. 2011). Viruses can also impact propagation through affecting cuttings used for planting reducing vigor and therefore yield potential. There is limited use of wild relatives directly as food due to the presence of poisonous compounds (Nassar 1978).

8.8.2 Crop Wild Relatives and Wild Use

The closest wild relatives are *Manihot flabellifolia* Pohl and *M. peruviana* Müll. Arg, but many members of the secondary genepool are also believed to spontaneously cross with cultivated material, including *M. irwinii* D. J. Rogers & Appan, *M. pruinosa*

Table 8.8 Cassava's crop wild relatives, genepool classification, and use in cassava breeding

Gene pool	Taxon	Native N.A. countries[a]	Breeding use	Number of accessions conserved in NPGS[b]	Number of accessions conserved in PGRC[c]	Number of accessions conserved in BGCI[d]	Number of accessions conserved in GENESYS[e]	Ex situ conservation status[f]	Reference
Secondary	*Manihot foetida* (Kunth) Pohl	M	NA	NA	NA	1	NA	Poorly conserved	NA
Tertiary	*Manihot aesculifolia* Pohl	M	Robustness	NA	NA	1	NA	Poorly conserved	Jennings (1995)
Tertiary	*Manihot angustiloba* (Torr.) Müll. Arg.	M, U	Drought tolerance; gene transfer	NA	NA	1	NA	Poorly conserved	Jennings (1995); Narina et al. (2011)
Tertiary	*Manihot auriculata* McVaugh	M	NA	NA	NA	NA	NA	Poorly conserved	NA
Tertiary	*Manihot caudata* Greenm.	M	NA	NA	NA	3	NA	Poorly conserved	NA
Tertiary	*Manihot chlorosticta* Standl. & Goldman	M	Soil salinity tolerance	NA	NA	NA	5	Poorly conserved	Narina et al. (2011)
Tertiary	*Manihot crassisepala* Pax & K. Hoffm.	M	NA	NA	NA	NA	NA	Poorly conserved	NA
Tertiary	*Manihot davisiae* Croizat	M, U	Drought tolerance	NA	NA	1	NA	Poorly conserved	Jennings (1995)
Tertiary	*Manihot mcvaughii* Steinmann	M	NA	NA	NA	NA	NA	Poorly conserved	NA
Tertiary	*Manihot michaelis* McVaugh	M	NA	NA	NA	NA	NA	Poorly conserved	NA
Tertiary	*Manihot oaxacana* D. J. Rogers & Appan	M	NA	NA	NA	NA	NA	Poorly conserved	NA

(continued)

Table 8.8 (continued)

Gene pool	Taxon	Native N.A. countries[a]	Breeding use	Number of accessions conserved in NPGS[b]	Number of accessions conserved in PGRC[c]	Number of accessions conserved in BGCI[d]	Number of accessions conserved in GENESYS[e]	Ex situ conservation status[f]	Reference
Tertiary	*Manihot obovata* J. Jimenez Ram.	M	NA	NA	NA	NA	NA	Poorly conserved	NA
Tertiary	*Manihot pauciflora* Brandegee	M	NA	NA	NA	1	2	Poorly conserved	NA
Tertiary	*Manihot pringlei* S. Watson	M	Low cyanide content	NA	NA	NA	NA	Poorly conserved	Nassar et al. (2008)
Tertiary	*Manihot rhomboidea* Müll. Arg.	M	NA	NA	NA	1	NA	Poorly conserved	NA
Tertiary	*Manihot rhomboidea* Müll. Arg. subsp. *microcarpa* (Müll. Arg.) D. J. Rogers & Appan	M	NA	NA	NA	NA	1	Poorly conserved	NA
Tertiary	*Manihot rhomboidea* Müll. Arg. subsp. *rhomboidea* Müll. Arg.	M	NA	NA	NA	1	NA	Poorly conserved	NA
Tertiary	*Manihot rubricaulis* I. M. Johnst. subsp. *isoloba* (Standl.) D. J. Rogers & Appan	M	NA	NA	NA	NA	1	Poorly conserved	NA

Tertiary	*Manihot rubricaulis* I. M. Johnst. subsp. *rubricaulis* I. M. Johnst.	M	NA	NA	NA	NA	NA	Poorly conserved	NA
Tertiary	*Manihot rubricaulis* I. M. Johnst.	M	Cold tolerance	NA	NA	NA	1	Poorly conserved	Jennings (1995)
Tertiary	*Manihot subspicata* D. J. Rogers & Appan	M	NA	NA	NA	NA	NA	Poorly conserved	NA
Tertiary	*Manihot tomatophylla* Standl.	M	NA	NA	NA	NA	NA	Poorly conserved	NA
Tertiary	*Manihot triloba* (Sessé ex Cerv.) Miranda	M	NA	NA	NA	1	NA	Poorly conserved	NA
Tertiary	*Manihot walkerae* Croizat	M, U	Postharvest physiological deterioration tolerance	NA	NA	3	NA	Poorly conserved	CIAT (2006). CIAT Annual Report (2006). CIAT, Cali, Colombia
Tertiary	*Manihot websteri* D. J. Rogers & Appan	M	NA	NA	NA	NA	NA	Poorly conserved	NA

[a] Canada (C), Mexico (M), USA (U), according to USDA, ARS (2017)

[b] USDA, ARS (2017)

[c] AAFC (2017)

[d] BGCI (2017)

[e] Global Crop Diversity Trust (2014) GENESYS

[f] Based on occurrence points relative to distribution maps and published literature

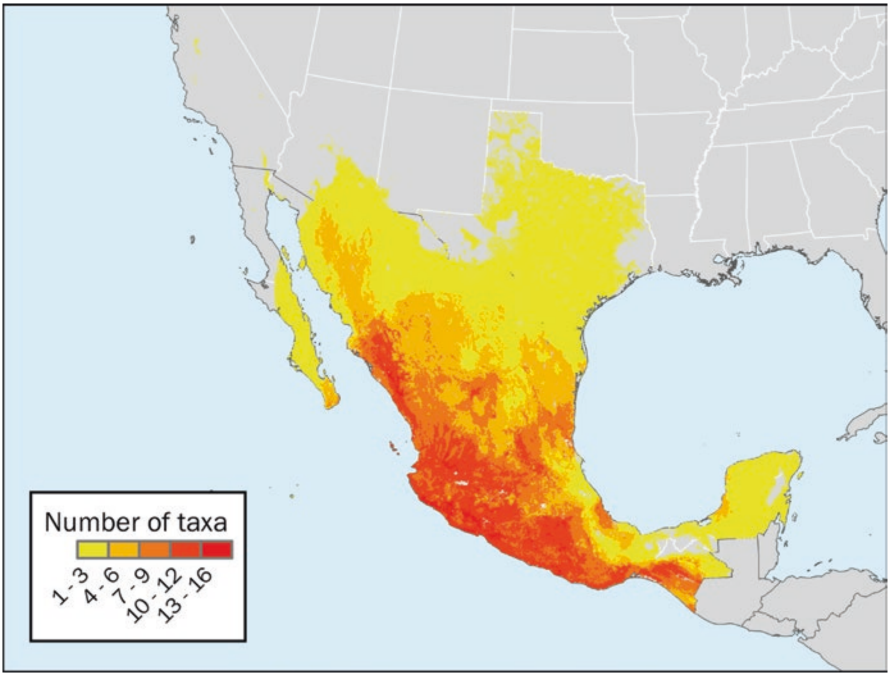

Fig. 8.5 Species richness map of modeled potential distributions of North American *Manihot* taxa, based on climatic and edaphic similarities with herbarium and genebank reference localities. Warmer colors indicate areas where greater numbers of taxa potentially occur in the same geographic localities. Full methods for generation of maps and data providers are given in Appendix 1

Pohl, *M. triphylla* Pohl, and *M. tristis* Müll. Arg (Allem et al. 2001). The wild relatives are distributed across southern North America (Fig. 8.5).

8.8.3 Conservation Status

The largest collection of cassava is housed at International Center for Tropical Agriculture (CIAT) consisting of 6024 accessions (Hershey 2010). Conservation and utilization can be improved by increasing the amount of information available on specific accessions to both conservationists and breeders. The wild relatives of cassava are all in need of further conservation; they are poorly represented in germplasm banks despite their well-characterized potential in breeding. *Manihot walkerae* Croizat is listed as endangered by the US Fish and Wildlife Service (ECOS 2016), as well as globally imperiled (critically imperiled in Texas) by NatureServe (www.natureserve.org; NatureServe 2017). The rest of the species are either secure or not well explored in situ.

8.9 Beet (*Beta vulgaris* L.)

8.9.1 Introduction

Beet (*Beta vulgaris* L.), termed "nature's candy" due to its high sugar content, is an important vegetable, leaf, and forage crop. Cultivated beet was domesticated from wild sea beet (*Beta vulgaris* L. subsp. *maritima* (L.) Arcang.), with references to its uses dating back to ancient Rome and China (Panella and Lewellen 2007; Biancardi 2005). Beet breeding for high sucrose production increased rapidly when Napoleonic France needed a source of sugar after their access to sugarcane was cut off by the British blockade (McGrath et al. 2011). The cultivated beet originated in the Mediterranean, but the *Beta* genus contains species that are located all over the world. Europe currently cultivates the most beets with the highest production concentrated in France, Germany, and Russia, although there is substantial production in North America (FAO Stat 2014). Sugar beet, currently the most profitable cultigen, is a hybrid utilizing a cytoplasmic male sterility system and is generally grown as a biennial. Due to the importance of sugar, initial breeding efforts focused almost solely on this trait, which led to many early varieties having poor insect and disease resistance.

8.9.2 Crop Wild Relatives and Wild Use

By the mid-twentieth century there were many systematic efforts to screen wild beet species from around the world for resistance to beet leafhopper, nematodes, and leaf spot disease (Panella and Lewellen 2007). Only a few beet relatives are commonly gathered in the wild and used in cuisine, and they are generally in the primary germplasm (Ghirardini et al. 2007). Only one species is native to North America (Table 8.9).

8.9.3 Conservation Status

Increased conservation efforts for the North American wild beet species are needed (Table 8.9); while many wild relatives have been used, there is room to better conserve and characterize this species. *Aphanisma blitoides* Nutt. ex Moq. is ranked globally vulnerable by NatureServe (www.natureserve.org; NatureServe 2017) and would benefit from in situ conservation in protected areas as well as ex situ conservation.

Table 8.9 Sugar beet crop wild relatives, genepool classification, and use in sugar beet breeding

Gene pool	Taxon	Native N.A. countries[a]	Breeding use	Number of accessions conserved in NPGS[b]	Number of accessions conserved in PGRC[c]	Number of accessions conserved in BGCI[d]	Number of accessions conserved in GENESYS[e]	Ex situ conservation status[f]	Reference
Tertiary	*Aphanisma blitoides* Nutt. ex Moq.	M, U	NA	NA	NA	NA	NA	Poorly conserved	NA

[a] Canada (C), Mexico (M), USA (U), according to USDA, ARS (2017)
[b] USDA, ARS (2017)
[c] AAFC (2017)
[d] BGCI (2017)
[e] Global Crop Diversity Trust (2014) GENESYS
[f] Based on occurrence points relative to distribution maps and published literature

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Part III
Fruits and Nuts

Chapter 9
North American Crop Wild Relatives of Temperate Berries (*Fragaria* L., *Ribes* L., *Rubus* L., and *Vaccinium* L.)

Kim E. Hummer, Karen A. Williams, and Jill M. Bushakra

Abstract The crop wild relatives of temperate berry species abound on the North American continent, where more than 180 species are endemic. The development and production of berry crops, such as strawberries (*Fragaria* L.), currants and gooseberries (*Ribes* L.), raspberries and blackberries (*Rubus* L.), and blueberries and cranberries (*Vaccinium* L.), have global economic importance. The cultivated crops derived from these species have a total global annual farm gate value of roughly USD $3.7 billion, with production on the rise. Global strawberry production is more than twice the combined production of other temperate berry crops. Berries are highly nutritious and positively impact consumer health and vitality. Significant North American genetic resources have contributed to the development and cultivation of these globally produced and consumed crops.

Keywords Germplasm · Genetic resources · Small fruit · Soft fruit · *Fragaria* · *Ribes* · *Rubus* · *Vaccinium* · Strawberries · Currants · Gooseberries · Raspberries · Blackberries · Blueberries · Cranberries

9.1 Introduction

The North American landscape is rich with endemic species that are crop wild relatives (CWR) of the berry crops of *Fragaria*, *Ribes*, *Rubus*, and *Vaccinium*. Compared to grain crops that have been cultivated for millennia, temperate berry crops are much younger; selection, development, and domestication of the berries

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K. E. Hummer (✉) · J. M. Bushakra
USDA, Agricultural Research Service,
National Clonal Germplasm Repository, Corvallis, OR, USA
e-mail: kim.hummer@ars.usda.gov; jill.bushakra@ars.usda.gov

K. A. Williams
USDA, Agricultural Research Service, Beltsville Agricultural Research Center,
National Germplasm Resources Laboratory, Beltsville, MD, USA
e-mail: karen.williams@ars.usda.gov

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began between 100 and 750 years ago, depending on the crop. More than 180 species are endemic to North America (Table 9.1). The primary, secondary, and tertiary gene pools of the berry species were delineated by Wiersema and León (2016) and are presented (Table 9.1). Maps of the geographic distribution of the North American berry taxa are provided.

9.2 Strawberries (*Fragaria* L.)

9.2.1 Origin and Brief History of Use

The genus *Fragaria* is a member of the rose family (Rosaceae) and includes 22 species worldwide (Liston et al. 2014), although some subspecific designations remain unresolved at the molecular level (Hokanson et al. 2006). The cultivated strawberry of present-day commerce, *Fragaria* × *ananassa*, has a North and South American origin and is recent for a globally cultivated economically important crop. Its hybrid origin is specifically documented between 1714 and 1759 (Staudt 1962). Antoine Duchesne (1766) was first to observe the accidental hybrid and name this species. The mother of the large-fruited strawberry was a white-fruited South American landrace of *F. chiloensis* (L.) Mill. subsp. *chiloensis* f. *chiloensis*, and the pollen parent was the small, red-fruited North American *F. virginiana* Mill. subsp. *virginiana*. The original pollen parent was likely brought to France from the St. Lawrence River Basin, either from Quebec or Nova Scotia, Canada, by either Samuel Champlain or Louis Hébert in the early 1600s (Desjardins, personal communication, 2016). Thus, it had been "waiting" in Europe for over 100 years before the arrival of the South American landrace. Both of these American strawberry species and the resulting accidental hybrid offspring are octoploid.

9.2.2 Modern-Day Use and Agricultural Importance

In 2014, about 8,114,373 MT of strawberries were produced in about 78 countries (UNFAO 2017). In 2014, the US strawberry crop of about 1.36 billion MT was valued at $2.9 billion, with the fresh market value comprising about 81% (value $2.6 billion) and the remainder (value $241.8 million) used for processing (USDA-NASS 2015). California leads the USA in strawberry production with about 68% of the acreage, followed by Florida (USDA-NASS 2015). However, because strawberries are highly perishable, they are grown widely throughout the USA. Strawberries rank as the fifth most popular fresh market fruit in the USA, with per capita consumption increasing steadily to 3 kg per year in 2010 (USDA-ERS 2010). The USA is followed by the other major producing countries of Spain, Turkey, Mexico, Egypt, Russian Federation, Japan, Republic of Korea, and Poland (UNFAO 2017).

Table 9.1 Taxa and ex situ conservation of temperate berry crop wild relatives

Genus	Taxon	Ploidy	Gene pool	Number of accessions in NPGS[a]	Number of accessions in PGRC (Canada)[b]	Number of accessions in BGCI[c]	Number of accessions in GENESYS[d]
Fragaria L.	*Fragaria cascadensis* K. E. Hummer	10	2	52		2	33
Fragaria L.	*Fragaria chiloensis* (L.) Mill.	8	1	18	829	43	169
Fragaria L.	*Fragaria chiloensis* (L.) Mill. subsp. *chiloensis* f. *chiloensis*	8	1	22			23
Fragaria L.	*Fragaria chiloensis* (L.) Mill. subsp. *chiloensis* f. *patagonica* Staudt	8	1	283			276
Fragaria L.	*Fragaria chiloensis* (L.) Mill. subsp. *lucida* (E. Vilm. ex Gay) Staudt	8	1	26			20
Fragaria L.	*Fragaria chiloensis* (L.) Mill. subsp. *pacifica* Staudt	8	1	38			35
Fragaria L.	*Fragaria chiloensis* L. subsp. *sandwicensis* (Decne.) Staudt	8	1	2			2
Fragaria L.	*Fragaria mexicana* Schltdl. (=*Fragaria vesca* f. *bracteata* (A. Heller) Staudt)	2	3			1	
Fragaria L.	*Fragaria vesca* L. subsp. *bracteata* (A. Heller) Staudt	2	3	75			58
Fragaria L.	*Fragaria vesca* L. subsp. *americana* (Porter) Staudt	2	3	15			18
Fragaria L.	*Fragaria vesca* L. f. *bracteata* (A. Heller) Staudt	2	3	2		1	58
Fragaria L.	*Fragaria vesca* L. subsp. *californica* (Cham. & Schltdl.) Staudt	2	3	11		5	10
Fragaria L.	*Fragaria virginiana* Mill.	8	1	246	186	58	376
Fragaria L.	*Fragaria virginiana* Mill. subsp. *glauca* (S. Watson) Staudt	8	1	56			52
Fragaria L.	*Fragaria virginiana* Mill. subsp. *grayana* (Vilm. ex J. Gay) Staudt	8	1	50			50
Fragaria L.	*Fragaria virginiana* Mill. subsp. *platypetala* (Rydb.) Staudt	8	1	26		6	49
Fragaria L.	*Fragaria virginiana* Mill. subsp. *virginiana*	8	1	62			58
Fragaria L.	*Fragaria* × *ananassa* Duchesne ex Rozier (cultivated)	8	1	575	781	24	1552
Fragaria L.	*Fragaria* × *ananassa* Duchesne ex Rozier nothosubsp. *ananassa*	8	1	1			
Fragaria L.	*Fragaria* × *ananassa* Duchesne ex Rozier nothosubsp. *cuneifolia*	8	1	58		6	21
Fragaria L.	*Fragaria* × *bringhurstii* Staudt	4, 5, 6, 9	2	16		1	16
Ribes L.	*Ribes acerifolium* Howell	2	3	3		1	3

(continued)

Table 9.1 (continued)

Genus	Taxon	Ploidy	Gene pool	Number of accessions in NPGS[a]	Number of accessions in PGRC (Canada)[b]	Number of accessions in BGCI[c]	Number of accessions in GENESYS[d]
Ribes L.	*Ribes affine* Kunth	2	3			2	
Ribes L.	*Ribes amarum* McClatchie	2	3	2		10	2
Ribes L.	*Ribes americanum* Mill.	2	2	9		61	12
Ribes L.	*Ribes aureum* Pursh	8	2	48	7	128	68
Ribes L.	*Ribes binominatum* A. Heller	2	1	3		1	3
Ribes L.	*Ribes bracteosum* Douglas	2	1	25		25	30
Ribes L.	*Ribes californicum* Hook. & Arn.	2	2			5	
Ribes L.	*Ribes californicum* var. *hesperium* (McClatchie) Jeps.	2	2	1		3	1
Ribes L.	*Ribes cereum* Douglas	2	2	32		28	54
Ribes L.	*Ribes cereum* Douglas var. *inebrians* (Lindl.) C. L. Hitchc. (=*Ribes cereum* var. *cereum*)	2	2			1	
Ribes L.	*Ribes cereum* Douglas var. *cereum*	2	2	1		4	3
Ribes L.	*Ribes cereum* Douglas var. *colubrinum* C. L. Hitchc.	2	2	2		1	1
Ribes L.	*Ribes ciliatum* Humb. & Bonpl. ex Willd.	2	2	1		2	2
Ribes L.	*Ribes coloradense* Coville (=*Ribes laxiflorum* Pursh)	2	2			1	
Ribes L.	*Ribes cruentum* Greene (=*Ribes roezlii* var. *cruentum* (Greene) Rehder)	4	2	1		3	4
Ribes L.	*Ribes curvatum* Small	2	2	3		2	3
Ribes L.	*Ribes cynosbati* L.	2	1	7		32	13
Ribes L.	*Ribes diacanthum* Pall.	4	2	3		35	6
Ribes L.	*Ribes divaricatum* Douglas	6	2	1	1	53	7
Ribes L.	*Ribes echinellum* (Coville) Rehder	2	3	3		8	3
Ribes L.	*Ribes erythrocarpum* Coville & Leiberg	2	3	4		2	19
Ribes L.	*Ribes glandulosum* Grauer	2	3	7		30	20

Ribes L.	*Ribes hirtellum* Michx.	2	1	2		18	4
Ribes L.	*Ribes hudsonianum* Richardson	2	1	9		23	60
Ribes L.	*Ribes hudsonianum* Richardson var. *petiolare* (Douglas) Jancz.	2	1	21		5	22
Ribes L.	*Ribes indecorum* Eastw.	2	2			12	2
Ribes L.	*Ribes inerme* Rydb.	2	2	18		10	27
Ribes L.	*Ribes inerme* Rydb. var. *klamathense* (Coville) Jeps.	2	2			1	
Ribes L.	*Ribes irriguum* Douglas (=*Ribes oxyacanthoides* subsp. *irriguum* (Douglas) Q. P. Sinnott)	2	2			3	
Ribes L.	*Ribes lacustre* (Pers.) Poir.	2	3	35		32	53
Ribes L.	*Ribes lasianthum* Greene	2	3			1	
Ribes L.	*Ribes laxiflorum* Pursh	2	2	8		16	11
Ribes L.	*Ribes leptanthum* A. Gray	2	2	3		11	6
Ribes L.	*Ribes lobbii* A. Gray	2	2	7		9	10
Ribes L.	*Ribes malvaceum* Sm.	2	2	5		23	8
Ribes L.	*Ribes menziesii* Pursh	2	2	3		15	3
Ribes L.	*Ribes mescalerium* Coville	2	2	3		1	3
Ribes L.	*Ribes missouriense* Nutt.	2	2	17		16	30
Ribes L.	*Ribes montigenum* McClatchie	2	2	8		10	17
Ribes L.	*Ribes nevadense* Kellogg	2	2	5		14	8
Ribes L.	*Ribes niveum* Lindl.	2	2	9		14	24
Ribes L.	*Ribes odoratum* H. L. Wendl. (=*Ribes aureum* var. *villosum* DC.)	2	1			74	2
Ribes L.	*Ribes oxyacanthoides* L.	2	1	3	1	14	5
Ribes L.	*Ribes oxyacanthoides* subsp. *irriguum* (Douglas) Q. P. Sinnott	2	1	5			5
Ribes L.	*Ribes oxyacanthoides* subsp. *setosum* (Lindl.) Q. P. Sinnott	2	1	1		4	1
Ribes L.	*Ribes pinetorum* Greene	2	2	2		5	2
Ribes L.	*Ribes quercetorum* Greene	2	2	6		6	9
Ribes L.	*Ribes roezlii* Regel	2	2	10		10	14

(continued)

Table 9.1 (continued)

Genus	Taxon	Ploidy	Gene pool	Number of accessions in NPGS[a]	Number of accessions in PGRC (Canada)[b]	Number of accessions in BGCI[c]	Number of accessions in GENESYS[d]
Ribes L.	*Ribes roezlii* var. *amictum* (Greene) Jeps.	2	2			2	1
Ribes L.	*Ribes roezlii* var. *cruentum* (Greene) Rehder	2	2	6		1	6
Ribes L.	*Ribes rotundifolium* Michx.	2	2	9		4	10
Ribes L.	*Ribes sanguineum* Pursh	2	1	29		85	38
Ribes L.	*Ribes sanguineum* Pursh var. *glutinosum* (Benth.) Loudon	2	1	2		18	4
Ribes L.	*Ribes sanguineum* Pursh var. *sanguineum*	2	1	2		5	4
Ribes L.	*Ribes speciosum* Pursh	2	2	2		47	5
Ribes L.	*Ribes thacherianum* (Jeps.) Munz	2	2	1		7	1
Ribes L.	*Ribes triste* Pall.	2	1	15		23	23
Ribes L.	*Ribes velutinum* Greene	2	2	4		4	8
Ribes L.	*Ribes viburnifolium* A. Gray	2	2	6		22	9
Ribes L.	*Ribes viscosissimum* Pursh	2	2	27		8	48
Ribes L.	*Ribes watsonianum* Koehne	2	2	1		6	3
Ribes L.	*Ribes wolfii* Rothr.	2	2	2		2	2
Rubus L.	*Rubus adenoleucus* Chaboiss.	2	3	2		1	3
Rubus L.	*Rubus allegheniensis* Porter	2, 3	1	39		29	47
Rubus L.	*Rubus alumnus* L. H. Bailey	3, 4	4	1		2	2
Rubus L.	*Rubus anglocandicans* A. Newton (introduced)	4	3	1		2	2
Rubus L.	*Rubus arcticus* L.	2, 3	1	4	1	33	8
Rubus L.	*Rubus arcticus* L. nothosubsp. *stellarcticus* G. Larss.	2	1	6			6
Rubus L.	*Rubus arcticus* L. subsp. *stellatus* (Sm.) B. Boivin	2	1			2	
Rubus L.	*Rubus arcticus* L. subsp. acaulis (Michx.) Focke	2	1			3	
Rubus L.	*Rubus arcticus* L. subsp. *arcticus*	2	1	7			7

Rubus L.	*Rubus arcticus* × *saxatilis*	2	1			1	
Rubus L.	*Rubus arcticus* × *stellatus*	2	1			1	
Rubus L.	*Rubus argutus* Link	2, 3, 4	1	7		3	9
Rubus L.	*Rubus arizonensis* (Greene.) Rydb.	0	1			1	
Rubus L.	*Rubus allegheniensis* Porter	2	2	39			
Rubus L.	*Rubus armeniacus* Focke (introduced)	4	1	25		3	26
Rubus L.	*Rubus baileyanus* Britton	?	2				1
Rubus L.	*Rubus bartonianus* M. Peck	4	3	3		2	2
Rubus L.	*Rubus canadensis* L.	2	1	17		4	17
Rubus L.	*Rubus chamaemorus* L.	8	1	29		23	48
Rubus L.	*Rubus cuneifolius* Pursh	2, 4	1	1		1	1
Rubus L.	*Rubus deliciosus* Torr.	2, 3	3	5		33	7
Rubus L.	*Rubus flagellaris* Willd.	4, 5, 7, 8, 9	2	12		19	14
Rubus L.	*Rubus frondosus* Bigelow	2, 3, 4	3			1	1
Rubus L.	*Rubus hawaiensis* A. Gray	2	3	14		4	15
Rubus L.	*Rubus hispidus* L.	2, 5, 8	2	11		12	15
Rubus L.	*Rubus idaeus* L. subsp. *strigosus* (Michx.) Focke	2	1	129			122
Rubus L.	*Rubus idaeus* L. var. *canadensis*	2	1			4	
Rubus L.	*Rubus idaeus* L. var. *strigosus* (Michx.) Focke	2	1		100	24	14
Rubus L.	*Rubus kennedyanus* Fernald	4	3	1		1	1
Rubus L.	*Rubus laciniatus* Willd. (introduced)	4	2	10		26	11
Rubus L.	*Rubus lasiococcus* A. Gray	2	3	10		1	14
Rubus L.	*Rubus leucodermis* Douglas ex Torr. & A. Gray	2	1	50		20	62
Rubus L.	*Rubus leucodermis* Douglas ex Torr. & A. Gray var. *bernardinus*	2	1			1	
Rubus L.	*Rubus leucodermis* Douglas ex Torr. & A. Gray var. *leucodermis*	2	1			1	
Rubus L.	*Rubus macraei* A. Gray	6	3			1	2

(continued)

Table 9.1 (continued)

Genus	Taxon	Ploidy	Gene pool	Number of accessions in NPGS[a]	Number of accessions in PGRC (Canada)[b]	Number of accessions in BGCI[c]	Number of accessions in GENESYS[d]
Rubus L.	*Rubus macvaughianus* Rzed. & Calderón	2	3	3		1	10
Rubus L.	*Rubus malifolius* (introduced)	?	3			3	
Rubus L.	*Rubus neglectus* Peck	2	1	15			15
Rubus L.	*Rubus neomexicanus* A. Gray	2	3	2		3	2
Rubus L.	*Rubus nivalis* Douglas	6	2	2		2	2
Rubus L.	*Rubus niveus* Thunb.	2, 4, 5	2	16		10	26
Rubus L.	*Rubus occidentalis* L.	2	2	227		30	260
Rubus L.	*Rubus odoratus* L.	2	3	11		125	18
Rubus L.	*Rubus parviflorus* Nutt.	2	3	32	1	69	42
Rubus L.	*Rubus parvifolius* L. (introduced)	2	1	37		27	50
Rubus L.	*Rubus pedatus* Sm.	2	3	14		9	20
Rubus L.	*Rubus pensilvanicus* Poir.	4	3	1		8	2
Rubus L.	*Rubus phoenicolasius* Maxim. (introduced)	2	1	4		56	12
Rubus L.	*Rubus praecox* Bertol. (introduced)	4	3	2		1	2
Rubus L.	*Rubus procerus* auct. (=*Rubus armeniacus* Focke) (introduced)	4	3			1	
Rubus L.	*Rubus pubescens* Raf.	2, 4	3	2		12	3
Rubus L.	*Rubus recurvans* Blanch.	3	3				1
Rubus L.	*Rubus repens* (=*Dalibarda repens* L.)	?	3			1	
Rubus L.	*Rubus riograndis* L. H. Bailey	4	2	1		1	1
Rubus L.	*Rubus semisetosus* Blanch.	?	3			1	1
Rubus L.	*Rubus spectabilis* Pursh	2	3	54	9	57	58
Rubus L.	*Rubus subtercanens* W.C.R. Watson (introduced)	2	3			1	1
Rubus L.	*Rubus trilobus* Ser.	2	2			5	

Rubus L.	*Rubus trivialis* Michx.	2, 3	1	25		7	29
Rubus L.	*Rubus ulmifolius* Schott (introduced)	4	2	25		34	64
Rubus L.	*Rubus ursinus* Cham. & Schltdl.	6, 8, 9, 10, 11, 12	1	84		17	79
Rubus L.	*Rubus urticifolius* Poir.	2	3	4		1	4
Rubus L.	*Rubus vermontanus* Blanch.	2	1	1		1	1
Vaccinium L.	*Vaccinium angustifolium* Aiton	4	1	61		75	66
Vaccinium L.	*Vaccinium arboreum* Marshall	2	1	30		32	42
Vaccinium L.	*Vaccinium boreale* I. V. Hall & Aalders	2	1	9		3	10
Vaccinium L.	*Vaccinium caesariense* Mack.	4	1	3		3	3
Vaccinium L.	*Vaccinium cespitosum* Michx.	4, 6	1	10		12	12
Vaccinium L.	*Vaccinium calycinum* Sm.	2	2	7		2	9
Vaccinium L.	*Vaccinium confertum* Kunth	2	3	1		3	
Vaccinium L.	*Vaccinium corymbosum* L.	2, 4, 6	1	290	18	133	494
Vaccinium L.	*Vaccinium crassifolium* Andrews	2	3	4		10	4
Vaccinium L.	*Vaccinium darrowii* Camp	2	1	44		9	83
Vaccinium L.	*Vaccinium deliciosum* Piper	4	2	11		8	12
Vaccinium L.	*Vaccinium elliottii* Chapm.	2	1	22		14	52
Vaccinium L.	*Vaccinium erythrocarpum* Michx.	2	3	7		6	6
Vaccinium L.	*Vaccinium formosum* Andrews	4	1	3		1	4
Vaccinium L.	*Vaccinium fuscatum* Aiton	2	1	22	1	17	26
Vaccinium L.	*Vaccinium hirtum* Thunb.	4	3	1		3	5
Vaccinium L.	*Vaccinium macrocarpon* Aiton	2	1	146	1	70	166
Vaccinium L.	*Vaccinium membranaceum* Douglas ex Torr.	2	1	71		20	81
Vaccinium L.	*Vaccinium myrsinites* Lam.	8	1	2		13	7
Vaccinium L.	*Vaccinium myrtilloides* Michx.	2	1	10		26	15

(continued)

Table 9.1 (continued)

Genus	Taxon	Ploidy	Gene pool	Number of accessions in NPGS[a]	Number of accessions in PGRC (Canada)[b]	Number of accessions in BGCI[c]	Number of accessions in GENESYS[d]
Vaccinium L.	*Vaccinium myrtillus* L.	2, 4, 6	1	43		98	332
Vaccinium L.	*Vaccinium ovalifolium* Sm.	4,6	1	93		36	117
Vaccinium L.	*Vaccinium ovatum* Pursh	2	3	35		48	41
Vaccinium L.	*Vaccinium oxycoccos* L.	2	3	77		66	203
Vaccinium L.	*Vaccinium pallidum* Aiton	2, 4	2	31		35	39
Vaccinium L.	*Vaccinium parvifolium* Sm.	2	3	38		29	49
Vaccinium L.	*Vaccinium reticulatum* Sm.	2	1	32		1	35
Vaccinium L.	*Vaccinium scoparium* Leiberg ex Coville	2	3	17		11	25
Vaccinium L.	*Vaccinium simulatum* Small	4	3	29		5	32
Vaccinium L.	*Vaccinium stamineum* L.	4	2	13		35	29
Vaccinium L.	*Vaccinium tenellum* Aiton	2	2	8		3	14
Vaccinium L.	*Vaccinium uliginosum* L.	2, (3), 4, 6	3	111	1	69	157
Vaccinium L.	*Vaccinium virgatum* Aiton	6	1	64	1	14	83
Vaccinium L.	*Vaccinium vitis-idaea* L.	2	1	108		116	184

[a] USDA, ARS (2017a)
[b] AAFC (2017)
[c] BGCI (2017)
[d] Global Crop Diversity Trust (2017)

9.2.3 Challenges in Cultivation: Pests, Diseases, and Edaphic and Climatic Limitations

Virus diseases are ubiquitous wherever strawberries are cultivated (Maas 1998). Extensive testing and certification programs have been developed for the strawberry nursery industry in many countries (Diekmann et al. 1994). The recommended procedures for detection of berry viruses include bioassays on indicator plants, sap and graft inoculation, enzyme-linked immunosorbent assay (ELISA), and double-stranded RNA detection with the polymerase chain reaction (PCR). Cultivated plantings should be started from certified pathogen-negative sources.

Common insects and diseases should be managed to maintain healthy and vigorous plants. Diekmann et al. (1994) and Maas (1998) describe symptoms, host range, geographical distribution, biology, and transmission of common strawberry diseases. Nearly 200 species of insects and mites have been reported to infect strawberry plants in North America (Maas 1998). Not only do arthropods cause direct plant damage, but they can also vector viruses and other diseases. Suggested control measures for arthropod pests combine cultural, biological, and chemical methods in an integrated plant production approach. These pests must be controlled in genebanks.

Abiotic stresses can be increased by factors as diverse as climate change and market dynamics. Changes in timing and duration of seasonal progressions can affect flowering time, movement of pollinators, and chilling hours.

9.2.4 Nutritional and Functional Use

Fresh strawberries are a low-calorie source of vitamin A, vitamin C, vitamin K, folate, potassium, dietary fiber, and polyphenols and other phytonutrients (USDA-NDL 2017). Most analytical biochemical studies of fruits have relied on specific extraction/separation methods to identify and quantify compounds of interest.

9.2.5 Crop Wild Relatives and Wild Utilized Species

9.2.5.1 Distribution, Habitat, and Abundance

Four strawberry species and two hybrid species are endemic to North America and Hawaii (Hummer et al. 2011; Lee 1964; Staudt 1999, 2009) (Table 9.1, Fig. 9.1). Strawberry species cover the North American landscape, ranging across Alaska and Canada in the north, along the western ocean beaches from Alaska through the fog zone of California, across the continent from West to East, and south through Mexico. *Fragaria chiloensis* (L.) Mill., the beach strawberry, is plentiful along sandy beaches of the Pacific Ocean from Alaska to California. *Fragaria chiloensis*

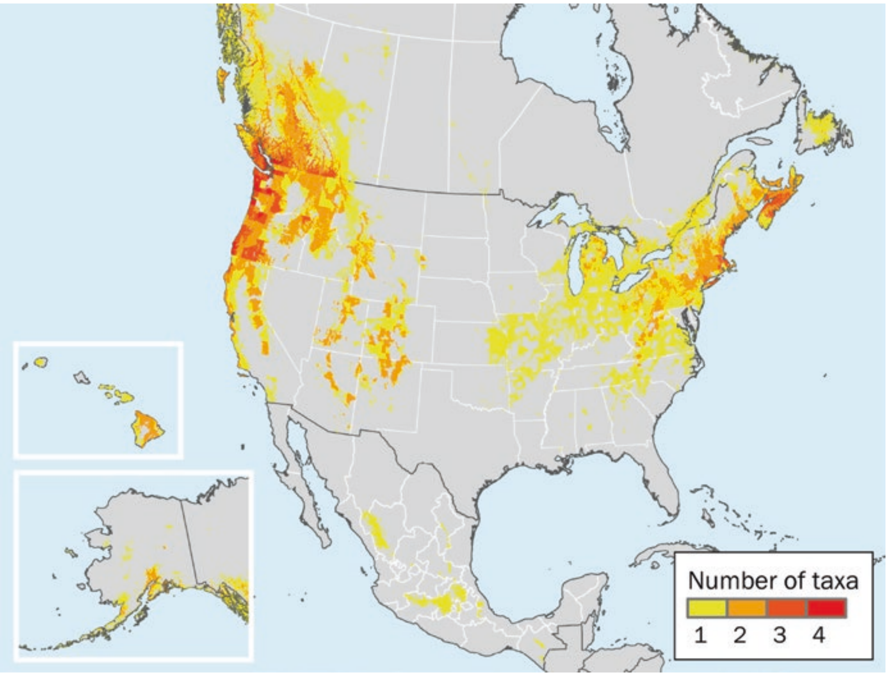

Fig. 9.1 Species richness map of modeled potential distribution of *Fragaria* taxa in North America, based on climatic and edaphic similarities with herbarium and genebank reference localities. Warmer colors indicate areas where greater numbers of taxa potentially occur in the same geographic localities. Full methods for generation of map and data providers are given in Appendix 1

(L.) Mill. subsp. *sandwicensis* (Decne.) Staudt is distributed in mountainous regions of the big island of Hawaii and on Maui (Staudt 1999). *Fragaria virginiana* Mill. is native throughout much of the USA and Canada.

Fragaria × *ananassa* Duchesne ex Rozier nothosubsp. *cuneifolia* (Nutt. ex Howell) Staudt is a natural hybrid of *F. chiloensis* (L.) Mill. subsp. *pacifica* Staudt or subsp. *lucida* (E. Vilm. ex Gay) Staudt and *F. virginiana* Mill. subsp. *platypetala* (Rydb.) Staudt (Staudt 1999) (Fig. 9.2). This hybrid has smaller leaves, flowers, and fruits than the cultivated strawberry. The distribution of *F.* × *ananassa* subsp. *cuneifolia* extends from the coastal regions of British Columbia (Vancouver Island), Canada, south to Fort Bragg and Point Arena lighthouse in California, USA. Hybrids of *F.* × *ananassa* subsp. *cuneifolia* and the two octoploids, *F. chiloensis* subsp. *pacifica* and *F. virginiana* subsp. *platypetala*, have been seen in Oregon, Washington, and California (Staudt 1999).

North American indigenous peoples used and consumed wild strawberries. Primarily, the whole plant of several species of strawberries, including the beach, the woodland (*F. vesca* L.), and the Virginia strawberries, were collected and used. Most of these plants were obtained for medicinal purposes. Moerman (2009) cites

Fig. 9.2 Flower and leaves of *Fragaria virginiana* Mill. subsp. *platypetala* (Rydb.) Staudt growing at the National Clonal Germplasm Repository, Corvallis, OR, USA. (Photo by K.E. Hummer, USDA ARS, 04/2011)

15 references for uses of strawberries by 11 tribes of indigenous peoples of North America. They were used as analgesic, antidiarrheal, dermatological, pediatric, gastrointestinal, kidney, liver, psychological, and sedative aids, as well as a remedy for toothache and a general disinfectant. Berries were also used as a deodorant. In some tribes the whole plant was kept in the home to ensure happiness. The plant was dried and used as a powder or poultice or prepared as a decoction of leaves or infusion of roots.

9.2.5.2 Utilization: North American Breeding Contributions

Research into trait discovery, including perpetual flowering and sex determination, in *Fragaria* species has been active since the eighteenth century (Richardson 1914). Many traits have been characterized, and genes associated with flowering (Gaston et al. 2013; Koskela et al. 2016), aroma, and flavor compounds (Chambers et al. 2014) have been cloned. Fruit firmness, a genetically complex trait, has been a focal point of many strawberry breeding programs during the past 50 years (Hancock et al. 2008b). As described by Salentijn et al. (2003), breeding to improve firmness and flavor simultaneously is a difficult task because of the inverse correlation between firmness and flavor volatiles. The increase in firmness developed through breeding has provided the industry with the capability to move fruit to the far reaches of the globe.

The flavor components of strawberries are complex. Schwab et al. (2009) summarize the genetic work concerning volatile and polyphenolic compounds, including metabolic routes and associated genetic mechanisms. The concentration of polyphenols varies among strawberry species and cultivars. Some breeding programs monitor the levels of these compounds to ensure maintenance of the already high levels. Other breeding programs favor development of cultivars that support year-round production and have fruit with good flavor to encourage increased consumption of an already nutritious fruit. Colquhoun et al. (2012) describe consumer preferences for sweetness and complex flavor in strawberry fruit.

Genetic linkage maps of diploid (Davis and Yu 1997; Sargent et al. 2006; Sargent et al. 2004) and octoploid (Bassil et al. 2015; Lerceteau-Köhler et al. 2012; van Dijk et al. 2014; Zorrilla-Fontanesi et al. 2011) populations have been developed using various marker types and platforms. Robust markers for molecular fingerprinting of species have been developed (Chambers et al. 2013), and the genome of the diploid woodland strawberry (*F. vesca*) has been sequenced (Shulaev et al. 2011). These advances provide tools for research and breeding of improved strawberry cultivars.

Since the mid-1800s, the efforts of over 35 breeding programs in Europe and the USA have resulted in thousands of cultivars (Faedi et al. 2000). In the late 1900s, strawberry breeding programs began in Asian countries and Oceania (Darrow 1966). During the past two decades, with the advent of improved genotypes and efficient knowledge-based cultivation techniques, private strawberry companies have globalized and now provide strawberries to markets in high population centers around the world, 365 days of the year. This multi-billion dollar success is predicated on the initial and continued improvement of cultivars resulting from the incorporation of wild germplasm into advanced cultivars through breeding.

Important historical breeders include the California breeders Albert Etter, Earl Goldsmith, Harold Thomas, and Harold Johnson (Sjulin 2006; Wilhelm and Sagen 1974). Their significant founding clones “Shasta,” “Sierra,” “Lassen,” “Tahoe,” “Donner,” and “Heidi” became the parental cultivars for subsequent public and private breeding programs in California. In the 1950s, Royce Bringhurst assumed management of the University of California strawberry breeding program, which had moved to the University of California, Davis (Hancock 2006a). He and his collaborator Victor Voth in southern California began breeding for large berries on plants adapted to California growing conditions. Bringhurst discovered a day-neutral *F. virginiana* Mill. subsp. *glauca* (S. Watson) Staudt (Fig. 9.3) growing in Hecker Pass, Utah. The day-neutral trait enabled production of strawberry fruit every day of the year somewhere in California. Strawberry breeders throughout the nation and throughout the world obtained this germplasm to breed cultivars with this valuable trait.

Additional traits have been transferred from wild North American genetic resources, including resistance to red stele (*Phytophthora fragariae* var. *fragariae* Hickman) and the strawberry aphid, drought and salinity tolerance, and winter hardiness. Other valuable traits that could be donated from wild American germplasm include higher photosynthetic rate, lower fertilizer requirement, heat tolerance, and resistance to soil pathogens and to powdery mildew. Hancock et al. (2010)

Fig. 9.3 Flower, flower buds, and leaves of *Fragaria virginiana* Mill. subsp. *glauca* (S. Watson) Staudt growing at the National Clonal Germplasm Repository, Corvallis, OR, USA. (Photo by K.E. Hummer, USDA ARS, 04/2011)

evaluated many American octoploids for their potential to expand the *F.* × *ananassa* gene pool. Stegmeir et al. (2010) identified hybrid genotypes from CWR that had high values for fruit color, firmness, and soluble solids, among other traits.

9.2.6 *In Situ Conservation Status of CWR and WUS*

NatureServe ranks the Hawaiian strawberry, *Fragaria chiloensi*s subsp. *sandwicensis*, which is endemic on the islands of Maui and Hawaii, as globally imperiled (NatureServe 2017). The population sizes of *F. chiloensis* subsp. *lucida* (Fig. 9.4) and *F. vesca* L. subsp. *californica* (Cham. & Schltdl.) Staudt (Fig. 9.5), growing along the valuable California coast, are being reduced due to human encroachment and invasive species (Hancock, personal communication 2016).

9.3 Currants and Gooseberries (*Ribes* L.)

9.3.1 *Origin and Brief History of Use*

The genus *Ribes* is placed in the family Grossulariaceae (previously in Saxifragaceae) and includes about 150 species worldwide (Brennan 2008). Breeders have incorporated germplasm from about 18 species in the pedigrees of modern fruit cultivars of currants and gooseberries (Harmat et al. 1990). Additional species have commercial ornamental landscape application or potential.

Fig. 9.4 Flowers and leaves of *Fragaria chiloensis* (L.) Mill. subsp. *lucida* (E. Vilm. ex Gay) Staudt growing at the National Clonal Germplasm Repository, Corvallis, OR, USA. (Photo by K.E. Hummer, USDA ARS, 04/2011)

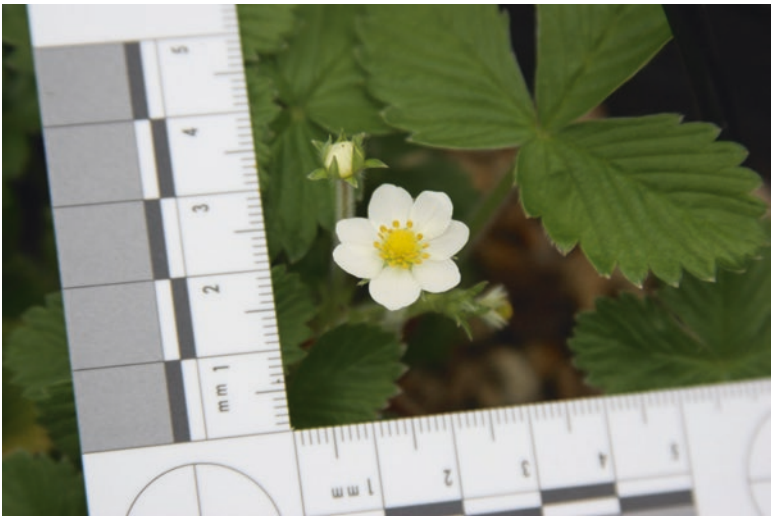

Fig. 9.5 Flower, flower buds, and leaves of *Fragaria vesca* L. subsp. *californica* (Cham & Schltdl.) Staudt growing at the National Clonal Germplasm Repository, Corvallis, OR, USA. (Photo by K.E. Hummer, USDA ARS, 04/2011)

Cultivated currants and gooseberries were initially derived from English and European species, although American species have been chosen as parents of the cultivated gooseberries to contribute disease resistance. For black currants, the primary species of commerce is *Ribes nigrum* L.; for red and white currants, *R. rubrum* L.; and for gooseberries, *R. uva-crispa* L.

The black currants were first selected for their fruits in the 1600s as recorded in early herbals (Brennan 1996). The first recorded cultivation of red and white currants for their fruit was in the 1400s and that of gooseberries in the 1200s. Recent improvements are the result of the crosses of black currant species with gooseberry species performed by Rudolf Bauer to produce the hybrid species *R.* × *nidigrolaria* Rud. Bauer & A. Bauer. "Josta," released in 1977, was the first of these types (Bauer 1986). Bauer released additional cultivars of this hybrid species so that cultivars of this group have become commonly known as jostaberries.

9.3.2 Modern-Day Use and Agricultural Importance

Globally, the most economically important *Ribes* crop is black currants. This crop is mechanically harvested for processing from intensive, large-scale farms, primarily in Russia, Ukraine, Poland, Austria, and France. World production varies from 500,000 to 600,000 MT annually with production in 2014 estimated at >659,000 MT (UNFAO 2017). The fruits are most often processed into juice, but other popular products include jams, jellies, liqueurs, and colorants used in yogurts and other dairy products. The main red currant producers are Poland and Germany. Germany, Russia, Poland, Ukraine, and the UK are the top producing countries for gooseberries with >170,000 MT produced in 2014. In North America, a small amount of acreage is used for growing black and red currants in Canada, the eastern USA, and Washington State, although not enough to be reported by the UNFAO (Hummer and Dale 2010).

9.3.3 Challenges in Cultivation: Pests, Diseases, and Edaphic and Climatic Limitations

While the major pest challenge for European black currant production is *Blackcurrant reversion virus*, this is not the case for North America. The European vector for this disease, the black currant gall mite [*Cecidophyopsis ribis* (Westw.)] (Adams and Thresh 1987), does not occur in North America (Brennan et al. 2009).

The key *Ribes* pest in North America is white pine blister rust (caused by *Cronartium ribicola* C J Fisher) (Barney and Hummer 2005). Originally from Asia, this rust was introduced into North America on infected white pine nursery stock in the late nineteenth and early twentieth centuries. It spread across North America during the early 1900s. This rust requires two co-hosts, a five-needle white pine and a currant or gooseberry, to complete its life cycle. To reduce infection of pines, *Ribes* production is prohibited or restricted by regulations in 12 states. Several black currant cultivars with resistance have been identified (Barney and Fallahi 2009; Barney and Hummer 2005).

Powdery mildew [*Podosphaera mors-uvae (Schwein.)*, formerly *Sphaerotheca mors-uvae*] is another primary problem in currant and gooseberry production plantations. Resistant cultivars are an effective control strategy. European gooseberries are most susceptible, followed by European black currants, American gooseberries, red and white currants, and jostaberries.

Common insect pests in North American *Ribes* and their origins include aphids [*Capitophorus ribis* L., North America and Europe; *Aphis grossulariae* Kalt., Europe; *Hyperomyzus pallidus* (H.R. L.) and *Nasonovia ribisnigri* (Mosley), Europe], currant borer (*Synanthedon tipuliformis*, North America), and gooseberry sawfly (*Nematus ribesii* Scop., North America).

9.3.4 Nutritional and Functional Use

Black currants are particularly rich in vitamin C, phenolics, anthocyanins, and other phytonutrients (Moyer et al. 2002). The primary anthocyanins present in black currants are 3-0-glucoside and 3-0-glutinoside. Black currant fruit extracts have been studied for use in cardiovascular health, as anticancer agents, to lower oxidative stress and postprandial glycemic responses (Mortaş and Şanlıer 2017).

9.3.5 Crop Wild Relatives and Wild Utilized Species

9.3.5.1 Distribution, Habitat, and Abundance

More than 50 *Ribes* species are native to North America (Table 9.1; Fig. 9.6). The Pacific Northwest in North America is a center of gooseberry species diversity.

Ribes species grow in a range of habitats in temperate woods and mountainous regions. They tend to be shade tolerant and can be found as elements of the understory in conifer forests and in disturbed sites along roadways and drainage ditches. Some species grow in moist areas or bogs.

Ribes species have been used medicinally for centuries. North American indigenous peoples used the fruits of wild currants and gooseberries as food, the inner bark as a poultice for sores and swelling, and the root for sore throats (Moerman 2009). *Gerard's Herbal*, an English herbal published in 1597, describes black and red currants and gooseberries and their medicinal uses (Woodward 1924).

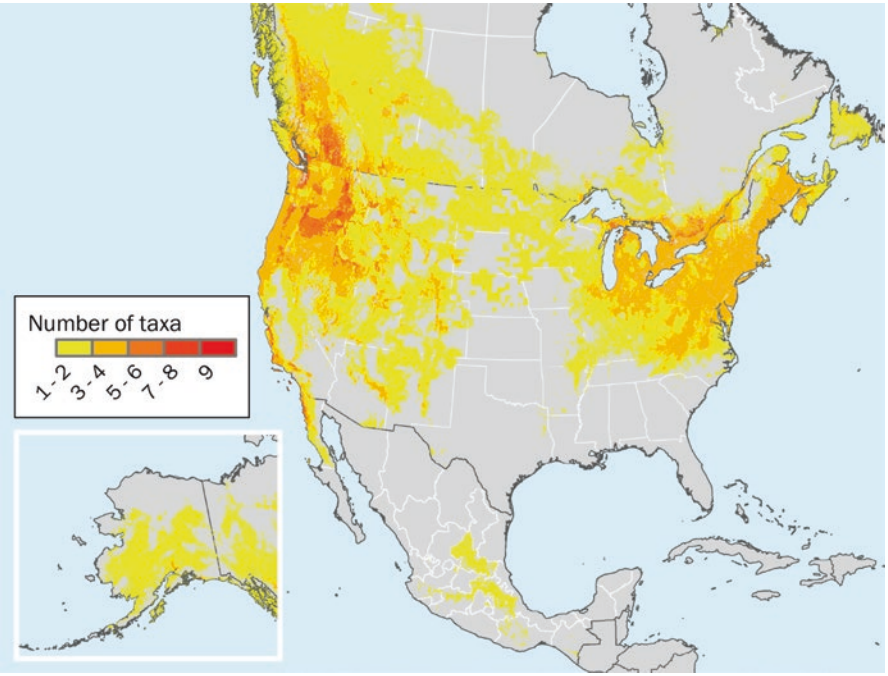

Fig. 9.6 Species richness map of modeled potential distribution of *Ribes* taxa in North America, based on climatic and edaphic similarities with herbarium and genebank reference localities. Warmer colors indicate areas where greater numbers of taxa potentially occur in the same geographic localities. Full methods for generation of map and data providers are given in Appendix 1

9.3.5.2 Utilization: North American Breeding Contributions

Active breeding programs are currently based in the UK, Russia, Poland, Estonia, Lithuania, and New Zealand (Brennan 2008). Early important cultivars include "Consort" from Canada that is resistant to white pine blister rust; "Laxton's No. 1," a red currant that is an important parent; and the "Ben" series of black currants from the UK breeding program in Scotland (Brennan 2008).

Genetic research into *Ribes* has revealed many species that have contributed key traits for improving cultivation (Barney and Hummer 2005; Brennan et al. 2009). The cluster length and yields of black currant cultivars have been improved by incorporating *Ribes bracteosum* Douglas ex Hook., the California black currant. *R. americanum* Mill. (Fig. 9.7), and the American black currant. These species also have the potential to provide powdery mildew resistance in interspecific hybrids (Brennan 2008). Other North American species that could broaden the gene pool are *R. hudsonianum* Richardson, the North American black currant, and *R. aureum* Pursh var. *villosum* DC. (Fig. 9.8), which has a large, sweet fruit that ripens much later than traditional black currant cultivars.

Fig. 9.7 Flowering branch of *Ribes americanum* Mill. growing at the National Clonal Germplasm Repository, Corvallis, OR, USA. (Photo by K.E. Hummer, USDA ARS, 04/2007)

Fig. 9.8 Flowering branch of *Ribes aureum* Pursh growing at the National Clonal Germplasm Repository, Corvallis, OR, USA. (Photo by K.E. Hummer, USDA ARS, 04/2007)

Fig. 9.9 (**a**) Flowering branch of *Ribes divaricatum* Douglas growing at the National Clonal Germplasm Repository, Corvallis, OR, USA. (**b**) Flower of *Ribes divaricatum* growing at the National Clonal Germplasm Repository, Corvallis, OR, USA. (Photos by K.E. Hummer, USDA ARS, 04/2007)

While the cultivated red currants have been derived from many European species (Barney and Hummer 2005), the North American red currant, *R. triste* Pall., has fruit quality similar to the European species but has not yet been utilized for breeding. The commercial gooseberry was primarily derived from the European gooseberry *R. uva-crispa* (synonym = *R. grossularia*) that is native to the UK. The North American gooseberry species *R. divaricatum* Douglas (Fig. 9.9), *R. hirtellum* Michx., and *R. oxyacanthoides* L. (Fig. 9.10) have contributed to improved disease resistance and decreased spines when bred with the larger fruited European species. Many North American gooseberry species have fuchsia-like flowers and are planted for their ornamental features (Brennan 1996).

Various methods have been used to develop molecular markers (Brennan et al. 2002; Cavanna et al. 2009; de Mattia et al. 2008; Russell et al. 2011, 2014) and to create linkage maps (Brennan et al. 2008; Russell et al. 2014) for *Ribes*.

Fig. 9.10 Flowering branch of *Ribes oxyacanthoides* L. growing at the National Clonal Germplasm Repository, Corvallis, OR, USA. (Photo by K.E. Hummer, USDA ARS, 04/2007)

9.3.6 In Situ Conservation Status of CWR and WUS

Ribes echinellum (Coville) Rehder, the Miccosukee gooseberry (Fig. 9.11), is listed as threatened by the US Fish and Wildlife Service (2015) and critically imperiled by NatureServe (2017). It is known only from the two localities of Jefferson County, Florida (USA), near Lake Miccosukee, and McCormick County, South Carolina (US); thus it is vulnerable to human encroachment and regional development in the areas. The PLANTS Database (USDA-NRCS 2017) lists 12 additional *Ribes* taxa of concern under state laws in a total of 13 states.

9.4 Raspberries and Blackberries (*Rubus* L.)

9.4.1 Origin and Brief History of Use

The genus *Rubus*, a member of the rose family (Rosaceae), is one of the most diverse in the plant kingdom. More than 740 named species have been divided into 15 subgenera, including artificial hybrid groups (USDA, ARS 2017a). Raspberries

Fig. 9.11 Flowering branch of *Ribes echinellum* (Coville) Rehder growing at the National Clonal Germplasm Repository, Corvallis, OR, USA. (Photo by K.E. Hummer, USDA ARS)

and blackberries are the economically important cultivated crops in the genus. Red raspberry cultivation for fruit became widespread in European countries by the sixteenth century (Jennings 1988). Red raspberries have been selected mostly from European species, but the American red raspberry subspecies, *R. idaeus* L. subsp. *strigosus* (Michx.) Focke (synonym = *R. strigosus* Michx.), has significantly contributed to the cultivated red raspberry gene pool. Black raspberry cultivars were developed from the eastern North American black raspberry, *R. occidentalis* L. Purple raspberries (hybrids of black raspberry with red raspberry) were also developed from American germplasm.

Blackberry species, while distributed in Europe and America, were most intensely selected and bred from the widely diverse forms of American species. Cultivars developed in the USA were derived from different multi-species, germplasm pools centered in either the Pacific coastal regions or east of the Rocky Mountains. Innovative breeding has produced hybrid berries, combining blackberry and raspberry species, despite great ploidy incongruities.

9.4.2 Modern-Day Use and Agricultural Importance

Russia, Poland, the USA, Serbia, and Mexico are the top producing countries for red raspberries, with >612,570 MT produced in 2014. Black raspberry production is much less, ~900 MT, and production is centered in Oregon (USDA-ERS 2018), although a great deal of fruit is grown or imported for production of liqueurs in Korea.

Blackberry production is not large enough to be recorded through the UNFAO statistical database. Strik et al. (2007) surveyed world production of blackberries and reported 140,292 MT in 2005, with production increasing. The central highlands of Mexico have seen a dramatic increase in production for export of off-season fresh fruit into the USA, and they are now the world's leading blackberry producer.

9.4.3 Challenges in Cultivation: Pests, Diseases, and Edaphic and Climatic Limitations

Spotted wing drosophila (*Drosophila suzukii* Matsumura), a recent introduction to berry production areas outside of eastern Asia, has become a devastating problem for many berry growers, especially those growing raspberries and blackberries (Bolda et al. 2010). At this time, there are no known sources of resistance in wild germplasm.

Virus diseases are found throughout *Rubus*-growing regions and can be transmitted via insects, nematodes, or pollen (*Compendium of Raspberry and Blackberry Diseases and Pests* 2017). In red raspberry, *Raspberry bushy dwarf virus*, verticillium wilt, phytophthora root rot, and powdery mildew are among the biggest disease concerns. Black raspberry growers face similar disease problems, and *Black raspberry necrosis virus* is a serious problem for growers.

Generally, blackberries have fewer devastating diseases than raspberries; however, in newer, generally warmer production areas, new-to-blackberry diseases such as *Fusarium oxysporum* Schltdl. 1824 (Gordon et al. 2015) have become a problem. Efforts are being made by the breeding community to identify and incorporate genetic sources of resistance to virus vectors, especially aphids (Bushakra et al. 2015; Dossett and Finn 2010; Dossett and Kempler 2012) and diseases.

High temperatures and/or intense ultraviolet light can injure ripening raspberry and blackberry fruit, and there is a genetic variability for tolerance to these stresses (Finn and Clark 2012). Breeding efforts are going into improving plant tolerances to heat, cold, and drought to expand and extend the growing range.

9.4.4 Nutritional and Functional Use

Raspberries and blackberries are low-calorie sources of dietary fiber, calcium, potassium, vitamin A, vitamin C, vitamin K, and folate (USDA-NDL 2017). Whole fruits and fruit extracts of the cultivated *Rubus* species have been shown to decrease cancer cell proliferation in animal models (Ash et al. 2011; Mace et al. 2014; Montrose et al. 2011; Rodrigo et al. 2006; Stoner et al. 2005, 2007; Zhang et al. 2011; Zikri et al. 2009).

9.4.5 Crop Wild Relatives and Wild Utilized Species

9.4.5.1 Distribution, Habitat, and Abundance

Rubus species are diverse in morphology, cytology, and genetics. The GRIN database lists 34 species native to North America. The *Rubus* treatment in the Flora of North America (Alice et al. 2015) reports 27 *Rubus* species native to North America, with eight species introduced from Europe or Asia (Table 9.1, Fig. 9.12). Because *Rubus* is one of the most taxonomically challenging of plant genera (Aalders and Hall 1966; Alice and Campbell 1999), many names of species have been published and submerged as synonyms. Species definition is complicated by hybridization, polyploidy, agamospermy, and lack of a universal species concept (Alice and Campbell 1999).

Indigenous peoples of North America have used *Rubus* species for a range of edible and medicinal purposes (Moerman 1996; USDA-NRCS 2017). For example, the bark and leaves of salmonberry (*R. spectabilis* Pursh) (Fig. 9.13) were used in various ways to relieve general pain and relieve labor pains and as an antiseptic (Stevens and Darris 2003).

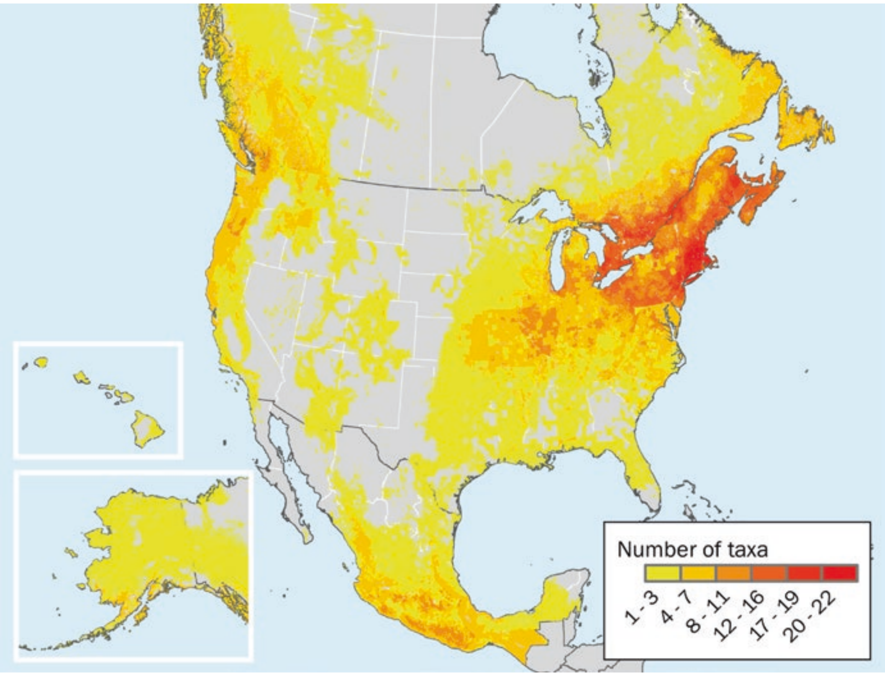

Fig. 9.12 Species richness map of modeled potential distribution of *Rubus* taxa in North America, based on climatic and edaphic similarities with herbarium and genebank reference localities. Warmer colors indicate areas where greater numbers of taxa potentially occur in the same geographic localities. Full methods for generation of map and data providers are given in Appendix 1

Fig. 9.13 Ripening fruit and leaves of *Rubus spectabilis* Pursh growing in the wild in Oregon. (Photo by K.E. Hummer, USDA ARS)

The many species of *Rubus* are adapted to different climates and growing conditions (Daubeny 1996; Thompson 1995). They can be found in the forest understories, disturbed habitats, and wetlands and are often pioneer species that can become weedy and invasive (Amsellem et al. 2001; Caplan and Yeakley 2013). At least eight European and Asian species have been introduced into North America and are now naturalized in the USA.

9.4.5.2 Utilization: North American Breeding Contributions

Public North American breeding programs for *Rubus* are based primarily at the University of Arkansas and the USDA-ARS in Corvallis, Oregon. Newer public breeding programs are housed at the University of North Carolina; the USDA-ARS in Poplarville, Mississippi; and Agriculture and Agri-Foods Canada in Agassiz, British Columbia. Important early North American cultivars include red raspberry “Lloyd George,” “Early Red,” “Meeker,” “Washington,” and “September”; black raspberry “Munger” (Fig. 9.14), “Jewel,” and “Bristol”; and blackberry “Brazos,” “Darrow,” “Thornfree,” and “Eldorado” (Jennings 1988).

Of the 34 species listed in GRIN-Global as native to North America, 15 have been used in breeding (USDA, ARS 2017b). While the predominant germplasm resource for the development of the cultivated red raspberry has been the European *R. idaeus*, North American *R. idaeus* subsp. *strigosus* crosses freely with this material and has been a source of disease resistance and adaptive traits

Fig. 9.14 Fruit of black raspberry cultivar Munger. (Photo from USDA NCGR)

(Daubeny 1996; Jennings et al. 1991; Weber 2013). The germplasm pool used in black raspberry breeding has been all North American in origin and was extremely narrow until recently (Dossett 2011; Dossett et al. 2012a, b; Weber 2003). Recent *R. occidentalis* collections and evaluations have brought a wealth of diversity for vegetative and reproductive traits as well as aphid resistance, which can convey virus resistance, into breeding programs (Bushakra et al. 2015; Dossett 2011; Dossett and Finn 2010).

In the eastern USA, *R. allegheniensis* and *R. argutus* have been the primary species used to develop the erect and semi-erect-type blackberries, while in the west, *R. ursinus* has been the most important species contributing to the development of the trailing-type blackberries (Clark and Finn 2011; Clark et al. 2007; Finn 2001; Finn and Clark 2012). These North American raspberry and blackberry species have been collected and evaluated with varying degrees of rigor but provide a diverse and valuable source of germplasm that can readily be incorporated into advanced breeding material.

Breeding with these species has resulted in cultivars with introgressed traits from wild relatives. Current breeding programs are interested in improving fruit quality (flavor, skin firmness, color, color retention), postharvest characteristics (reduced fruit color reversion in blackberry, shelf life), yield, machine-harvest ability, and tolerance to biotic and abiotic stresses.

Research into trait discovery in *Rubus* species has been active since 1931. Studies were conducted on many species to identify if traits were controlled by single loci or controlled quantitatively (reviewed by Daubeny (1996)). Many traits have been characterized, although no genes have been identified. Recent advances in genome sequencing technologies are bringing us closer to gene discovery. The black raspberry genome sequence (VanBuren et al. 2016) and genetic linkage maps (Bushakra et al. 2015; Bushakra et al. 2012), red raspberry genetic linkage maps

(Graham et al. 2004; Sargent et al. 2007; Ward et al. 2013; Woodhead et al. 2010), and blackberry genetic linkage maps (Castro-Lopez et al. 2013) and expressed sequence tag libraries of *Rubus* sp. (Garcia-Seco et al. 2015; Lewers et al. 2008) are narrowing the focus for gene identification. Researchers now have a large molecular toolbox with which to address questions on genetics, genomics, and breeding of these important berry crops.

9.4.6 In Situ Conservation Status of CWR and WUS

The PLANTS Database (USDA-NRCS 2017) lists 17 *Rubus* species as having protected status in a total of 14 US states and Canadian provinces. *Rubus aliceae* L. H. Bailey is presumed to be globally extinct (NatureServe 2017). *Rubus bartonianus* M. Peck (Fig. 9.15), endemic to western Idaho and eastern Oregon, is ranked by NatureServe (2017) as globally imperiled. The two Hawaiian species, *Rubus hawaiensis* A. Gray (Fig. 9.16) and *R. macraei* A. Gray, are also ranked as globally imperiled. These two species are the only *Rubus* species endemic to the Hawaiian Archipelago, although five introduced species encroach upon their niche (Howarth et al. 1997; Morden et al. 2003).

Fig. 9.15 Flowering branch of *Rubus bartonianus* M. Peck collected from the Snake River Canyon, ID. (Photo by K.E. Hummer, USDA ARS)

Fig. 9.16 Flowers and ripening fruit of *Rubus hawaiensis* A. Gray growing in the wild. (Photo by J.D. Postman, USDA ARS)

9.5 Blueberries, Cranberries and Lingonberries (*Vaccinium* L.)

9.5.1 Origin and Brief History of Use

Vaccinium is a member of the heath family (Ericaceae). More than 450 *Vaccinium* species have been described in more than 31 subgenera (Song and Hancock 2011), although the taxonomy of the genus is controversial (Vander Kloet 2004). North American *Vaccinium* species have been improved through selection and breeding to become economically important cultivated crops (Brazelton and Young 2017).

The three main crops of commerce are blueberries (*V. corymbosum* L. and hybrids, *V. angustifolium* Aiton, and *V. virgatum* Aiton [synonym = *V. ashei* J.M. Reade]), cranberries (*V. macrocarpon* Aiton), and lingonberries (*V. vitis-idaea* L.); most of the *V. angustifolium* and *V. vitis-idaea* are harvested from managed wild stands. Blueberries were derived initially from section *Cyanococcus*, predominantly from selections and hybrids of *V. corymbosum*, the highbush blueberry); these North American-derived blueberries have been selected for many climatic regions and are now globally produced and grown. Selections of elite wild northern highbush blueberry (Coville 1921) led to the establishment of field plantations, and breeding to improve fruit production has been underway for the past 100 years. In the latter half of the twentieth century, breeders began to incorporate the southern US species *V. darrowii* Camp into breeding material to develop blueberries with a low chilling requirement (Hancock et al. 2008a). The development of blueberries that could be grown in no-chill or low-chill environments has been the most important development in blueberry since the release of the first cultivars 100 years ago as it has allowed the rapid expansion of the crop into new regions.

The American cranberry (*V. macrocarpon*), a diploid, is native to eastern North America. When colonists arrived in Massachusetts in 1614, they found and described these large-fruited cranberries growing on the peat bogs of Cape Cod (Eck 1990) and were taught by the indigenous peoples of the area to prepare food from them. The American cranberry was first domesticated and cultivated in Cape Cod in 1810. Breeding and research efforts have been conducted over the past 100 years for improvement of cranberry cultivation (Hancock et al. 2008a). Modern cultivated cranberries are wild selections of *V. macrocarpon* or cultivars specifically bred to be grown in managed bogs. Some efforts at field cultivation have been made but have not been successful on an ongoing large scale.

Most lingonberries (*V. vitis-idaea*) are harvested from the wild. While most cultivars are superior selections from the wild, cultivars have also been developed by breeding programs. This species is native in northern Canada and the USA. Cultivated production of lingonberries is under trial in the USA but has not been very successful.

Efforts to cultivate other native *Vaccinium* species, such as the oheloberry (*V. reticulatum* Sm.) (Figs. 9.17 and 9.18) and its wild relatives endemic to Hawaii, are in the early stages (Hummer et al. 2012).

9.5.2 Modern-Day Use and Agricultural Importance

In 2014, the USA, Canada, Mexico, Poland, and Germany were the top producing countries for blueberries, with a total of 525,621 MT. In 2014, a global total of 303 MT of cultivated and wild blueberries, valued at $824.9 million, were produced and utilized (USDA-NASS 2015). In 2015, the leading US state for production was Washington, followed by Oregon, Georgia, and Michigan (USDA-ERS 2018). Maine is the leading producer of lowbush “wild” blueberries that are gathered from managed native stands rather than cultivated fields. Fresh and processed wild blueberries were valued at $47.2 million in the USA in 2015.

In 2015, the value of the American cranberry crop was about $267 million (USDA-ERS 2018) for about 8.6 million barrels of fruit. Production was slightly higher in 2015 than in the previous year. Massachusetts, New Jersey, Oregon, Washington, and Wisconsin have the greatest production in the USA. This crop is now grown on approximately 40,000 acres (> 16,000 ha) across Canada and the northern USA (Song and Hancock 2011). Plantings are expanding in British Columbia, Michigan, Nova Scotia, Quebec, Chile, and Germany.

Fig. 9.17 Plant of *Vaccinium reticulatum* Sm. growing on lava in Hawaii, USA. (Photo by K.E. Hummer, USDA ARS)

9.5.3 Challenges in Cultivation: Pests, Diseases, and Edaphic and Climatic Limitations

Spotted wing drosophila (SWD) is the greatest threat to blueberry and other soft fruit production in the USA. There is a zero tolerance threshold for SWD larvae in fresh market fruit, and potential berry crop losses can be as high as $511 million annually in western states (Bolda et al. 2010). No one has yet found sources of resistance to this pest.

Throughout North America, blueberry production is threatened by many viruses that are regionally located. Some of the most important viruses include *Blueberry shoestring virus*, *Tomato ringspot virus*, *Tobacco ringspot virus*, *Blueberry leaf mottle virus*, *Blueberry red ringspot virus*, blueberry stunt phytoplasma, *Blueberry scorch virus*, and *Blueberry shock virus* (Martin et al. 2012).

Fig. 9.18 Branch with fruits and flowers of *Vaccinium reticulatum* Sm. growing at the National Clonal Germplasm Repository, Corvallis, OR, USA. (Photo by K.E. Hummer, USDA ARS)

In terms of climatic limitations in North America, blueberry germplasm has a range of environmental adaptations, with the exceptions of tolerance to the coldest regions of the north and to hot dry conditions. During the past 100 years, innovative breeders have combined North American CWR with the highbush blueberry to produce named cultivars for a range of environments. Blueberries were first selected from cold-hardy, northeastern-adapted elite clones from New Hampshire and New Jersey (Coville 1937). Now growers can plant blueberries throughout many climatic zones of North America, ranging from areas with minimum temperatures of about −40 °C to freeze-free locations when sufficient moisture is present. Breeders have been collaborating to evaluate mineral soil adaptation in blueberry cultivars (Scheerens et al. 1999a, b). Grafting cultivars onto mineral-adapted rootstock is another approach (Basey 2017).

Cranberry plants and fruit are affected by several major fungal diseases including root rots caused by *Phytophthora cinnamomi*; diebacks caused by *Phomopsis vaccinia*, *Fusicoccum putrefaciens*, and *Synchronoblastia crypta*; and leaf spots caused by *Pyrenobotrys compacta* and *Protoventuria myrtilli*. In addition, ringspot virus and false blossom phytoplasma reduce plant growth and yield. Insect pests include the black-headed fireworm *Rhopobota naevana* (Hübner), cranberry fruitworm

(*Acrobasis vaccinii* Riley), Sparganothis fruitworm (*Sparganothis sulfureana* Clemens), cranberry weevils (*Anthonomus musculus* Say), cutworms, and green and brown span worm.

9.5.4 Nutritional and Functional Use

Vaccinium fruits are a healthful and nutritious food for humans. The fruits are low in fat and salt content and contain only about 80 calories per cup. The berries contain phytonutrients called polyphenols including the pigments called anthocyanins. Blueberries have high contents of vitamin C, manganese, and dietary fiber and are preserved as jams, jellies, and syrups. The North American cranberry also has multiple health benefits linked to phytochemicals in the fruit (Neto et al. 2008).

9.5.5 Crop Wild Relatives and Wild Utilized Species

9.5.5.1 Distribution, Habitat, and Abundance

Crop wild relatives of blueberries are a diverse taxonomic group. The genus is polyphyletic (Kron et al. 2002), and species delineation is taxonomically complex (Song and Hancock 2011). A global taxonomic reassessment of the definition of the genus is needed. About 34 species of *Vaccinium* are indigenous to North America (Table 9.1, Fig. 9.19), many of which have been gathered from the wild for centuries by Native Americans.

Lowbush blueberry, sometimes called “wild” or “Maine” blueberry, is harvested from managed wild mixed stands of unselected *V. angustifolium* and *V. myrtilloides* Michx. genotypes throughout northeastern North America. While mostly grown in commercial fields today, *V. corymbosum* and *V. virgatum* were historically harvested by indigenous people, and pickers still harvest from the wild.

The little leaf cranberry, *V. oxycoccos* L., with a polyploid series from diploid to hexaploid, has a broad, circumboreal distribution. It is gathered from wild stands in Russia and Eastern Europe and across North America and, as in the cases of lingonberry and lowbush blueberry, has not undergone breeding for domestication.

Blueberry plants are shrubs, small trees, or vines that grow on acidic, sandy, peaty, or organic soils. They are pioneer plants, expanding in disturbed regions, on the edges of forests, where burning has occurred or where the upper tree story has been cut. Some temperate species, but not the highbush blueberry species, tend to grow in large clonal colonies with intricate, fibrous, and shallow rhizomes that can spread over large areas under forest or in open fields.

The American cranberry is a woody perennial vine that is found in sphagnum bogs, swamps, mires, wet shores, headlands, and upland meadows. It has a

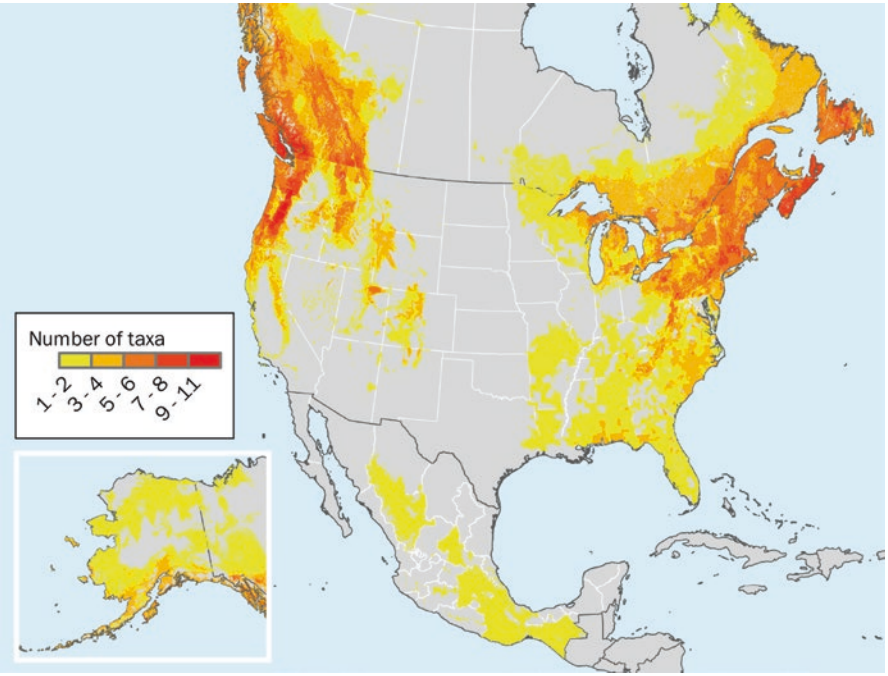

Fig. 9.19 Species richness map of modeled potential distribution of *Vaccinium* taxa in North America, based on climatic and edaphic similarities with herbarium and genebank reference localities. Warmer colors indicate areas where greater numbers of taxa potentially occur in the same geographic localities. Full methods for generation of map and data providers are given in Appendix 1

widespread distribution in eastern Canada and the northeastern and north-central USA, and south to the Appalachian Mountains of eastern Tennessee and North Carolina.

9.5.5.2 Utilization: North American Breeding Contributions

In North America, the highbush blueberry, *V. corymbosum* (Fig. 9.20), has been bred for 107 years, with significant historical contributions from Frederick Coville, George Darrow, and Arlen Draper (Hancock 2006b). Coville initiated highbush blueberry breeding in 1909 and produced "Bluecrop," "Jersey," and "Rubel" and many others. Darrow worked to understand the interspecific crosses and taxonomy. Arlen Draper extensively used native material in his crosses and was able to make crosses between individuals of different ploidy to produce, among others, the very important US 75 and "O'Neal." Breeders have chosen a wide range of species within section *Cyanococcus* to develop hybrids with the highbush blueberry that are adapted to a broad range of environments: from the cold north to hot climates without winter. The tetraploid lowbush blueberry, *V. angustifolium*, was crossed with the

Fig. 9.20 Fruiting shrub of *Vaccinium corymbosum* L. growing at the National Clonal Germplasm Repository, Corvallis, OR, USA. (Photo by K.E. Hummer, USDA ARS)

highbush to create half-high blueberries that survive winter by growing beneath the snow line. In contrast, southern-adapted species, such as *V. darrowii*, were incorporated to produce plants whose buds require much fewer dormant chilling hours to successfully break and develop. New "evergreen" production systems allow fruit development at any time throughout the year in subtropical-tropical locations. These interspecific crosses created cultivars that facilitated robust production from Canada to Mexico thanks to genes contributed from North American germplasm.

Northern highbush blueberries are primarily selected from elite plants of tetraploid *V. corymbosum* or crosses between them. Southern highbush blueberries are hybrids of the northern *V. corymbosum* crossed with a combination of southern species such as *V. darrowii* (Fig. 9.21), so that they are adapted to conditions with fewer winter chilling hours. Rabbiteye blueberries are selections of *V. virgatum* that originally were bred and cultivated in southern North America but now are bred by a number of breeding programs and grown in other areas like the Pacific Northwest that are mild wintered, where they ripen extremely late.

Genetic research into *Vaccinium* species has led to the development of linkage maps for diploid (Rowland et al. 2014) and tetraploid (McCallum et al. 2016) blueberry populations based on various marker types (Bian et al. 2014; McCallum et al. 2016). The tetraploid blueberry genome has been sequenced and annotated (Gupta et al. 2015). The genome of cranberry has been sequenced (Polashock et al. 2014). Genetic linkage maps have been constructed for cranberry (Georgi et al. 2013) based on various marker types (Covarrubias-Pazaran et al. 2016; Fajardo et al. 2013; Schlautman et al. 2015).

Fig. 9.21 *Vaccinium darrowii* Camp growing in the wild in Florida. (Photo by Paul Lyrene, 05/2007)

Beginning in 1929, cultivars of the American cranberry were first bred by the United States Department of Agriculture-Agricultural Research Service (USDA-ARS) working with the New Jersey and Massachusetts Agricultural Experiment Stations. They began their breeding programs with selections from wild stands in Massachusetts, New Jersey, and Wisconsin. Today cranberry breeding efforts are focused on early fruit with a uniformly large size. Major cranberry breeding efforts continue in New Jersey, Wisconsin, and Massachusetts.

9.5.6 In Situ Conservation Status of CWR and WUS

The USDA Plants Database (USDA-NRCS 2017) lists 11 *Vaccinium* species, including *V. boreale* I.V. Hall & Aalders, northern blueberry, with some type of protected status in a total of 15 states. The limited distribution of *V. boreale* is protected in Maine and New York. Populations of *V. boreale* are not threatened in Canada (NatureServe 2017). *Vaccinium crassifolium* Andrews subsp. *sempervirens* (D. A. Rayner & J. Hend.) W. B. Kirkman & Ballington is listed as endangered in

Fig. 9.22 Bog of *Vaccinium macrocarpon* Aiton at Green Pond, George Washington National Forest, VA, USA. (Photo by K.A. Williams, USDA ARS)

South Carolina, where it is endemic, and ranked as critically imperiled by NatureServe (2017). *Vaccinium macrocarpon*, the American cranberry, is endangered in Illinois and threatened in Tennessee. The limited populations in these states warrant protection.

Vaccinium macrocarpon (Fig. 9.22) and *V. oxycoccos* (Fig. 9.23), the two native species of cranberry, are the focus of a project to identify sites for in situ conservation under the *US Forest Service(USFS)/Agricultural Research Service (ARS) Joint Strategic Framework on the Conservation and Use of Crop Wild Relatives in the United States*. Collaborators from the USFS, the USDA-ARS, and the University of Wisconsin have identified and documented populations of these species on National Forests and conducted population genetic analyses using molecular markers.

9.6 Ex Situ Conservation Status of CWR and WUS of Berry Species

The Multilateral System (MLS) of access and benefit sharing established by the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA 2017) covers genetic resources of the crops listed in its Annex 1. Strawberry, which was recognized as a crop of global horticultural significance, is

Fig. 9.23 Fruiting branch of *Vaccinium oxycoccos* L. from the Olympic Peninsula, WA, USA. (Photo by K.A. Williams, USDA ARS)

included, but the other berry crops are not because they were not recognized as globally significant in 2004 when the ITPGRFA was established. A global conservation strategy for strawberry genetic resources was developed through the cooperation of the Global Crop Diversity Trust, the Bioversity International, the International Society for Horticultural Science, and international scientists (Hummer 2008).

The largest ex situ collection of North American berry genetic resources is held at the US national berry genebank located at the USDA-ARS National Clonal Germplasm Repository (NCGR) in Corvallis, Oregon. Their collection includes a broad diversity of *Fragaria*, *Ribes*, *Rubus*, and *Vaccinium* of not only North American taxa (Table 9.1) but also representatives of global species and cultivars (Postman et al. 2006; USDA, ARS 2017a). Primary collections are maintained on-site as living plants. Backup secondary collections of subgroups are maintained in different forms. Medium-term tissue cultures are maintained on-site and remotely; meristems have been placed in cryogenic storage at the base location, USDA-ARS National Laboratory for Genetic Resource Preservation, Ft. Collins, CO, USA. Protocols for dormant bud preservation in cryopreservation are under research (Jenderek et al. 2011).

At the NCGR, primary collections of major taxa are maintained in containers in screenhouses or planted in the field. Seed lots are stored in −18 °C. Plants are tested for common viruses, viroids, and phytoplasmas as funding allows. Plant identity is checked by comparison with written description, review by botanical and horticultural taxonomic experts, and evaluation by molecular markers, such as simple sequence repeat markers. Single nucleotide polymorphism (SNP) markers and genotyping by sequencing (GBS) approaches are being tested.

The collections have been documented for accession, inventory, voucher images, and morphological and genetic observations on the Germplasm Resources Information Network (USDA, ARS 2017a). Accessions of more than 22,770 strawberry, 9,900 currant and gooseberry, 14,800 blackberry and raspberry, and 12,700 blueberry, cranberry, and lingonberry CWR have been distributed to international and domestic requestors from NCGR-Corvallis during the past four decades.

Other collections of berry genetic resources are conserved by the Canadian Clonal Genebank, botanic gardens in the Botanical Gardens Conservation International (BGCI) network, and genebanks whose holdings are listed in GENESYS (GCDT 2017) (Table 9.1). Other international genebanks have invested only limited conservation efforts for small fruit and temperate berry CWR.

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Chapter 10
Crop Wild Relatives of Grape (*Vitis vinifera* L.) Throughout North America

Claire C. Heinitz, Jake Uretsky, Jean C. Dodson Peterson, Karla G. Huerta-Acosta, and M. Andrew Walker

Abstract Although cultivated grapevines (*Vitis vinifera* L.) were domesticated from their closest relative in Central Asia, grape wild relatives from North America are vital due to their use as grafted rootstocks. Rootstocks derived from North American *Vitis* species are critical to the global wine, table, and raisin grape industries for resistance to the root pest phylloxera (*Daktulosphaira vitifoliae*). These rootstocks can also provide other benefits such as cold and drought tolerance, nematode and disease resistance, and control over vigor and phenology. Phylogenetic studies of the many *Vitis* species native to North America often disagree on the number of species and their boundaries, specifically in the Southwestern United States and Mexico. The wild vines are all dioecious and, with the exception of subgenus *Muscadinia* Planchon, interfertile – allowing for interspecific hybridization wherever ranges overlap. A better understanding of the relationships between North American *Vitis* species is needed to identify gaps in the current ex situ germplasm collections. Additionally, efforts must be made to safeguard dwindling populations of some species in their native environments. Conservation of these valuable genetic resources will ensure that grape breeders throughout the world have the necessary diversity to adapt to a changing environment.

Keywords Crop wild relatives · Grapevine breeding · Vitis · Genetic resources

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C. C. Heinitz (✉)
USDA Agricultural Research Service, National Arid Land Plant Genetic Resources Unit, Parlier, CA, USA
e-mail: claire.heinitz@ars.usda.gov

J. Uretsky · K. G. Huerta-Acosta · M. A. Walker
Department of Viticulture & Enology, University of California-Davis, Davis, CA, USA

J. C. Dodson Peterson
Wine and Viticulture, California Polytechnic State University, San Luis Obispo, CA, USA

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10.1 Introduction

Cultivated grapes are one of the most valuable and diverse horticultural crops in the world. As of 2013, grape production (for wine, fresh fruit, raisins, juice, and distilled products) accounted for over 5 billion dollars in annual revenue in the United States alone (USDA 2013). The most widely cultivated grape species, *Vitis vinifera* L., was domesticated in modern-day Northern Iran (Chataigner 1995; McGovern and Michel 1995; Zohary 1996; Zohary and Hopf 2000) between 6000 and 5000 BC during the Neolithic era (Amerine and Singleton 1977; Mullins et al. 1992; McGovern et al. 1996; McGovern 2013). *Vitis vinifera* was domesticated from its antecedent, *V. sylvestris*, which is now considered a subspecies of *V. vinifera* (Levadoux 1956; Mullins et al. 1992). Prior to domestication, wild *V. vinifera* ssp. *sylvestris* (C.C. Gmel) Hedi selections were found and collected along the banks of the Caspian and Black Seas (Zohary and Spiegel-Roy 1975; Ketsa and Verheij 1992) and in the region's semi-deciduous forests (Levadoux 1956; Arnold et al. 1998). The defining aspect of wild grapevine domestication was the selection of a hermaphroditic, rather than dioecious, mode of reproduction. This move to self-pollination in cultivated vines ensured high fruit set without the need for an external male (pollinator) vine. With the exception of rare mutations, cultivated *V. vinifera* is still unique among the near-universally dioecious wild *Vitis* species.

Following domestication, the Greeks and Phoenicians distributed cultivated vines as clonal cuttings across the rest of the Middle and Near East as well as Europe over the next few thousand years (Grassi et al. 2003; Arroyo-García et al. 2006). Distribution followed trade routes and the movement of civilizations, and during this period of expansion, the practice of grape growing and importance of wine became deeply integrated into various cultures and religions. Cortez introduced *V. vinifera* into the new world via Mexico about 1525 AD (Mullins et al. 1992). By the late 1600s, grape growing had spread across Latin America and north along the western coast of North America as Catholic missionaries cultivated grapes to supply sacramental wines (Mullins et al. 1992). During this time, European colonists were also introducing *V. vinifera* varieties from their home countries to the eastern coast of North America. Early plantings of *V. vinifera* vines in this area quickly died as a result of pests, diseases, and abiotic stress such as cold. The failure of *V. vinifera* caused the early settlers to look to the better-adapted wild grape species native to North America. This recognition eventually led to large-scale breeding efforts by the mid-nineteenth century to incorporate the pest and disease resistance of the American species with the high fruit and wine quality of the *V. vinifera*-derived varieties, resulting in a new class of grape cultivars called American hybrids in the United States and the hybrid direct producers in France.

Unfortunately, one of the unintended consequences of the movement of plant material between the New and Old World was the introduction of powdery (*Erysiphe necator* Schwein.) and downy mildew (*Plasmopara viticola* (Berk & Curt.) Berl. & de Toni) and the root pest phylloxera (*Daktulosphaira vitifoliae* Fitch) from North America into England in 1845 (Campbell 2006). The mildews and phylloxera devastated the European grape and wine industry. In 1873, phylloxera was also detected in a Sonoma county, California vineyard (Bioletti et al. 1921; Campbell 2006). Rootstock breeding programs began in response to the phylloxera invasion of Europe, as a way to combine the desirable fruit characteristics of *V. vinifera* with the resistance to phylloxera in the roots of North American *Vitis* species. These programs evaluated multiple wild species from North America and quickly became focused on two species that were easy to root and propagate from dormant cuttings, *V. riparia* Michaux and *V. rupestris* Scheel (Viala and Ravaz 1903; Bioletti et al. 1921). Later, *V. berlandieri* Planchon was also integrated into rootstock breeding programs as a response to the need for lime tolerance (Viala and Ravaz 1903). Rootstock selection today still revolves primarily around *V. rupestris*, *V. riparia*, and *V. berlandieri* as pure species and in hybrid combinations.

Although it was widely assumed at the time that all native North American grapevine species would be equally resistant to phylloxera feeding, these initial rootstock breeding and establishment efforts soon discovered that some species were more resistant than others (Lider 1958). This prompted much of the initial evaluation work designed to classify the resistance and viticultural attributes of rootstocks by genetic parentage (Ramming 2010). The initial work on phylloxera resistance in California was supported by the State Viticulture Commission (Doyle 1894). This work resulted in the discovery that rootstock performance was greatly influenced by site, although a detailed classification of rootstock influence on scion attributes and characteristics was not thoroughly explored at that time.

A second era of rootstock and wild species evaluation began in California in the 1980s after the widely used but inadequately resistant rootstock AXR#1 (*V. vinifera* 'Aramon' x *V. rupestris* 'Ganzin') began failing to phylloxera (Granett et al. 1985, 1987). AXR#1's failure was due to the *V. vinifera* parentage in its background and the existence and selection of phylloxera strains capable of feeding aggressively on its root system. Wine grape growers were forced to replant the damaged acreage and select from a range of different phylloxera-resistant rootstocks with very little current knowledge as to the impact any given rootstock would have on scion growth and development. Current rootstock breeding is shifting to a focus on rootstock-scion interactions and expanding beyond phylloxera resistance.

In addition to the continued threat of phylloxera and fungal pathogens, the global expansion of viticulture into diverse environments has resulted in additional pressures such as nematodes, Pierce's disease (caused by an insect-vectored bacterium, *Xylella fastidiosa*; Wells et al. 1987), viruses and virus complexes, and the need for cold and drought tolerance. *Vitis vinifera*, though broadly adapted to conditions throughout Europe, does not carry tolerance or resistance to New World pests and diseases that have been spread throughout the world on plant material. For the industry to continue to thrive, new sources of resistance and mechanisms for tolerance must be identified and incorporated into both rootstock and scion breeding programs. Wild *Vitis* species from North America have coevolved with a broad range of pressures currently challenging the global viticulture industry and can continue to provide valuable traits for breeding. In addition to their value to the viticulture industry, many of these species have a long history of wild utilization by indigenous groups and present opportunities for the production of industrial and medicinal compounds. North American *Vitis* species have very high value, and their conservation and utilization present an opportunity for crucial contributions to global agriculture.

10.2 Grapevine Wild Relatives in North America

North America is home to about 30 species of wild *Vitis*, and recent studies have suggested that it is the center of origin of the genus (Wan et al. 2013). These species are all dioecious, and with the exception of subgenus *Muscadinia* from the Southeastern United States, all of the species are interfertile. This missing reproductive barrier encourages species diversity and has helped *Vitis* species to inhabit a wide range of environments throughout the continent. However, it has also created a complicated scenario of closely related species and interspecific hybrids in areas where ranges overlap. Despite several species descriptions for *Vitis* (Munson 1909; Brizicky 1965; Moore 1991), a detailed phylogenetic reconstruction of the genus has not yet been published.

Most of the species richness is concentrated in the Eastern United States (Fig. 10.1), with high levels of diversity in central Texas. Legendary viticulturist T.V. Munson first documented the rich diversity of *Vitis* species in Texas in his 1909 treatise, "Foundations of American Grape Culture" (Munson 1909). The number of morphologically distinct species that occur together across Texas is unprecedented globally, perhaps with the exception of certain areas of China. Texas is also critical to the history of rootstock breeding, as it has the only grape habitat in North America with significant limestone deposits. Limestone soils dominate the viticultural regions of Europe, and the first generation of rootstocks bred from *V. rupestris* and *V. riparia* was incapable of growing well on those soils. French grape breeders contacted Munson for advice, and he suggested the use of *V. berlandieri* (now *Vitis cinerea* (Engelm. in Gray) Engelm. ex Millardet var. *helleri* (Bailey) M.O. Moore), a species endemic to the limestone hills of central Texas. This led to the hybridization of this species with *V. riparia* and *V. rupestris* and the development of most of the rootstocks used around the world (Campbell 2006). Texas is also home to the only known grape species to grow away from any apparent permanent water source, *V. monticola* Buckley, and two species of suspected hybrid origin: *V.* X *champinii* Planchon and *V.* X *doaniana* Munson ex Viala (Munson 1909; Pavek et al. 2003).

Historical and current breeding efforts have focused on a relatively small group of species – these are profiled in detail below as either "rootstock species" (Fig. 10.2) or "scion species" (Fig. 10.3), though some overlap these categories. The majority of North American *Vitis* species are either less utilized or less understood, however, and fall under a more traditional definition of "crop wild relatives." They represent useful genetic diversity in traits of interest for breeding and could form the basis of future work but will only be introduced here in the interest of brevity (Table 10.1).

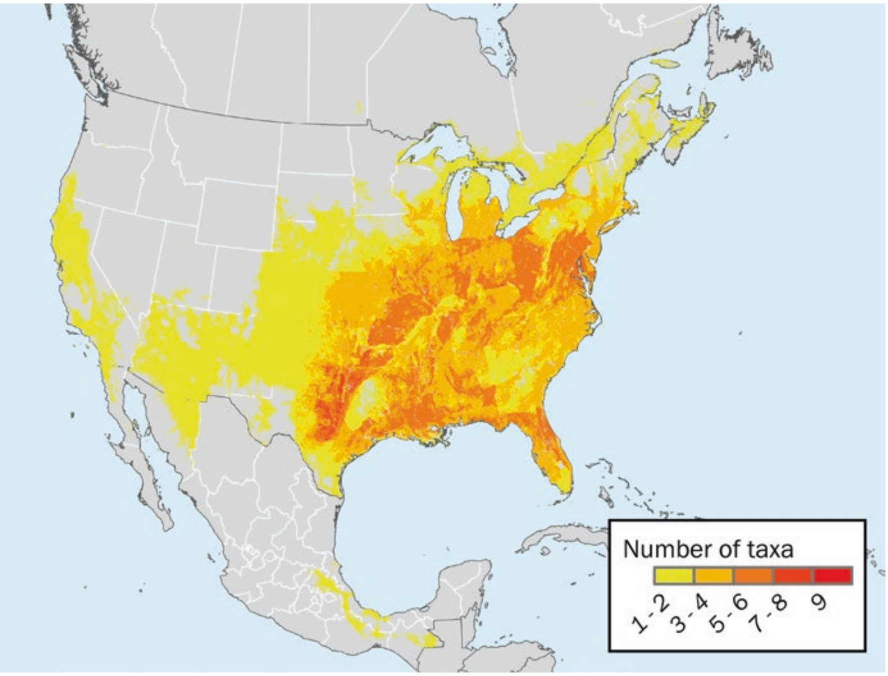

Fig. 10.1 Species richness map of modeled potential distributions of North American *Vitis*. The map displays overlapping potential distribution models for assessed taxa. Warmer colors indicate areas where greater numbers of taxa potentially occur in the same geographic localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

10.2.1 Rootstock Species

Vitis riparia It typically grows in moist, fertile soils near bodies of water. Its broad range extends across most of eastern North America: from the Rocky Mountains to the Atlantic Ocean, from northern Texas, Mississippi, and Louisiana to Southern Canada, and from New Brunswick to Saskatchewan (Pongracz 1983; Moore 1991). This species was essential in reestablishing European vineyards after the importation of phylloxera (Viala and Ravaz 1903; Pongracz 1983), and still many of the most important rootstocks in use today are derived from *V. riparia*.

Beyond phylloxera resistance, *V. riparia* is associated with several viticulturally significant traits. For example, rootstocks with *V. riparia* parentage (i.e., “101–14 Mgt”) exhibit relatively early phenology compared with other *Vitis* species and are associated with early ripening of berries and early senescence (Dodson Peterson and Walker 2017). In addition, the low vigor associated with *V. riparia* is frequently exploited in choosing rootstocks for vineyard sites with deep, moist, fertile soil to restrict scion vigor and maintain high fruit quality.

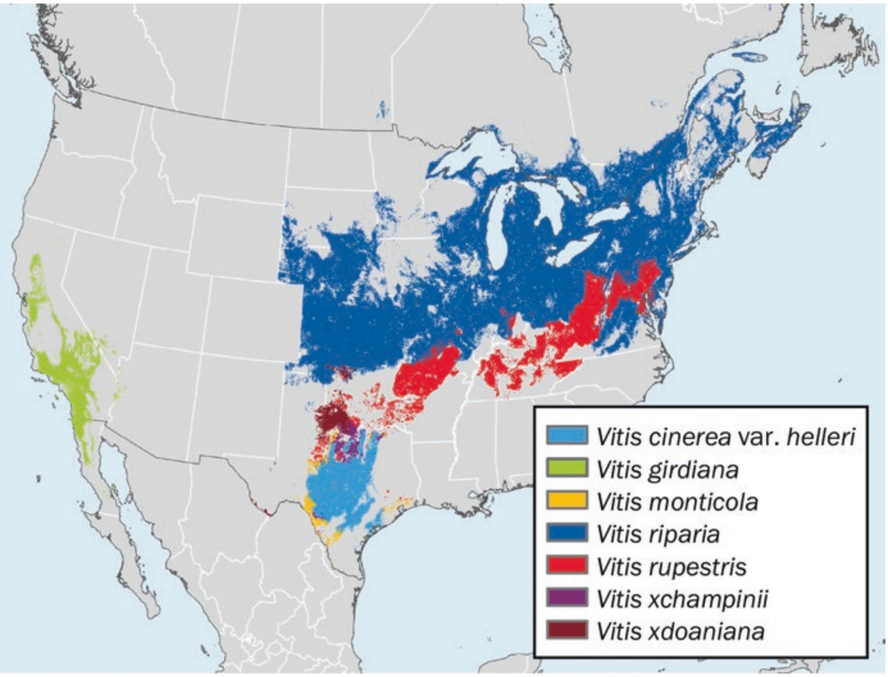

Fig. 10.2 Modeled potential distribution of *Vitis* species used in rootstock breeding: *V. riparia* Michx., *V. rupestris* Scheele, *V. cinerea* (Engelm.) Millardet var. *helleri* (L. H. Bailey) M. O. Moore, *Vitis xchampinii* Planch., *V. girdiana* Munson, *V. xdoaniana* Munson ex Viala, and *V. monticola* Buckley, based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

The exceptional range of this species has resulted in a broad adaptation to various environmental conditions, particularly in temperature. In fact, Viala and Ravaz (1903) reported that specimens were found in regions with low temperatures reaching −30 °C, an observation supported by the work of Pierquet and Stushnoff (1980), who tested the association of low temperature exotherms with the viability/death of primary and secondary buds in *V. riparia*. Most grape breeding programs focusing on developing scion cultivars for colder climates have utilized *V. riparia* in complex hybrids (Fisher 1980; Luby 1991), with newer cultivars developed at the University of Minnesota showing hardiness to almost −40 °C (Hemstad and Luby 2000). Interestingly, *V. riparia* accessions from more southerly locations might exhibit better winter hardiness than those from northerly locations, due to reduced response to temperature fluctuations during winter (Londo and Martinson 2015).

While *V. riparia* is generally considered drought sensitive, there is limited evidence for adaptation to drier conditions in some forms the species. For instance, the dune grape (*V. riparia* var. *syrticola*) is restricted to the dunes along the Great Lakes shoreline in Southern Ontario and might be a germplasm source for combined cold and drought tolerance (Catling and Mitrow 2005; Rahemi et al. 2016).

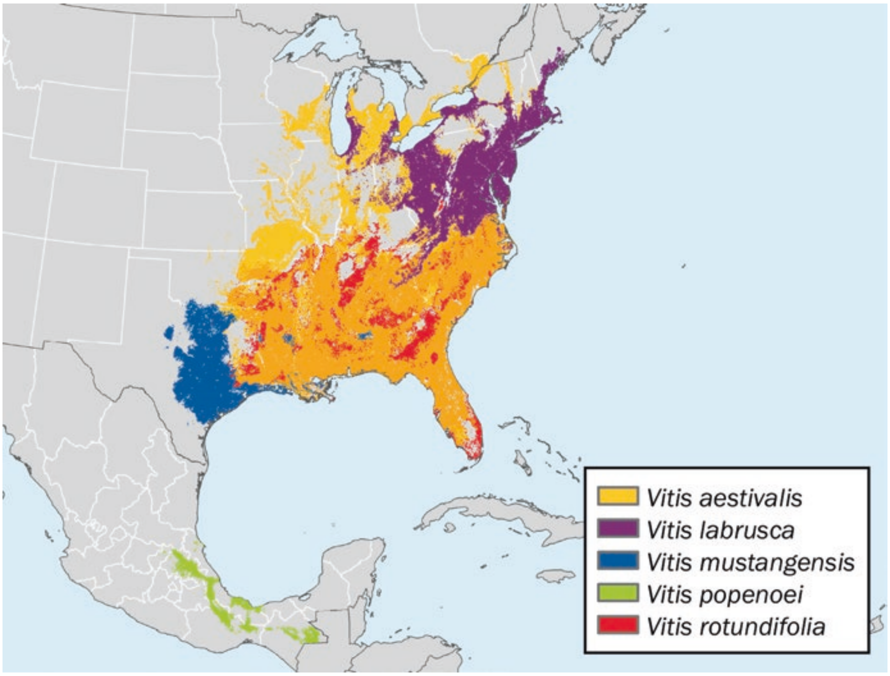

Fig. 10.3 Modeled potential distribution of *Vitis* species used in scion breeding: *V. aestivalis* Michx., *V. labrusca* L., *V. mustangensis* Buckley, *V. popenoei* J. H. Fennel, and *V. rotundifolia* Michx. based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

Vitis riparia is one of several North American grape species resistant to the fungal disease downy mildew (*Plasmopara viticola*) (Alleweldt 1980; Alleweldt et al. 1990; Staudt and Kassemeyer 1995) and has been used in studies aimed at identifying quantitative trait loci (QTL) for downy mildew resistance (Marguerit et al. 2009). The species has also been cited as a potential source for resistance to fungal diseases including botrytis bunch rot (*Botrytis cinerea* Pers.), black rot (*Guignardia bidwellii* (Ellis) Viala & Ravaz), and powdery mildew (*Erysiphe necator*) (Alleweldt 1980; Alleweldt et al. 1990).

In 2015, USDA-ARS researchers reported the discovery of a novel polysaccharide in the stem exudate of *V. riparia* and named it Frost Grape Polysaccharide (FGP) (Price et al. 2015). FGP has potential for the food and cosmetic industries as an emulsifier similar to currently imported gum arabic but without the potential for allergy sensitization (Hay et al. 2017). More research is necessary to determine the exact properties and uses for this compound and whether or not it is produced in other related *Vitis* species (Leathers et al. 2017).

Vitis rupestris It has a low-growing, shrubby habit and is native to rocky streambeds. At one time it was abundant along a narrow band from southwestern Texas, through Oklahoma, Arkansas, Missouri, and continuing northeast to the Pennsylvania

Table 10.1 Introduction and key traits for select North American grape wild relatives

Species	Native area	Key traits and references
V. acerifolia Raf. Syn.: *V. longii* Prince, *V. solonis* Hort. Berol. ex Planchon	North-central Texas and Western Oklahoma, extending to parts of Kansas, Colorado, and New Mexico	Salt tolerance (Heinitz 2016) Drought (Padgett-Johnson et al. 2003)
V. arizonica Engelm.	Arizona, New Mexico, north-central Mexico, extending into Texas	Drought tolerance (Padgett-Johnson et al. 2003; Knipfer et al. 2015) Pierce's Disease (*Xylella fastidiosa*) resistance (Riaz et al. 2006) Dagger nematode (*Xiphinema index* Thorne and Allen, 1950) resistance (Xu et al. 2008)
V. californica Bentham	Central and Northern California, extending into Oregon	Hybridization with cultivated *V. vinifera* (Dangl et al. 2015)
V. cinerea (Engelm. in Gray) Engelm. ex Millardet (excl. var. *helleri*)	Broadly through central and eastern Mexico and Southeastern United States, extending north to Pennsylvania	General fungal disease resistance genes (Mahanil et al. 2007) Tropical root-knot nematode (*Meloidogyne javanica* Treub, 1885) resistance (Smith et al. 2014) Strong phylloxera resistance (Zhang et al. 2009)
V. shuttleworthii House	Northern Florida, rare	Anthracnose (*Elsinoe ampelina* Shear) resistance (Mortensen 1981)
V. treleasei Munson ex L.H. Bailey	Arizona and New Mexico	Salt tolerance (Heinitz 2016) Drought tolerance (Padgett-Johnson et al. 2003)
V. vulpina L. Syn.: *V. cordifolia* Michaux	Broadly in Eastern United States, south of the Great Lakes and New York, south to Texas, and east to the Atlantic	Cold tolerance (Luby 1991)

Ozarks – but the range is now much more restricted. By 1909, Munson noted that the populations of this species were shrinking due to grazing (Munson 1909). The current range is restricted to the Ozark Plateau in southern Missouri and northern Arkansas and a small number of isolated populations in Oklahoma and Texas (Moore 1991; Pap et al. 2015) (Fig. 10.4). The shrubby, non-climbing growth habit makes these vines particularly susceptible to grazing, though riparian habitat degradation is also a serious factor in the decline of this species (Moore 1991). Due to the increasing vulnerability of wild populations and the great historical and potential value of the species for the viticulture industry, four locations in Missouri and Oklahoma were established as the first NPGS in situ conservation sites for an American crop wild relative (Pavek et al. 2003).

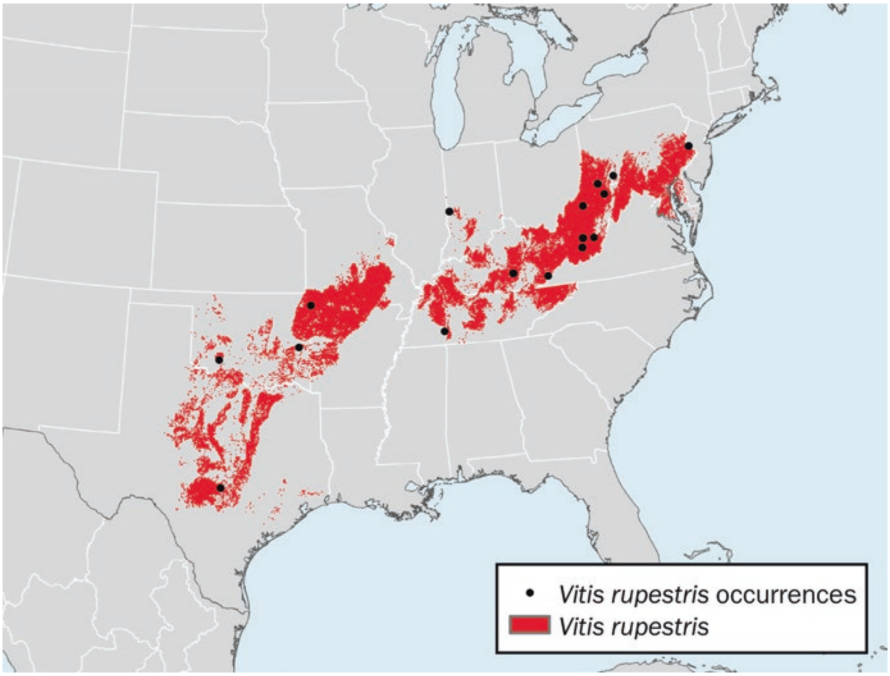

Fig. 10.4 Red shading indicates the modeled potential distribution of *V. rupestris* Scheele collections based on climatic and edaphic similarities with historic herbarium and genebank reference localities. Black circles indicate remaining occurrences of known wild populations. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

Vitis rupestris was one of the first North American *Vitis* species utilized for grapevine breeding, initially as a source of downy mildew resistance and later, with *V. riparia*, as the foundation of the first phylloxera-resistant rootstocks (Viala and Ravaz 1903; Galet 1988; Di Gaspero et al. 2012). In addition to durable phylloxera resistance, the species possesses other important characteristics that are likely derived from its adaptation to nutrient-poor, gravelly soils (Pongracz 1983; Reisch et al. 2012). Rootstocks with *V. rupestris* parentage are effective at excluding chloride from the scion, an indication of salt tolerance (Sauer 1968; Tregeagle et al. 2006; Fort et al. 2015), and have a deep rooting profile (Morano and Kliewer 1994; Fort et al. 2017). *Vitis rupestris* is also still an important source of powdery mildew resistance (Barba et al. 2014).

Vitis cinerea var. *helleri* It has been extensively used in rootstock breeding. Originally named *V. berlandieri*, it is now considered to be a variety of *V. cinerea*. *Vitis cinerea* is a wide-ranging species, found throughout the Eastern United States south of the 40th parallel (Moore 1991), and *V. cinerea* var. *helleri* is restricted to central Texas and has been used extensively in grape rootstock breeding, due to its tolerance of limestone soils. This latter taxon was considered an independent species, *Vitis berlandieri* in early texts (Munson 1909; Bailey 1934; Galet 1988), but Comeaux (1987) proposed reducing the species to a variety of *V. cinerea* based on field observations of intergradation between the two taxa. Despite possessing distinct characteristics in morphology, vigor, native habitat, and, crucially, lime tolerance (Viala and Ravaz 1903; Pongracz 1983; Schmid et al. 2009), the inclusion of *V*. *berlandieri* within *V. cinerea* has so far been supported by molecular evidence (Aradhya et al. 2013; Wan et al. 2013). Moore (1991) proposed the name 'var. *helleri*' for consistency with previous literature.

The small natural range of *V. cinerea* var. *helleri* is due to its adaption to the shallow, limestone-derived soils of the Edwards Plateau of central Texas southwest of the Brazos River and, sparsely, southwest toward the Rio Grande (Munson 1909; Hatch et al. 1990; Moore 1991). Although the region receives acute periods of precipitation, *V. cinerea* var. *helleri* is often found growing among dead or dormant grasses in dry soils (Morano and Walker 1995). Notably, much of the Edwards Plateau is historically rangeland, and the region holds one of the largest deer populations in North America (Hatch et al. 1990), suggesting that grazing has inhibited the proliferation of *V. cinerea* var. *helleri*.

Vitis cinerea var. *helleri* is remarkable for the narrowness of its ecological niche. Although the Edwards Plateau is a severe environment characterized partly by erratic precipitation, environmental factors including mean annual precipitation, seasonal temperature, and soil attributes are relatively uniform across the range of *V. cinerea* var. *helleri* (Hijmans et al. 2005; Hengl et al. 2017). The region, particularly the Hill Country west of Austin and north of San Antonio, is undergoing rapid residential and commercial development threatening the survival of this vital species. For this reason, ex situ conservation efforts might be most appropriate for maintaining *V. cinerea* var. *helleri* germplasm.

The lime-tolerant *V. cinerea* var. *helleri* was incorporated into rootstock breeding in the late 1800s when scions grafted to *V. riparia*- and *V. rupestris*-based rootstocks expressed lime-induced iron chlorosis on the limestone-derived soil common in the viticultural regions of Europe (Pongracz 1983). Because *V. cinerea* var. *helleri* is difficult to propagate, commercially viable rootstock cultivars utilizing this species are selected from crosses with *V. riparia* and *V. rupestris*. Other traits associated with *V. cinerea* var. *helleri*-based rootstocks, particularly hybrids with *V. rupestris*, include increased scion vigor, delayed phenology and senescence, drought resistance, and, in some instances, salinity tolerance. There is also evidence for reduced potassium uptake and/or transport in *V. cinerea* var. *helleri*-based rootstocks compared with other rootstocks in high-potassium soils (Rühl 1991, 1992; Wolpert et al. 2005).

Vitis xchampinii It is usually described as a natural hybrid between *V. mustangensis* Buckley x *V. rupestris*; however, there is disagreement among authors regarding its origin, which might also include hybridization with *V. cinerea var. helleri* and *V. monticola* Buckley. *Vitis* X *champinii* has been utilized in rootstock breeding, most notably for the cultivars 'Ramsey,' 'Dog Ridge,' 'Harmony,' and 'Freedom.' The species has also been used in developing fruit-bearing varieties such as the *V.* X *champinii x V. labrusca* L. hybrid 'Champanel' (Munson 1909). While associated with the Edwards Plateau in south-central Texas (Munson 1909; Moore 1991), the species has become very rare in natural settings, and herbarium samples of this taxon were mostly deposited prior to 1900 (Comeaux 1987). The rapid development of the Texas Hill Country, intense herbivory from deer and cattle populations, and diminishing range of *V. rupestris* make the continued existence of this important species precarious, except in ex situ germplasm collections.

Both climate change and expansion of viticultural regions are causing the viticulture industry to look toward rootstock-scion combinations that tolerate or avoid drought and marginal soils. Recently, rootstock breeders have been developing interest in species native to arid regions of the Southwestern United States and Mexico for salt and drought tolerance (Heinitz et al. 2015). In this region, wild *Vitis* are restricted to isolated mountain ranges and riparian corridors. Seeds are dispersed primarily by birds and small mammals, and vines propagate vegetatively by layering during seasonal flooding, allowing gene flow between otherwise isolated habitats. Unfortunately grazing, drought, invasive species in riparian zones, and herbicide use along highways threaten much of the prime *Vitis* habitat in the Southwest.

Vitis girdiana Munson and *V.* X *doaniana* Munson ex Viala both performed well in initial screens for chloride exclusion (a measure of salt tolerance) (Heinitz 2016) and drought tolerance (Padgett-Johnson et al. 2003). *Vitis girdiana* is native to Southern California, Baja (Mexico), and Southern Nevada and has been observed in Southwest Utah (Wada 2008). It displays high vigor and growth rate even under high temperatures in its native habitat and remains prevalent in the landscape, though it is under threat of genetic erosion from hybridization with cultivated *V. vinifera* (Dangl et al. 2015). *Vitis* X *doaniana* is a well-accepted hybrid of *V. mustangensis* and *V. acerifolia* Raf., which occurs in a narrow region where the parent species co-occur near the Red River at the border of Texas and Oklahoma (Munson 1909; Moore 1991; Peros et al. 2011). Although this hybrid species has unique characteristics and great potential for breeding, it is not well represented in ex situ collections, and native populations are under threat from drought and land use change on both sides of the Red River. *Vitis monticola* is another unique species with a restricted natural range. Found exclusively in well-drained, upland sites in the Edwards Plateau in central Texas, the slow-growing *V. monticola* is among the grape species with the narrowest range (Moore 1991). Unlike nearly all other *Vitis* species that are associated with either seasonal or permanent water, *V. monticola* is frequently found growing without obvious water sources. This makes it a potentially important genetic resource for drought tolerance, but difficulty of propagation from woody cuttings and very slow growth are drawbacks in using this unique species in breeding programs.

10.2.2 Scion Species

Vitis aestivalis Michaux It is found on well-drained sites throughout the Eastern United States and Southern Canada (Munson 1909; Moore 1991). The species is composed of three subspecies (vars. *aestivalis*, *bicolor* Deam, and *lincecumii*

(Buckley) Munson) that were variously designated in early texts (Munson 1909; Bailey 1934; Galet 1988; Moore 1991). The original form identified as *V. aestivalis*, now designated var. *aestivalis*, is found in the Southeastern United States, from eastern Texas, north to southern Iowa, east to the Atlantic Coastal Plain, and south to Florida (Munson 1909; Moore 1991). The subspecies *bicolor* comprises the northern range of *V. aestivalis* but is also found in northern Alabama and Georgia (Munson 1909; Moore 1991). Finally, *V. aestivalis* var. *lincecumii* (the Post Oak Grape) is mostly restricted to East Texas and Western Louisiana (Munson 1909; Moore 1991).

Historically, *V. aestivalis* was important in developing the French-American hybrids, with *V. aestivalis* var. *lincecumii* playing a central role in complex hybrids among American species and *V. vinifera* (Reisch et al. 1993; Robinson et al. 2012). Indeed, Munson (1909) utilized this subspecies extensively in his breeding efforts, and it might be useful as a source of heat tolerance in modern breeding efforts (Reisch and Pratt 1996). *Vitis aestivalis* accessions show partial resistance to downy mildew (Staudt and Kassemeyer 1995; Cadle-Davidson 2008), and the early American cultivar 'Norton,' likely a *V. aestivalis* x *V. vinifera* hybrid (Stover et al. 2009), is resistant to powdery mildew (Fung et al. 2008). Although several French-American hybrids derived from *V. aestivalis* show disease resistance, the complex parentage of those cultivars makes associations among traits, alleles, and species difficult (Dalbó et al. 2001; Fischer et al. 2004), further bolstering the need for conservation based on adaptive, phenotypic, and genetic diversity, as opposed to conservation based on taxonomy. Currently, *V. aestivalis* and hybrids with *V. aestivalis* parentage are used in breeding programs for eastern and northern climates, particularly in the Cornell program at Geneva (Reisch et al. 1993).

Vitis labrusca It is a vigorous vine that grows in a wide variety of wet habitats from Maine, New Hampshire, and Vermont to northern Georgia, Alabama, west to Mississippi, and north to Eastern Illinois and Southern Michigan (Munson 1909; Moore 1991). The species produces relatively large berries, which probably attracted human foragers and those attempting to improve North American grapes by selection and hybridization with European cultivars.

Early cultivars derived from *V. labrusca*, frequently from *V. labrusca* x *V. vinifera* hybrids but also from hybrids between *V. labrusca* and other North American species, were introduced in the first half of the nineteenth century (Hedrick et al. 1908; Munson 1909). The most well-known of these is 'Concord,' a seedling derived from a cross between *V. labrusca* and 'Catawba,' an early American hybrid with *V. labrusca* x *V. vinifera* parentage (Huber et al. 2016). Introduced in 1854, 'Concord' remains important for producing grape juice and preserves, with utilized US production exceeding 360,000 t in 2015 (USDA 2016).

Vitis labrusca was utilized in some early French-American hybrid wine grape cultivars of the early twentieth century (Robinson et al. 2012); however, the species was often avoided in crosses because of its undesirable "foxy" flavor (Reisch et al. 1993).

For this reason, cultivars with *V. labrusca* parentage are mainly utilized for juice and preserves, and several breeding programs utilize the species for table grape development (Clark and Moore 2015). Traits for which *V. labrusca* might serve as valuable germplasm include resistance to the fungal diseases powdery and downy mildew (Pearson and Goheen 1988; Alleweldt et al. 1990) and anthracnose (Mortensen 1981) and the phytoplasma disease Flavescence dorée (Pearson and Goheen 1988).

Subgenus *Muscadinia* The genus *Vitis* is currently divided into two subgenera: *Vitis* ($2n = 38$) and *Muscadinia* ($2n = 40$). The mostly subtropical *Muscadinia*, or muscadine grape, is comprised of *V. rotundifolia* Michaux and *V. popenoei* J.H. Fennel, with *V. rotundifolia* further divided into var. *rotundifolia* (found from Texas to Virginia and south to Florida), var. *munsoniana* (J.H. Simpson ex Planch.) M.O. Moore (found throughout Florida and in southern Georgia and Alabama), and var. *pygmaea* McFarlin ex D.B. Ward (found only in Central Florida) (Comeaux 1984; Moore 1991; Aradhya et al. 2013). The distribution of *V. popenoei* is limited to southern Mexico (Aradhya et al. 2013). Fossil (Kirchheimer 1939; Tiffney and Barghoorn 1976) and molecular evidence (Trondle et al. 2010; Aradhya et al. 2013) indicate that the two subgenera once occupied similar ranges before diverging during the Tertiary period which lasted from ~66 million to 2.6 million years ago. Restriction of *Muscadinia* to the Southeastern United States and Mexico probably occurred during periods of glaciation.

The muscadine grape is historically important in the southern United States, where it has been used for wine, preserves, and table fruit (Olien 1990). The ‘Scuppernong’ grape is the best-known *V. rotundifolia* cultivar and was thought to be planted in the mid-1500s in Sir Walter Raleigh’s colony (Hedrick et al. 1908; Munson 1909). While muscadine grapes have been cultivated since then, the vine that became the cultivar ‘Scuppernong’ was probably discovered in Northeastern North Carolina by Isaac Alexander about 200 years later in the mid-eighteenth century (Reimer 1909). Significant efforts to develop improved muscadine and muscadine x *vinifera* hybrids have been documented since the early twentieth century (Munson 1909; Reimer 1909; Dearing 1917), and public muscadine breeding programs continue in the United States, including at the University of Arkansas (Clark and Barchenger 2014), Georgia State University (Conner 2010), and North Carolina State University (NC State Extension 2016). In 2006, muscadine grapes were produced on approximately 2000 ha (5000 acres) in 12 states, with production trending upward (Cline and Fisk 2006).

Vitis rotundifolia is an important potential germplasm source for a range of disease, insect, and nematode resistance absent in *V. vinifera* (Alleweldt et al. 1990; Olien 1990; Staudt and Kassemeyer 1995), but chromosomal differences between the two subgenera make hybridization difficult. Although some *V. vinifera* x *V. rotundifolia* combinations exist (Patel and Olmo 1955; Dunstan 1962; Jelenkovic and Olmo 1968; Bouquet 1980), successful pollination is difficult to predict, and most F_1 populations are mostly or entirely sterile. Embryo rescue techniques have been used to improve progeny yields after attempted hybridization (Lu et al. 2000), and colchicine has been used to induce tetraploidy in *V. vinifera* x *V. rotundifolia* hybrids for improved fertility in F_1 populations (Xie et al. 2015).

Jelenkovic and Olmo (1968) developed a partially fertile *V. vinifera* x *V. rotundifolia* population that exhibited tolerance to several important insects and diseases and was used in backcrosses to *V. vinifera* to develop new wine grape cultivars (Olmo 1971). *Vitis rotundifolia* has also been used in breeding programs for developing rootstocks resistant to dagger nematode (*Xiphinema index*) and, by extension, grapevine fanleaf virus, which is vectored by the nematode (Walker et al. 1991; Walker and Jin 2000; Esmenjaud and Bouquet 2009). Genes for powdery mildew resistance have been identified in *V. rotundifolia* and *V. vinifera* x *V. rotundifolia* populations (Pauquet et al. 2001; Riaz et al. 2011; Blanc et al. 2012), as well as downy mildew resistance (Merdinoglu et al. 2003).

Vitis mustangensis The mustang grape, *Vitis mustangensis* (syn. *V. candicans* Engelm. ex Gray), is the dominant grapevine taxon in eastern Texas, with an overall range that includes Western Louisiana and Southern Oklahoma, as well as a disjunct population in Alabama (Munson 1909; Moore 1991). The species is very vigorous and is often observed completely enshrouding and smothering trees and other structures. Although *V. mustangensis* has played only a limited and indirect role in global viticulture (rootstocks like ‘Ramsey’ and ‘Dog Ridge’ are selections of *V.* X *champinii*, a natural hybrid between *V. mustangensis* x *V. rupestris*), mustang wine is of local historical importance in Texas, and the species might be valuable in scion and fruit breeding. *Vitis mustangensis* inhabits common ranges with most other wild grapes in Texas, including the lime-tolerant *V. cinerea* var. *helleri* and the drought-resistant *V. monticola*, and therefore might act as a bridge among taxa and a source for genetic and phenotypic variation in other important taxa. Its utility in rootstock breeding is limited due to poor rooting from woody cuttings and excessive vigor.

10.3 Wild and Alternative Utilization of North American *Vitis* L.

Efforts to study and conserve wild grapevines are typically focused on assisting breeding programs for commercial viticulture. However, researchers in Mexico are investigating ways to continue the long tradition of direct utilization of wild grapevines, where there is great potential in the agricultural, pharmaceutical, and food industries (Franco-Mora and Cruz-Castillo 2012).

Historically, indigenous groups in central Mexico used wild grapevine stems as thread to build fishing nets, baskets, and fences (Franco-Mora and Cruz-Castillo 2012). Wild grapevines have been highly important in traditional medicine, where the fruit, leaf, root, and sap are used to prepare teas and infusions (Jiménez-Martinez et al. 2013). Historically, wild grapevines were used as a natural remedy to treat heart disease, gout, and inflammatory arthritis (Jiménez-Martinez et al. 2013).

Culturally, wild grapevines have a strong presence in Mexican cuisine. Flowers and fresh berries were used in regional dishes from the State of Mexico (Luna-Gaona et al. 2010; Sabas-Chavez et al. 2016). *Vitis tiliifolia* Humb. & Bonpl. ex Schult. has been used to produce wine in the state of Guerrero, and the states of Puebla and Mexico are producing grape liquor (Franco-Mora and Cruz-Castillo 2012). This species is also being used to produce jelly and optimized for sugar and phenolic compound content in the wild grapevine berries (Franco-Mora and Cruz-Castillo 2012).

Currently, wild grapevines are getting special attention for their potential as sources of antioxidants and fatty acids. Tobar-Reyes and collaborators (2009) are studying the presence of antioxidant compounds in wild grapevine leaves. Trans-resveratrol, a polyphenol that confers important health characteristics in wine, has been reported to be synthetized in wild *Vitis* leaves either wounded or infected by *Botrytis cinerea* Pers. Resveratrol has shown potential as an inhibitor in the development of cancer cells in vitro and in vivo (Jang et al. 1997; Alkhalaf 2007; Tobar-Reyes et al. 2009). Moreover, consumption of resveratrol has shown anti-inflammatory, antioxidant, and antifungal properties as well as preventative action against heart disease (Stein et al. 1999). Resveratrol content varies between accessions of wild grapes and is heavily affected by the environment (Tobar-Reyes et al. 2009; Franco-Mora and Cruz-Castillo 2012). It has been suggested that resveratrol might be the active ingredient in *Vitis* that makes it important in traditional medicine (Tobar-Reyes et al. 2009).

Vitis vinifera seeds contain up to 14% oil. This oil is already used in Italy, Spain, and France for culinary purposes due to its high smoke point. This oil can also be used in the cosmetic industry due to its moisturizing properties (Franco-Mora et al. 2015). Franco-Mora and collaborators (2015) determined that wild grapevine seeds also have significant oil content. The average percentage of oil in the seed was 16.7%, of which 71.5% was linoleic acid, 17.2% was oleic acid, 6.6% was palmitic acid, and 4.3% was stearic acid.

10.4 Conservation Status and Future Concerns

10.4.1 In Situ Conservation

Conservation of wild plants in their native habitats (in situ conservation) is beneficial in many ways – populations can continue to adapt in place to changing environmental stresses, unique hybrid forms can be maintained by continued gene flow between parent species, and large population sizes can be maintained at relatively low expense. However, in situ conservation requires the cooperation of landholders and sufficiently robust wild populations. Most wild *Vitis* species in the Eastern United States still maintain large populations over broad ranges, and specific conservation measures are not necessary. In some areas, wild grapevines are so prevalent that they are often considered nuisance plants, and the state of Ohio has designated all *Vitis* as a prohibited noxious weed when not maintained or controlled for 2 years (Ohio Admin. Code 901:5-37-01).

Unfortunately, many other species, particularly in the more arid Western United States, are becoming rarer in the wild. Grazing, development, and riparian habitat degradation through reduced water flow and invasion of non-native species all threaten grape wild relatives in certain areas. This is most evident in the case of *V. rupestris*, an important rootstock species which was once prevalent but now considered endangered in Indiana (Division of Nature Preserves 2002) and Pennsylvania (Thompson 1997), threatened in Kentucky (Kentucky State Nature Preserves Commission 2000), and of special concern in Tennessee (Tennessee Natural Heritage Program 2002). Other species currently on state concern lists are the following: *V. aestivalis*, endangered, Maine (Maine Natural Areas Program 1999); *V. cinerea* var. *baileyana* (Munson) Comeaux, endangered, Pennsylvania (Thompson 1997); *V. labrusca*, special concern, Kentucky (Kentucky State Nature Preserves Commission 2000); *V. X novae-angliae* Fernald (pro sp.) [*labrusca* x *riparia*], endangered, Pennsylvania (Thompson 1997) and Maryland (Maryland Natural Heritage Program 1997), and special concern, Connecticut (Connecticut Department of Environmental Protection 1998); *V. palmata* Vahl, rare, Indiana (Division of Nature Preserves 2002); and *V. vulpina*, endangered, New York (Department of Environmental Conservation 2000), and threatened, Michigan (Michigan Natural Features Inventory 1999).

Scientists in the USDA-ARS National Plant Germplasm System (NPGS) conducted a study in the late 1990s to determine appropriate in situ conservation sites for three *Vitis* species: *V. rupestris*, *V. shuttleworthii*, and *V. monticola* (Pavek et al. 2000). They negotiated agreements with the landholders for four of seven sites identified for *V. rupestris* in Oklahoma and Missouri (Pavek et al. 2003) and tentative agreements with public land administrators at four Florida sites for *V. shuttleworthii* and three Texas sites for *V. monticola* (Pavek et al. 2000). At the time, these were the first official in situ conservation sites to be added to the NPGS system for any crop wild relative, and they were intended to complement but not replace the ex situ collections.

10.4.2 Ex Situ Conservation

Maintaining viable collections of seed or clonal plant material (ex situ conservation) can help ensure the safety of wild plants that are threatened in their natural habitats and allows for rapid access to diverse germplasm. Though ex situ conservation of clonal plants is expensive, it does allow for specific wild accessions to be preserved and propagated indefinitely. Also, the high level of heterozygosity in *Vitis* means that it is possible to capture a greater amount of allelic diversity with fewer individual plants.

Though global grape genebank collections are comprised mainly of cultivated *V. vinifera* varieties, most contain at least a small number of North American *Vitis* species due to their important history in rootstock breeding. The Vassal-Montpellier Grapevine Biological Resources Center, hosted by the French National Institute for Agricultural Research (INRA), has maintained collections from the original French breeders of the first grape rootstocks in the mid-nineteenth century. The University of California, Davis Viticulture and Enology Department (UC Davis V&E), also maintains a large collection of North American *Vitis* for rootstock and scion breeding that has been collected over the last 30 years. The most accessible wild *Vitis* collection is maintained by the NPGS in the United States, both at the National Clonal Germplasm Repository in Davis, California (NCGR-Davis), and the Plant Germplasm Resources Unit in Geneva, New York (Aradhya et al. 2013). The number of accessions of various species in the NPGS collection and their availability for distribution is summarized in Fig. 10.5. While some species are well represented,

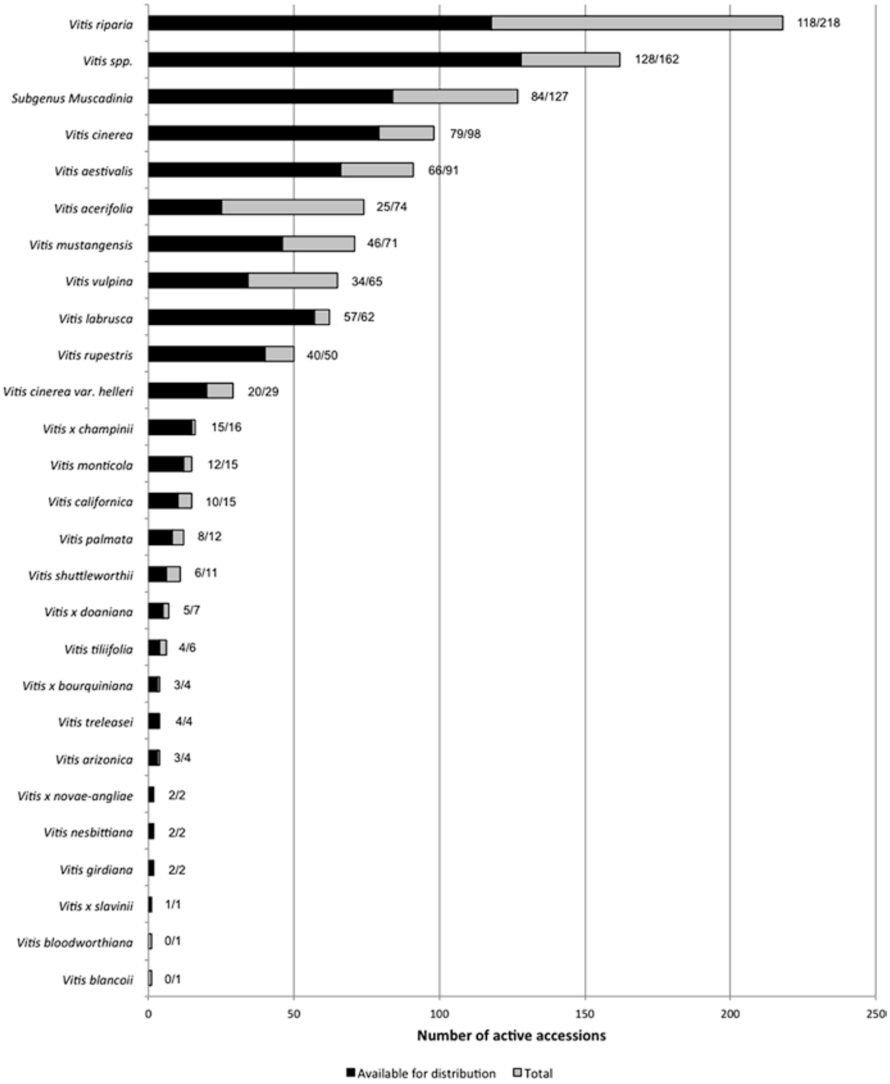

Fig. 10.5 Active accessions of North American *Vitis* in the National Plant Germplasm System (NPGS). Values are (number available for distribution)/(total number of accessions)

the lack of diversity in others such as *V. arizonica* and *V. girdiana* means that these species are often underrepresented in phylogenetic studies and other characterization efforts which rely on publicly available germplasm (e.g., Trondle et al. 2010; Peros et al. 2011). The addition of more diversity from the UC Davis V&E collection would help remedy this problem, but additional accessions cannot currently be added due to restricted field space and resources at NCGR-Davis.

10.4.3 Future Efforts

Characterization and utilization are key to the continued conservation of grape wild relatives in North America. More knowledge of the complex genetic relationships between species and unique populations of wild *Vitis* will allow for informed efforts at both ex situ and in situ conservation. Characterization of potentially useful traits will encourage utilization and can eventually lead to improved rootstock and scion varieties for a viticulture industry that is dealing with increasing environmental challenges.

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Chapter 11
Temperate Tree Fruits of North America: *Malus* Mill., *Prunus* L., *Diospyros* L., and *Asimina* Adans

Gayle M. Volk

Abstract North America has four native temperate tree fruit genera that have played key cultural roles due to their edible fruit and medicinal uses and have also been valuable as hardwood: *Malus* Mill. (apple), *Prunus* L. (cherry, plum, peach, etc.), *Diospyros* L. (persimmon), and *Asimina* Adans. (pawpaw). Some native North American species of these tree fruit genera also exhibit traits that are desirable for plant breeding targets. This chapter provides summary information about the geographic distribution, phylogenetic and taxonomic relationships, and conservation efforts for North American *Malus*, *Prunus*, *Diospyros*, and *Asimina* species. North American genebanks maintain vast collections of these genera that are among the largest in the world. Increased representation of North American native tree fruit species within genebanks will ensure global access to key genetic resources for future generations.

Keywords *Malus* · *Prunus* · *Diospyros* · *Asimina* · Ex situ conservation · In situ conservation · Genetic resources

11.1 Introduction

North America has members of four native temperate tree fruit genera that have played key cultural roles as a result of their edible fruit and medicinal uses and that have proven valuable as hardwood: *Malus* (apple), *Prunus* (cherry, plum, peach, etc.), *Diospyros* (persimmon), and *Asimina* (pawpaw). Some of these North American taxa have been recognized for their potential for use in plant breeding as crop wild relatives (CWR) of cultivated species (Khoury et al. 2013; Wiersema et al. 2012). A published global priority list for CWR genera includes two native North

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G. M. Volk (✉)
USDA-ARS National Laboratory for Genetic Resources Preservation,
Fort Collins, CO, USA
e-mail: Gayle.Volk@ars.usda.gov

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American tree fruit genera: *Malus* and *Prunus* (Vincent et al. 2013). In addition, members of *Malus*, *Prunus*, and *Diospyros* were classified as high-priority US CWR and wild utilized species (Khoury et al. 2013).

The indigenous people of North America have used a number of native fruit and nut species for nourishment including persimmons, pawpaws, plums, and cherries, as well as berries (Chap. 9), grapes (Chap. 10), tropical fruits (Chap. 12), and nuts (Chap. 13) (Abrams and Nowacki 2008). Wild mulberries were also widely consumed by indigenous peoples, but are not covered in this book.

The extent of information available for the North American species of *Malus*, *Prunus*, *Diospyros*, and *Asimina* varies widely. Summaries of each genus are provided herein, including introductory information about the North American species and their relationships to the cultivated crops, geographic distributions, phylogenetic and taxonomic relationships, and conservation efforts. Conservation effort information is focused on activities of the USDA-ARS National Plant Germplasm System (NPGS).

11.2 *Malus* Genetic Resources Native to North America

11.2.1 Introduction

Access to diverse apple genetic resources is critical for future apple fruit and rootstock breeding efforts (Volk et al. 2015a). The genus *Malus* includes at least 38 species that are either native to or are cultivated throughout many temperate regions of the world (Volk et al. 2015a). The cultivated apple, *Malus* × *domestica* Borkh., is the species grown and consumed for dessert, juice, and cider purposes. Its primary CWR and progenitor species include *Malus sieversii* (Ledeb.) M. Roem. (native to temperate Central Asia), *Malus orientalis* Uglitzk. (native to the Caucasus and western Asia), *Malus sylvestris* (L.) Mill. (native to Europe), and *Malus prunifolia* (Willd.) Borkh. (native to China) (Volk et al. 2015a). Taxonomic relationships based on chloroplast sequences reveal close genetic relationships among *M.* × *domestica* and its progenitor species as well as other species of Asian origin (Fig. 11.1).

Of 38 wild *Malus* species, 4 are native to North America. *Malus fusca* (Raf.) C. K. Schneid. is a thicket-forming shrub that occurs in mesic environments at low- to mid-elevations along the Pacific Coast from Northern California to the Kenai Peninsula in Alaska (Viereck and Little 1986; Routson et al. 2012) (Figs. 11.2 and 11.3). *Malus angustifolia* (Aiton) Michx. (North Central, Northeastern, South Central, and Southeastern USA), *Malus coronaria* (L.) Mill. (North Central, Northeastern, Southeastern USA, and Eastern Canada), and *Malus ioensis* (Alph. Wood) Britton (North Central, Northeastern, South Central, and Southeastern USA) (Figs. 11.2 and 11.3) are much more distantly related to the domesticated apple than *M. fusca* and are typically placed in its tertiary genepool (Fig. 11.1; Volk et al. 2015b; Wiersema et al. 2012).

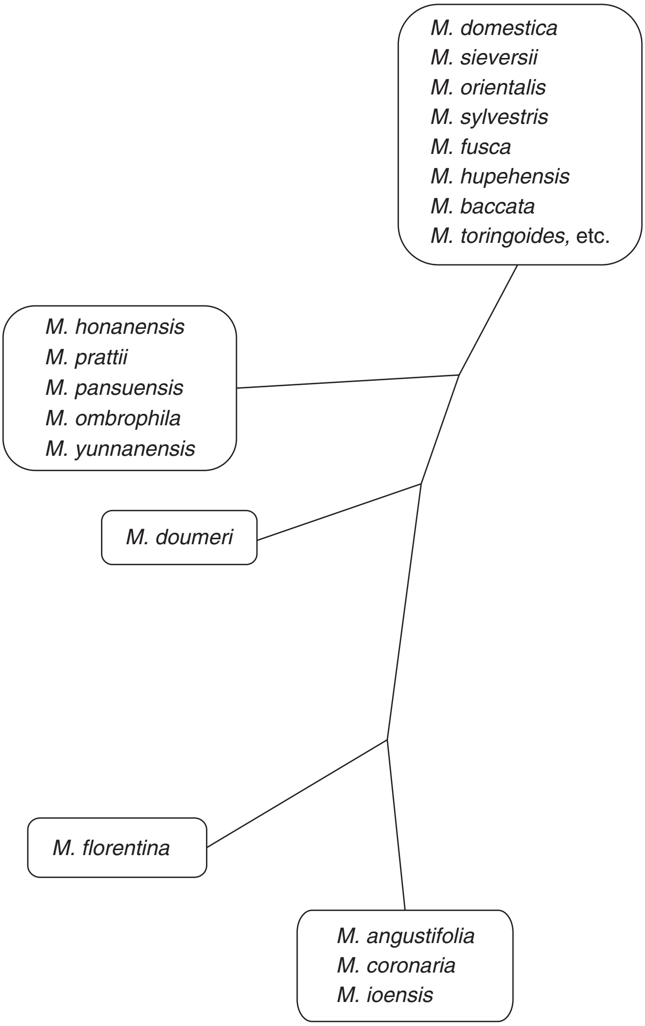


Fig. 11.1 Genetic relationships among *Malus* species based on chloroplast sequence data, adapted from Volk et al. (2015b)

Malus fusca was used extensively by the Saanich and Cowichan Coast Salish people of Southern Vancouver Island for digestive tract ailments and kidney trouble (Turner and Hebda 1990). In addition, the wood was used for halibut hooks, digging sticks, adze handles, bows, and fishing floats (Turner and Bell 1971). Native *M. angustifolia* fruits are consumed by deer and other mammals, as well as grouse, pheasants, and many small birds (USDA-NRCS 2009c). *M. fusca* has been used in breeding programs to improve resistance to fire blight (*Erwinia amylovora* (Burrill) Winslow) through the use of high-speed breeding technologies and transgenic methods (Flachowsky et al. 2011; Le Roux et al. 2012).

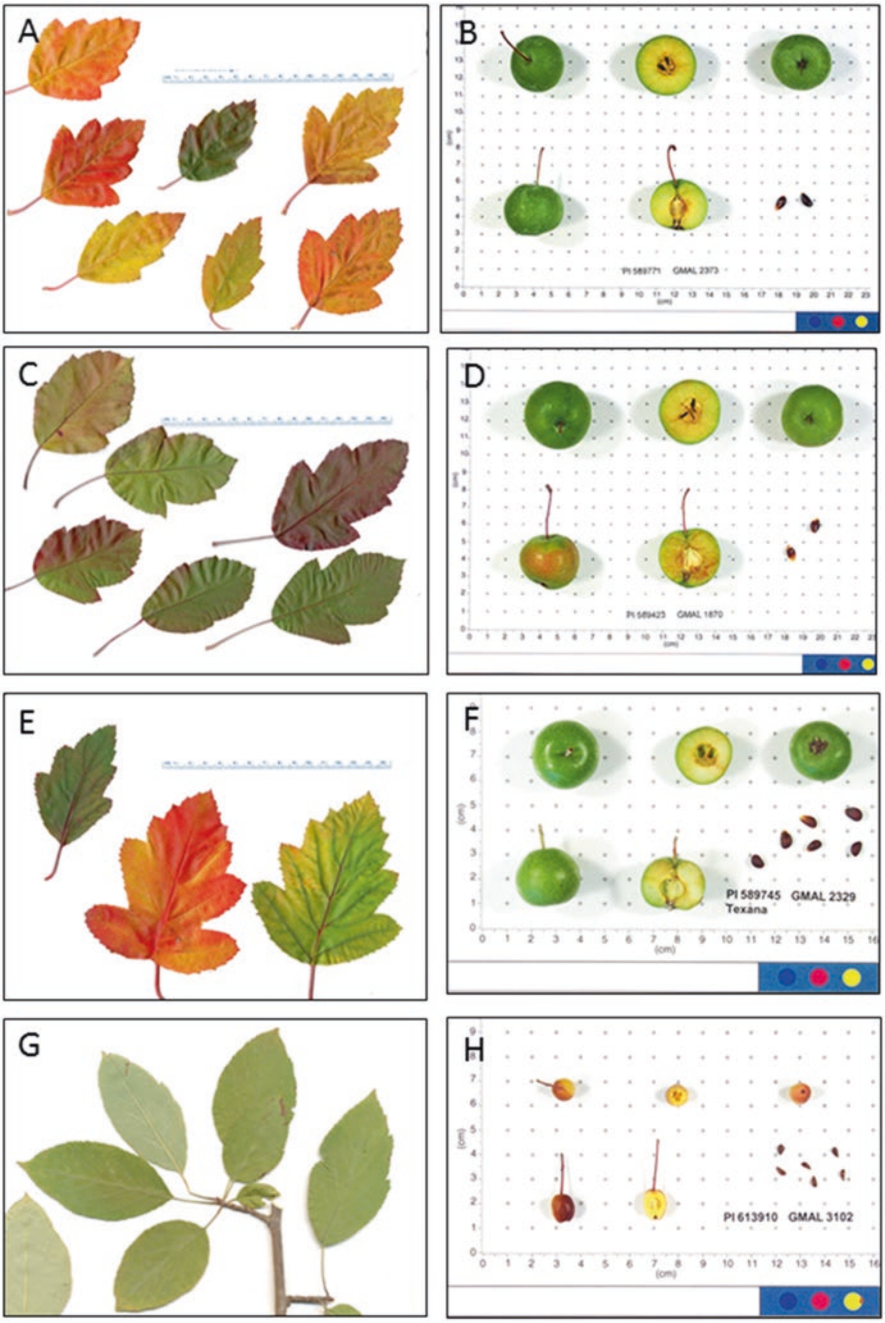


Fig. 11.2 Leaf and fruit images from North American apple species *Malus angustifolia* (Aiton) Michx. (PI 590175 **a**, **b**), *Malus coronaria* (L.) Mill. (PI 588927 **c**, **d**), *Malus ioensis* (Alph. Wood) Britton (PI 613906 **e**, **f**), and *Malus fusca* (Raf.) C. K. Schneid. (PI 613910 **g**, **h**). Identification numbers refer to accessions in the USDA-ARS National Plant Germplasm System. (Images **a**, **b**, **c**, **d**, **e**, **f**, and **h** were retrieved from GRIN-Global (USDA 2017). Image **g** was provided by Kanin Routson)

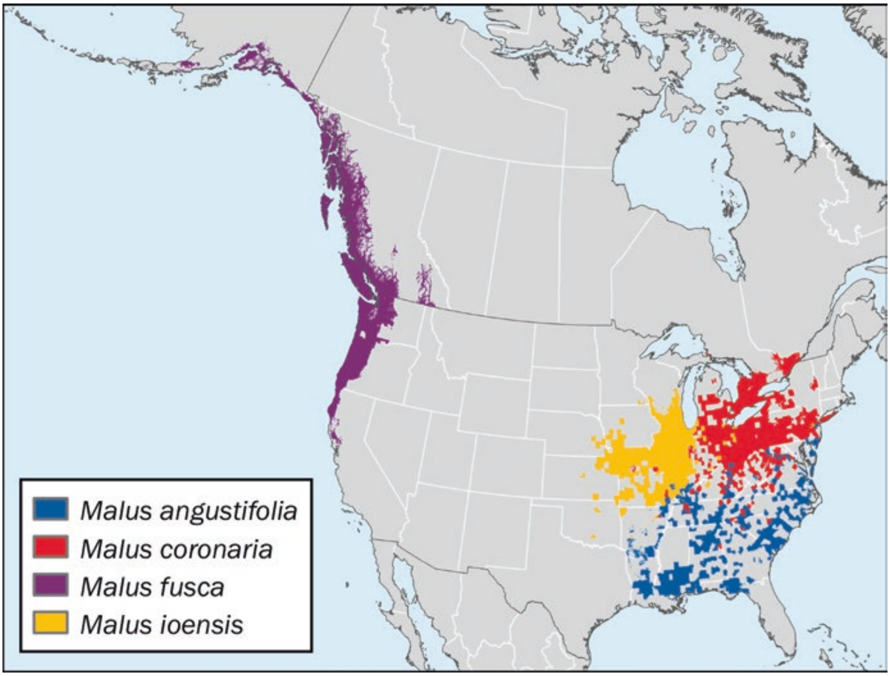


Fig. 11.3 Species distributions map of North American wild *Malus* species, based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are given in Appendix 1

11.2.2 Speciation and Taxonomic Relationships

Malus fusca is classified in *Malus* section *Kansuensis*, along with Chinese species *Malus kansuensis* (Batalin) C. K. Schneid., *Malus toringoides* (Rehder) Hughes, and *Malus transitoria* (Batalin) C. K. Schneid. (Robinson et al. 2001). *M. fusca* is believed to have arrived in North America by way of the Bering Strait (Williams 1982). Diploid *M. fusca* is genetically distinct from the three Eastern North American apple species, with species divergence between 30 and 46 million years ago in the early Oligocene epoch (Lo and Donoghue 2012).

The three eastern North American apple species are in *Malus* section *Chloromeles*. Genetic diversity assessments of *M. coronaria*, *M. ioensis*, and *M. angustifolia* using isozymes and chloroplast sequence data suggest that the species may be conspecific plant populations rather than congeneric species (Dickson et al. 1991; Volk et al. 2015b). Some literature suggested species differentiation based on ploidy level, but diploid, triploid, and tetraploid accessions have since been identified for each of the three species (Volk et al. 2015b). Further genotypic and phenotypic population assessments are needed (Fig. 11.2).

Due to the overlaps in geographic range and flowering time among *M.* × *domestica* and *M. angustifolia*, *M. coronaria*, and *M. ioensis*, there have been concerns about hybridization between domesticated and wild apple species in North America.

Hybridization is possible between *M.* × *domestica* and *M. coronaria* (Kron and Husband 2009), resulting in hybrid taxon *M.* × *platycarpa* Rehder progeny, but hybridization doesn't appear to occur commonly in the wild (Dickson et al. 1991). Likewise, *M.* × *dawsoniana* Rehder is the taxon of hybrids of *M.* × *domestica* and *M. fusca* and is grown as an ornamental crabapple.

11.2.3 Conservation

Most apple genebank collections are primarily comprised of grafted apple cultivars in field plantings. Accessions representing wild species materials may also be grown as seedlings on their own roots (Volk et al. 2015a). These field accessions are vulnerable to abiotic and biotic stresses, and some genebanks have implemented in vitro culture and cryopreservation technologies to secure their collections (Forsline et al. 1998; Höfer 2015; Towill et al. 2004; Volk et al. 2015a).

As *Malus* seeds exhibit an orthodox seed physiology, tolerating desiccation and low temperature, wild species can also be conserved in seed form. Seeds are expected to survive at least 100 years when stored at −18 °C using current genebanking technologies (Chapter 10; Kushnarenko et al. 2010). The USDA-ARS National Laboratory for Genetic Resources Preservation (NLGRP) in Fort Collins, Colorado, equilibrates *Malus* seeds at 23% relative humidity at 5 °C, and equilibrated seeds are kept in liquid nitrogen vapor (Vertucci and Roos 1990).

Although more than 28,000 apple accessions are maintained in more than 50 genebanks around the world (Volk, unpublished data), a survey of 35 major collections revealed that the USDA-ARS NPGS Plant Genetic Resources Unit in Geneva, NY, is the primary conservation site for native North American *Malus* species with 100 seedlots (sampled from either populations or single trees in the wild) and 55 unique field trees of *M. angustifolia*, 51 seedlots and 41 unique field trees of *M. coronaria*, 52 seedlots and 39 unique field trees of *M. ioensis*, and 193 seedlots and 36 unique field trees of *M. fusca* (Table 11.1). In the NPGS, hundreds

Table 11.1 *Malus* (apple) species that are native to North America

		NPGS			
Taxon	Common name	Seedlots	Unique Trees	BGCI	IUCN
Malus angustifolia (Aiton) Michx	Southern Crab	100	55	23	n/a
Malus coronaria (L.) Mill	Sweet crab	51	41	53	n/a
Malus fusca (Raf.) C. K. Schneid	Oregon Crab	193	36	54	Least concern
Malus ioensis (Alph. Wood) Britton	Iowa Crab	52	39	50	n/a

Common name, number of accessions in the USDA-ARS National Plant Germplasm System (NPGS), number of accessions in the Botanic Gardens Conservation International (BCGI 2017), number of accessions in the Genesys database (Genesys 2017), and Red list status according to the International Union for Conservation of Nature (IUCN 2017) are provided of thousands of *Malus* seeds are conserved from plant exploration collection trips and from hand-pollinated crosses among species representatives in the collection (Volk et al. 2015a).

Other national apple genebanks with North American *Malus* species are as follows: *Malus angustifolia* (1 accession in Germany), *M. coronaria* (5 accessions in Belarus, 9 accessions in Germany, 30 accessions in Lithuania, 2 accessions each in Russia and the UK, and 1 accession in the Netherlands), and *M. ioensis* (6 accessions in Germany, 5 accessions in Lithuania, 2 accessions in Russia, and 1 accession each in Belarus, Italy, Poland, and the Netherlands) (collection curators, personal communication). The PlantSearch Botanic Gardens Conservation International (BGCI) database reveals 23 accessions of *M. angustifolia*, 53 accessions of *M. coronaria*, 50 accessions of *M. ioensis*, and 54 accessions of *M. fusca* held at botanic gardens (BCGI 2017).

Malus angustifolia is classified as threatened in Florida, endangered in Illinois, and of special concern in Kentucky (USDA Plants 2017). *Malus coronaria* is endangered in the state of New York, while *M. ioensis* and *M. fusca* are not considered to be endangered (USDA Plants 2017). None of the North American *Malus* species are listed as a concern by the IUCN (IUCN 2017).

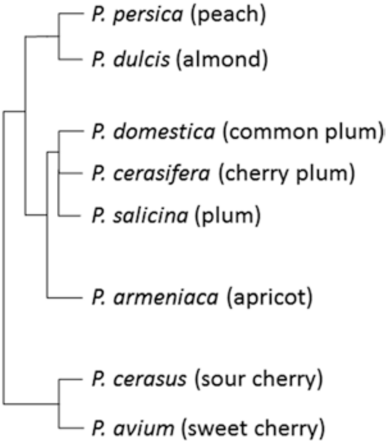
11.3 *Prunus* Genetic Resources Native to North America

11.3.1 Introduction

Prunus exhibits a wide range of environmental diversity, including species adapted to tropical to temperate climates and even taxa thriving in desert conditions (Liu et al. 2013). The most frequently cultivated species within the genus include *Prunus persica* (L.) Batsch (peach), *Prunus dulcis* (Mill.) D. A. Webb (almond), *Prunus domestica* L. (common plum), *Prunus cerasifera* Ehrh. (cherry plum), *Prunus salicina* Lindl. (plum), *Prunus armeniaca* L. (apricot), *Prunus cerasus* L. (sour cherry), and *Prunus avium* (L.) L. (sweet cherry) (Badenes and Parfitt 1995). Genetic relationships among these species are shown in Fig. 11.4, adapted from phylogenetic analyses performed by Badenes and Parfitt (1995) and Chin et al. (2014).

There are 154 wild species of *Prunus* that are globally distributed, including in regions of Africa, temperate Asia, tropical Asia, Europe, North America, and South America (USDA 2017). Of these wild *Prunus* species, 31 are native to North America, and many have potential for use in either scion or rootstock breeding (Figs. 11.5 and 11.6; USDA 2017). For example, *Prunus emarginata* (Douglas) Eaton exhibits disease resistance of interest for sweet cherry breeding, *Prunus geniculata* R. M. Harper and *Prunus subcordata* Benth. may provide drought resistance; *Prunus hortulana* L. H. Bailey and *Prunus umbellata* Elliott may offer disease resistance, and *Prunus nigra* Aiton may offer cold resistance for plum breeding; *Prunus maritima* Marshall may offer salt tolerance for peach breeding, and *Prunus serotina* Ehrh. may offer cold hardiness and disease resistance for sweet cherry breeding (Table 11.2; USDA 2017).

Fig. 11.4 Generalized genetic relationships among cultivated *Prunus* species, adapted from Chin et al. (2014) and Badenes and Parfitt (1995)



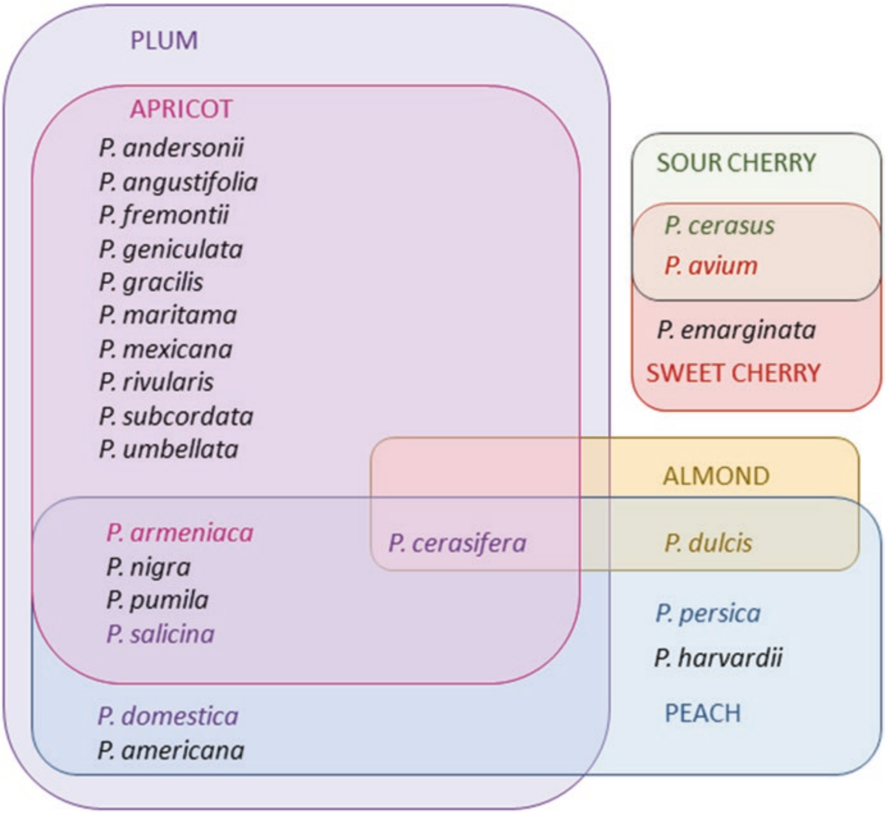


Fig. 11.5 North American *Prunus* species that are classified as crop wild relatives for scions of cultivated *Prunus* species plum, apricot, sour cherry, sweet cherry, almond, and peach. Species that share a region of the Venn diagram are crop wild relatives of the cultivated fruit listed for that shaded region in the chart. Crop wild relative data was acquired from GRIN-Global (USDA 2017)

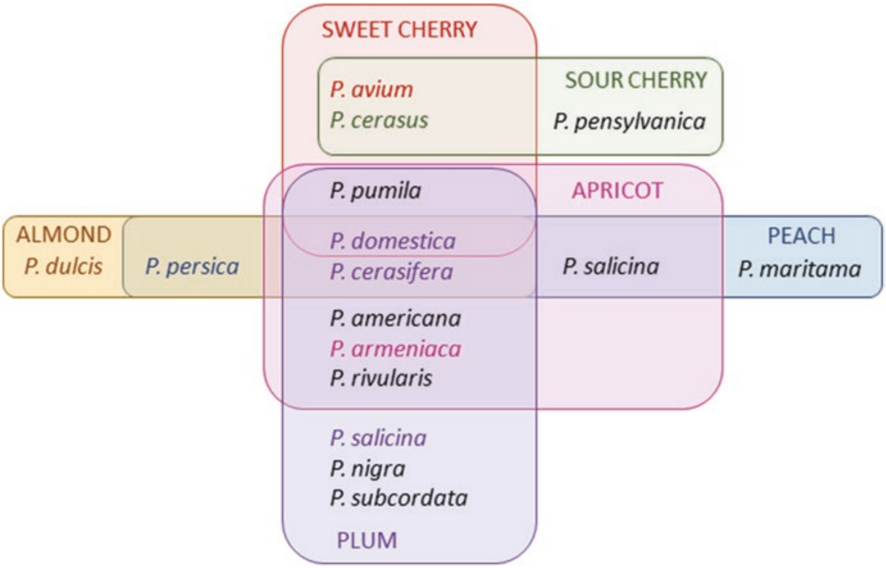


Fig. 11.6 North American *Prunus* species that are classified as crop wild relatives for rootstocks of cultivated *Prunus* species plum, apricot, sour cherry, sweet cherry, almond, and peach. Species that share a region of the Venn diagram are crop wild relatives of the cultivated fruit listed for that shaded region in the chart. Crop wild relative data was acquired from GRIN-Global (USDA 2017)

North American *Prunus* species have been utilized by indigenous peoples for millennia and continue to be important today. For example, *Prunus americana* Marshall fruit was eaten fresh or made into sauce by Native Americans on the prairies. *Prunus angustifolia* Marshall fruit was consumed fresh or dried and consumed by Native Americans as well as early explorers. Settlers cultivated *P. angustifolia* trees to use the fruit for wine, jam, and jelly (USDA-NRCS 2009c). *Prunus virginiana* L. was a staple for Native Americans on the plains and prairies, where it was cooked or dried to remove the bitter taste. Fruits were eaten whole or pulverized, shaped into balls, dried, and stored (USDA-NRCS 2016). *Prunus virginiana* was also included in recipes for pemmican (pounded dried meat, bone marrow, animal lard, and chokecherries). Settlers used *P. virginiana* fruit to make preserves by cooking, straining seeds and skins, and mixing them with wild plums and crabapples and adding sugar. *Prunus virginiana* fruits were also added to soups and stews as thickener. More recently, *P. virginiana* fruits have been consumed as preserves, juice, jelly, and syrup (USDA-NRCS 2016). *Prunus serotina* Ehrh. fruits have been consumed raw and as wine and jelly (USDA-NRCS 2008b). *Prunus ilicifolia* (Nutt. Ex Hook. & Arn.) D. Dietr. pits were first leached to remove hydrocyanic acid and were then ground into meal for use as a base for soup or to make tortilla or tamale-like foods. The fruits were also roasted and mashed into cakes or balls (USDA-NRCS 2008c).

Table 11.2 *Prunus* species that are native to North America

Taxon	Common name	Subgenus	Clade	NPGS	BGCI	IUCN	Conservation status (at the state level)	Use	Distribution
Prunus americana Marshall	American plum	*Prunus*	American	5	58	Least concern	NH (T), VT (T)	Ornamental, food, graft stock, tertiary relative of apricot, peach, and plum; secondary relative of myrobalan plum	
Prunus andersonii A. Gray	Desert peach	*Amygdalus*		0	10	n/a		Tertiary relative of apricot, Japanese plum, myrobalan plum, plum	
Prunus angustifolia Marshall	Cherokee or Chickasaw plum	*Prunus*	Chickasaw	1	17	n/a	NJ (E)	Ornamental, fruit, graft stock	N Central, NE United States, NW United States, South Central United States, SE United States
Prunus caroliniana (Mill.) Aiton	Carolina laurel cherry	*Laurocerasus*		0	37	n/a		Ornamental, vertebrate poison	
Prunus cercocarpifolia Villareal				0	0	n/a			
Prunus emarginata (Douglas) Eaton	Bitter cherry			0	21	Least concern		Host of crop pests, revegetator, disease resistance for sweet cherry, graft stock	Northern Mexico, NW United States, S Central United States, SW United States, W Canada

Prunus eremophila Prigge				0	0	n/a			SW United States
Prunus fasciculata (Torr.) A. Gray	Desert almond	*Amygdalus*		0	17	n/a			N Mexico, SW United States
Prunus fremontii S. Watson	Desert apricot	*Amygdalus*		0	11	n/a			N Mexico, SW United States
Prunus geniculata R. M. Harper	Scrub plum	*Prunus*	Beach	0	5	n/a	FL (E)	Drought resistance for plum	SE United States
Prunus gracilis Engelm. & A. Gray	Oklahoma plum	*Prunus*	Chickasaw	0	1	Least concern			N Central United States, NW United States, South Central United States, SE United States
Prunus havardii (W. Wight) S. C. Mason	Havard's plum	*Amygdalus*		0	2	Data deficient			S Central United States
Prunus hortulana L. H. Bailey	Hortulan plum	*Prunus*	American	0	6	Least concern		Ornamental, fruit, disease resistance for Japanese plum and myrobalan plum, graft stock for peach, plum	North Central United States, NE United States, SE United States
Prunus ilicifolia (Nutt. ex Hook. & Arn.) D. Dietr.		*Laurocerasus*		0	33	n/a			N Mexico, SW United States
Prunus maritima Marshall	Beach plum	*Prunus*	Beach	1	32	Data deficient	ME (E), MD (E), PA (E), CT (E)	Ornamental, fruit, graft stock relative for peach, salt tolerance in peach	NE United States, SE United States

(continued)

Table 11.2 (continued)

Taxon	Common name	Subgenus	Clade	NPGS	BGCI	IUCN	Conservation status (at the state level)	Use	Distribution
Prunus mexicana S. Watson	Mexican plum	*Prunus*	American	2	28	Least concern	OH (PRX)	Graft stock for peach	N Central United States, NE United States, N Mexico, South Central United States, SE United States
Prunus microphylla (Kunth) Hemsl.				0	0	n/a			Northern and Southern Mexico
Prunus minutiflora Engelm. ex A. Gray	Texas almond			0	2	n/a			N Mexico, S Central United States
Prunus murrayana E. J. Palmer	Murray plum	*Prunus*	Beach	0	0	Critically endangered			South Central United States
Prunus myrtifolia (L.) Urb.	Myrtle laurel cherry	*Laurocerasus*		0	2	n/a	FL (T)		Mexico, SE United States, Brazil, Caribbean, Western S America
Prunus nigra Aiton	Black plum	*Prunus*	Chickasaw	0	32	n/a	IA (E), OH (PRX)	Ornamental, fruit, cold tolerance for plum, graft stock for plum,	
Prunus x *orthosepala* Koehne				0	1	n/a			North Central United States

Prunus pensylvanica L. f.	Bird cherry	*Cerasus*		1	49	Least concern	IN (R)	Ornamental, graft stock for sour cherry, vertebrate poison	E Canada, N Central United States, NE United States, NW United States, SE United States, Subarctic Am, Western Canada
Prunus pumila L.	Dwarf cherry	*Prunus*		1	101	n/a	AR (T), PA (R), TN (T), MA (T), RI (SC), OH (PRX)	Graft stock for plum,	E Canada, N Central United States, NE United States, NW United States, SE United States, SW United States, W Canada
Prunus rivularis Scheele	Creek plum	*Prunus*	American	1	4	Data deficient		Ornamental, fruit, graft stock of apricot, plum	
Prunus salasii Standl.				0	5	n/a		Ornamental, shade/shelter	S Mexico, Central America
Prunus serotina Ehrh.	Black cherry	*Padus*		2	163	n/a		Ornamental, cold hardiness in sweet cherry, disease resistance in sweet cherry, wood, folklore, vertebrate poisons, weed	E Canada, N Central United States, NE United States, N Mexico, S Central United States, SE United States, S Mexico
Prunus subcordata Benth.	Pacific plum	*Prunus*		0	7	Least concern		Ornamental, fruit, drought resistance for plum, graft stock for plum,	NW United States, SW United States

(continued)

Table 11.2 (continued)

Taxon	Common name	Subgenus	Clade	NPGS	BGCI	IUCN	Conservation status (at the state level)	Use	Distribution
Prunus texana D. Dietr.	Peachbush	*Prunus*		0	2	n/a			S Central United States
Prunus umbellata Elliott	Allegheny plum	*Prunus*	Chickasaw	1	13	Least concern		Disease resistance in Japanese plum	
Prunus virginiana L.	Chokecherry	*Padus*		1	150	n/a	TN (SC)	Revegetator for land reclamation, potential for cold hardiness, wood, folklore, vertebrate poison	E Canada, N Central United States, NE United States, NW United States, South Central United States, SE United States, SW United States, Subarctic America, Western Canada

Common name, subgenus, clade, number of accessions in the USDA-ARS National Plant Germplasm System (NPGS), number of accessions in the Botanic Gardens Conservation International (BCGI 2017), number of accessions in the Genesys database (Genesys 2017), and Red list status according to the International Union for Conservation of Nature (IUCN), use, and distribution region are provided. State status data are classified as endangered (E), threatened (T), rare (R), special concern (SC), and presumed extirpated (PRX) (USDA Plants 2017)

Medicinally, *P. virginiana* juice has been used by Native Americans for postpardum hemorrhage, diarrhea, and sore throats. In addition, boiled bark infusions were used for coughs, chills, and fevers. Warm tea was provided for labor pains, colds, and rheumatism, to stop bleeding, stomach aches, diarrhea, and dysentery. Bark was used as a rinse for open sores, burns, and skin ulcers (USDA-NRCS 2016). In Appalachia, *P. serotina* inner bark was used as a cough remedy, tonic, and sedative (USDA-NRCS 2008b). *P. angustifolia* was used as a diarrhea remedy and for relief from canker sores (USDA-NRCS 2009c). Bark infusions of *P. ilicifolia* were used to treat colds and coughs. *Prunus emarginata* infusions were used to treat tuberculosis, heart troubles, and cure-all tonics, as well as respiratory ailments and contraceptives (USDA-NRCS 2008a; Turner and Hebda 1990).

Products from North American native *Prunus* species include brooms (*P. angustifolia*), bark baskets, joint coverings on underwater harpoons, spears, fishing lines and nets and the backing of the shafts of bows and covering for the joint between arrowheads and shafts (*P. emarginata*), and for arrow shafts and bows, tipi stakes and pins (*P. virginiana*) (Turner and Bell 1971; USDA-NRCS 2008a, 2009c, 2016). *P. virginiana* leaves and fruits were also used as dyes.

In the native landscape, *P. angustifolia* fruits are consumed by turkey, bear, wolves, foxes, grosbeaks, and ring-tailed cats (USDA-NRCS 2009c). *P. virginiana* fruits are consumed by birds, rabbits, hares, rodents, and bears (USDA-NRCS 2016). *P. serotina* fruits are consumed by birds, mammals, fox, black bear, raccoon, opossum, squirrels, and rabbits (USDA-NRCS 2008b). *Prunus emarginata* fruits are consumed by elk, mule deer, black bears, small mammals, and birds (USDA-NRCS 2008a). *P. maritima* has been used for stabilization and restoration of coastal sand dunes (USDA-NRCS 2009a), and *P. ilicifolia* is available from native plant nurseries for landscaping (USDA-NRCS 2008c). *Prunus pumila* is used for stream and lakeshore stabilization (USDA-NRCS 2009b).

11.3.2 Speciation and Taxonomic Relationships

The phylogenetic relationships among the genera within *Prunus* have recently been more clearly resolved. In the literature, taxonomic relationships have been described in many ways, usually dependent upon the markers selected for analyses. A generalized dendrogram illustrates genetic relationships among cultivated *Prunus* and North American native *Prunus* species based on nuclear and plastid DNA sequenced data published by Lee and Wen (2001), Shaw and Small (2004), Wen et al. (2008), Liu et al. (2013), and Chin et al. (2014) (Fig. 11.7).

Prunus taxonomists have identified three major clades of North American *Prunus* species that can be differentiated based on their ploidy and flower morphology. These include the diploid *solitary flower clade* (subgenera *Prunus*, *Amygdalus*), the diploid *corymbose clade* (subgenus *Cerasus*), and the polyploid *racemose clade* (subgenera *Padus*, *Laurocerasus*) (Fig. 11.8; Zhao et al. 2016). The solitary flower clade includes species with flowers that are borne individually. They are white, pink,

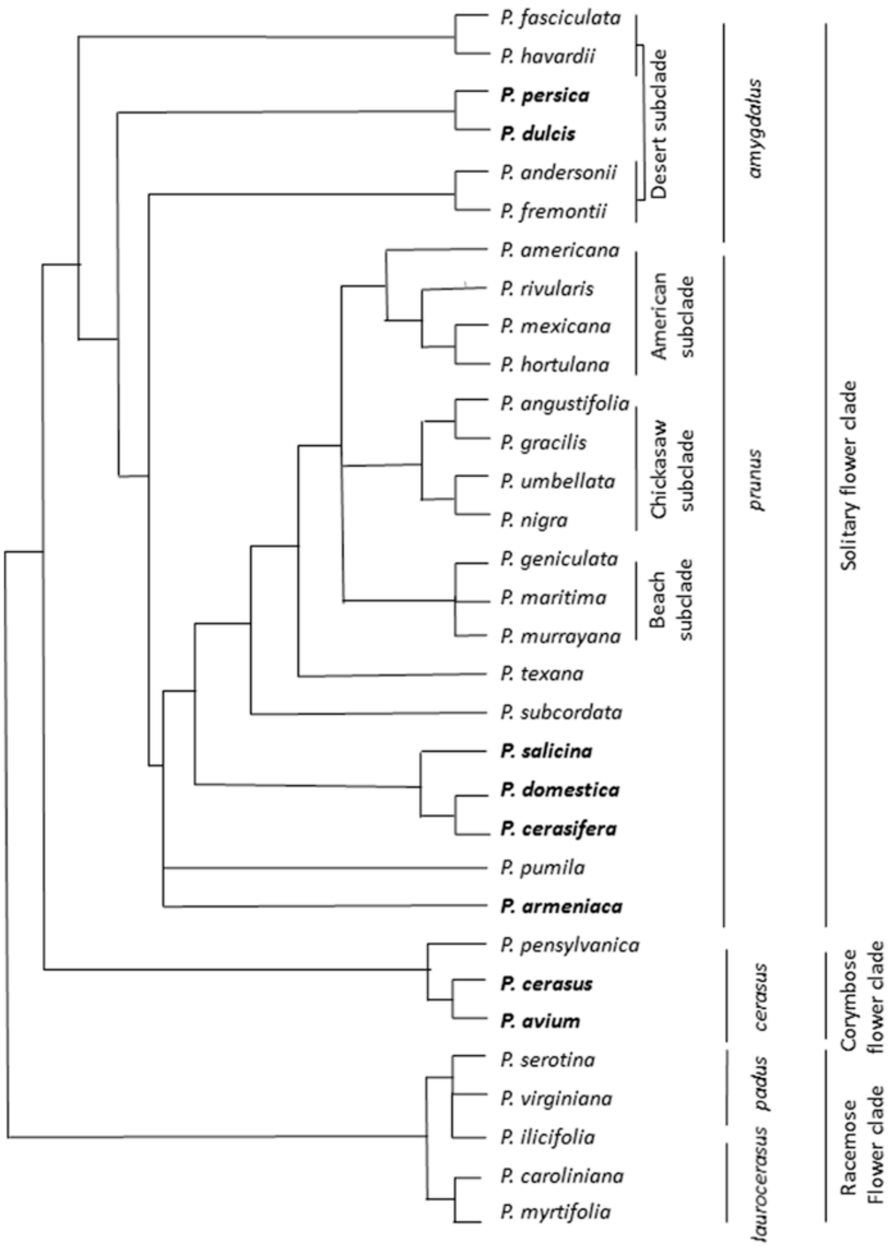


Fig. 11.7 Generalization of the genetic relationships among cultivated *Prunus* and North American native species based on nuclear and plastid DNA sequenced data published by Lee and Wen (2001), Shaw and Small (2004), Wen et al. (2008), Liu et al. (2013), and Chin et al. (2014). Branches are shown to demonstrate genetic relationships and their relative lengths are not significant. Cultivated species are in bold. Subgenera *Amygdalus*, *Prunus*, *Cerasus*, *Padus,* and *Laurocerasus* as well as American clade, Chickasaw clade, and Beach clades are indicated on the right

Fig. 11.8 Flower images of *Prunus* species classified as solitary ((**a**) *P. angustifolia* Marshall, (**b**) *P. andersonii* A. Gray), corymbose ((**c**) *P. pensylvanica* L. f., (**d**) *P. cerasus* L.), and racemose ((**e**) *P. virginiana* L., (**f**) *P. ilicifolia* (Nutt. ex Hook. & Arn.) D. Dietr.). Images were obtained online, made publicly available by (**a**) Homer Edward Price, (**b**) Matt Lavin, (**c**) Albert Herring, (**d**) Thomas Chao, (**e**) Nadia Talent, and (**f**) Curtis Clark

or red with five petals and five sepals. Corymbose clade flowers are on racemes, with the pedicels of the lower flowers longer than those of the upper flowers, such that the inflorescence is generally flat. In contrast, racemose clade flowers are distributed along an elongated raceme (Fig. 11.8). These clades are supported by plastid phylogenetic analyses (Fig. 11.7; Zhao et al. 2016).

The solitary flower clade can be further segregated into the Desert, American, Chickasaw, and Beach subclades. The North American solitary flower subclade species include Desert subclade *Prunus* species native to the Western and

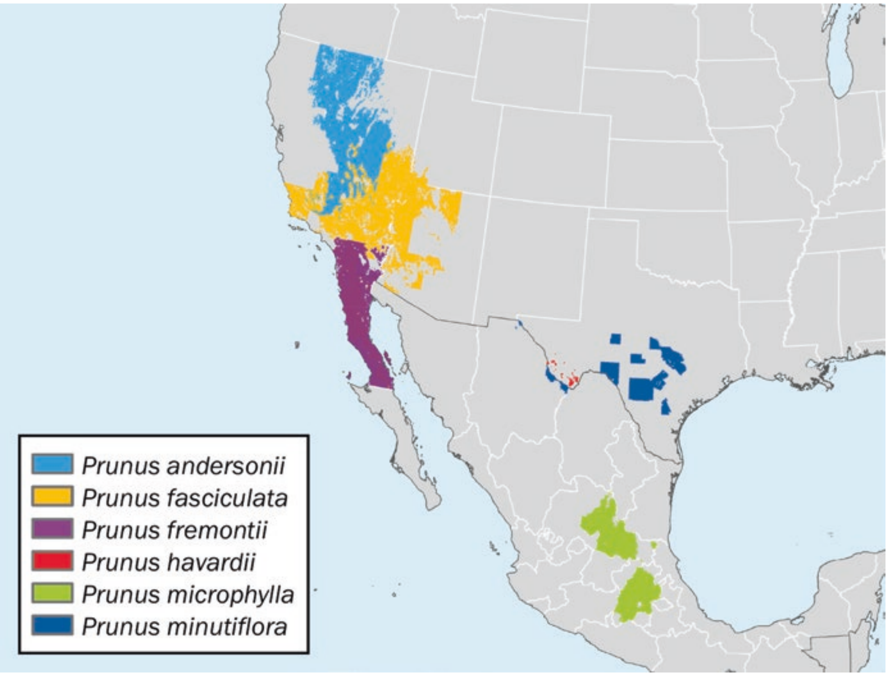


Fig. 11.9 Species distributions map of North American wild *Prunus* species in the solitary flower—desert species subclade for which geographic distribution data were available, including *P. andersonii* A. Gray, *P. fasciculata* (Torr.) A. Gray, *P. fremontii* S. Watson, *P. havardii* (W. Wight) S. C. Mason, *P. microphylla* (Kunth) Hemsl., and *P. minutiflora* Engelm. ex A. Gray. Potential distribution models are based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are given in Appendix 1

Southwestern United States and Mexico (subgenus *Amygdalus*): *Prunus fremontii* S. Watson, *Prunus fasciculata* (Torr.) A. Gray, *Prunus andersonii* A. Gray, *Prunus havardii* (W.Wight) S.C. Mason, *Prunus minutiflora* Engelm. Ex A. Gray, *Prunus eremophila* Prigge, and *Prunus microphylla* (Kunth) Hemsl. (Figs. 11.7 and 11.9) (Mason 1913; Chin et al. 2014; Wen et al. 2008). These desert species generally have pubescent fruit, deep taproots, and tolerance to extreme heat, cold, and/or drought conditions (Mason 1913). The American subclade *Prunus* species are *P. americana*, *Prunus Mexicana* S. Watson, *Prunus rivularis* Scheele, and *P. hortulana* (Northern and Eastern United States and Mexico) (Figs. 11.7 and 11.10). Chickasaw subclade *Prunus* species are *P. angustifolia*, *Prunus gracilis* Engelm. & A. Gray, *P. nigra*, *and P. umbellata* (Northern and Eastern United States) (Figs. 11.7 and 11.11). Beach subclade *Prunus* species are *P. maritima*, *P. geniculata*, and *Prunus murrayana* E. J. Palmer (Southern and Eastern United States) (Shaw and Small 2004, 2005) (Figs. 11.7 and 11.11). The solitary flower clade also includes *Prunus pumila* L. (sand cherry, Eastern and Central Canada, and Northern United States), *P. subcordata* (Pacific plum, Western United States), and *Prunus*

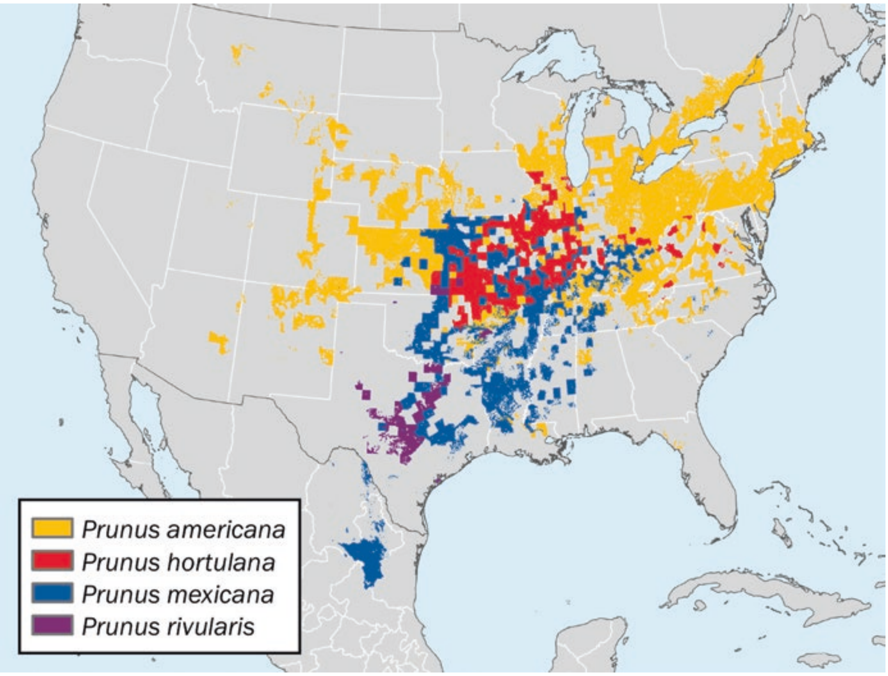


Fig. 11.10 Species distributions map of North American wild *Prunus* species in the solitary flower—American species subclade for which geographic distribution data were available, including *P. americana* Marshall, *P. hortulana* L. H. Bailey, *P. mexicana* S. Watson, and *P. rivularis* Scheele. Potential distribution models are based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are given in Appendix 1

texana D. Dietr. (wild peach, Texas) (Figs. 11.7 and 11.12). Classification information is incomplete for *P. cercocarpifolia*, *P. emarginata* (widespread), *Prunus eremophila* Prigge (Southwestern United States), and *Prunus salasii* Standl. (Mexico) and *Prunus* × *orthosepala* Koehne (North Central United States) (Fig. 11.13; USDA 2017; Villarreal 1989).

Prunus species with corymbose flower lineages (subgenus *Cerasus*) are native to Western North America (*P. emarginata*) and the Eastern United States (*Prunus pensylvanica* L. f.) (Figs. 11.7, 11.8, and 11.13).

The Racemose clade includes the *Prunus* subgenera *Laurocerasus* and *Padus* because they have racemose inflorescences, small flowers, and small floral bracts. They are differentiated because subgenus *Laurocerasus* is evergreen with naked peduncles and axillary inflorescences (Wen et al. 2008) and subgenus *Padus* is deciduous. Racemose flower-type lineages include *P. ilicifolia* (Western United States), *P. caroliniana*, and *P. myrtifolia* (subgenus *Laurocerasus*, Southeastern United States), with *Prunus caroliniana* (Mill.) Aiton and *Prunus myrtifolia* (L.) Urb., classified as a tropical racemose. *Prunus virginiana* and *P.*

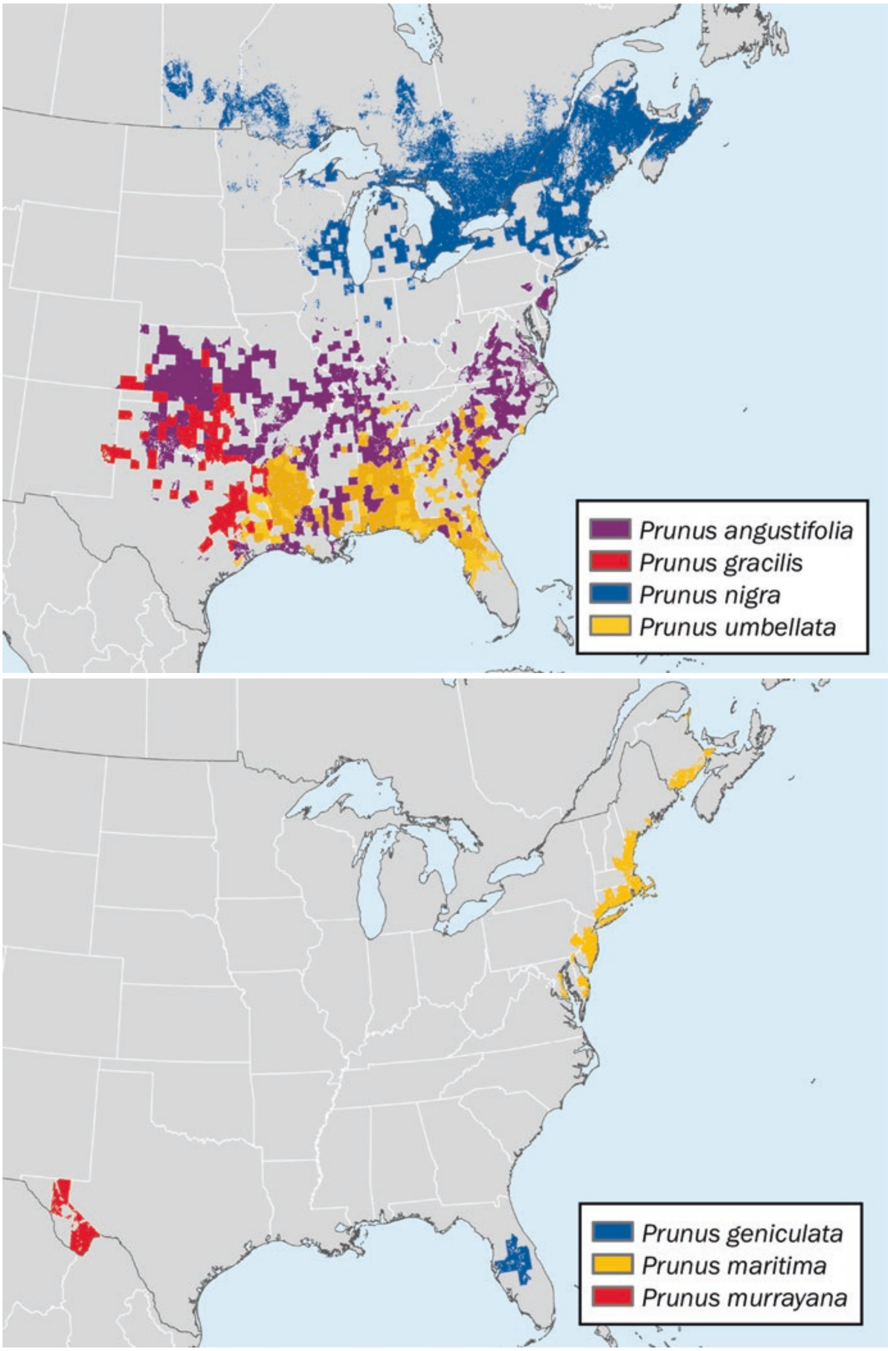


Fig. 11.11 Species distributions map of North American wild *Prunus* species in the solitary flower clade for which geographic distribution data were available, including (**a**) Chickasaw subclade species (*P. angustifolia* Marshall, *P. gracilis* Engelm. & A. Gray, *P. nigra* Aiton, and *P. umbellata* Elliott) and (**b**) Beach subclade species (*P. geniculata* R. M. Harper, *P. maritima* Marshall, and *P. murrayana* E. J. Palmer) clades. Potential distribution models are based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are given in Appendix 1

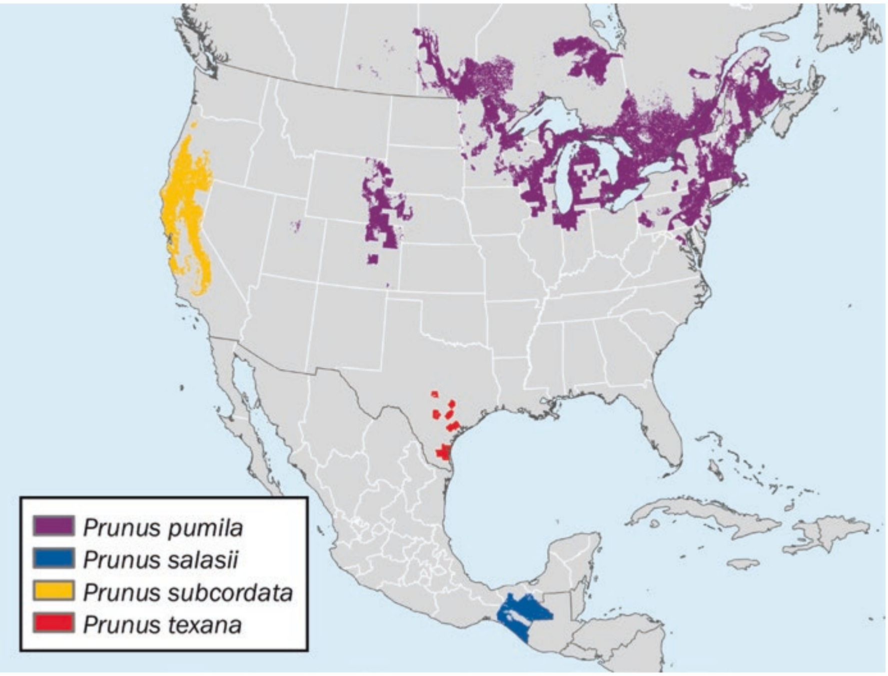


Fig. 11.12 Species distributions map of North American wild *Prunus* species in the solitary flower—other species for which geographic distribution data were available including *P. pumila* L., *P. salasii* Standl., *P. subcordata* Benth., and *P. texana* D. Dietr. Potential distribution models are based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are given in Appendix 1

serotina (subgenus *Padus*, East Coast of the United States) (Chin et al. 2014; Liu et al. 2013) (Figs. 11.7, 11.8 and 11.14) are temperate racemose.

The *Prunus* genus is believed to have appeared about 61 million years ago in eastern Asia, during the early Eocene epoch of the Paleogene period. During this time, the current North American and Asian continents were connected through the North Atlantic Land Bridge. The most recent common ancestor of the temperate *Prunus* was likely part of the boreotropical forests of the Northern hemisphere, while the most common recent ancestor of the tropical *Prunus* species was represented in remnants of boreotropical elements at lower latitudes (Chin et al. 2014).

The temperate forest flora were as far north as Alaska in the late Cretaceous period (99.6–65.5 mya) to the Eocene epoch (55.8–33.9 mya) and moved southward by the time of the Miocene epoch (23.03–5.332 mya). The cultivated solitary lineage (peach and almond) remained in Asia, traveling east to Europe (Eurasian plums *P. spinosa*), while the ancestors of the North American species traveled over the Bering Land Bridge to North America (*P. subcordata*, *P. fasciculata*, *P. havardii*, *P. americana*) (Chin et al. 2014). The corymbose lineage (*P. cerasus*) traveled from Central Asia to Europe (*P. mahaleb*, *P. avium*), over the North Atlantic Land Bridge into North America and down the east coast (*P. pensylvanica*), and over into the Western United States (*P. emarginata*) (Chin et al. 2014). The racemose lineage

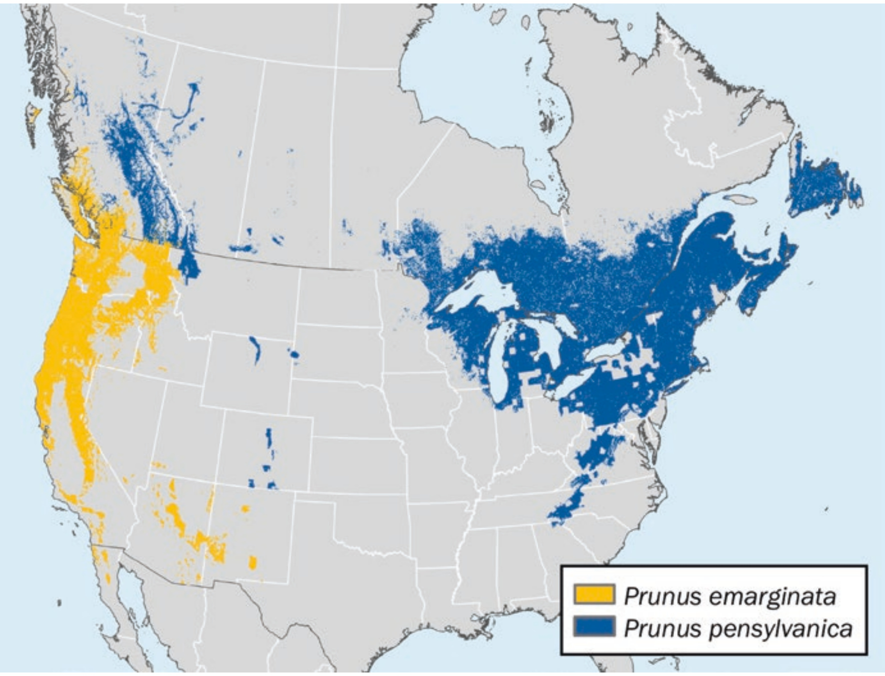


Fig. 11.13 Species distributions map of North American wild *Prunus* species in the corymbose flower clade for which geographic distribution data were available including *P. emarginata* (Douglas) Eaton and *P. pensylvanica* L. f. Potential distribution models are based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are given in Appendix 1

started in Asia and went over the North Atlantic Land Bridge into Eastern North America (*P. virginiana* and *P. serotina*). It also traversed over the Bering Land Bridge into the Western United States (*P. ilicifolia*, *P. caroliniana*) and south to Central America (Chin et al. 2014).

11.3.3 Conservation

Prunus cultivars and wild species are valued for their edible, ornamental, and native landscape value and, as such, are conserved in genebanks, in botanical gardens, and on public lands. The USDA-ARS NPGS *Prunus* collection is maintained at the National Clonal Germplasm Repository for Tree Fruit and Nuts and Grapes in Davis, California (all *Prunus* species except *P. cerasus*), and at the Plant Genetic Resources Unit in Geneva, New York (*P. cerasus*). The NPGS collections include many accessions of cultivated *Prunus* species (*P. armeniaca*, 146 accessions; *P. avium*, 70 accessions; *P. cerasifera*, 29 accessions; *P. cerasus*, 111 accessions; *P.*

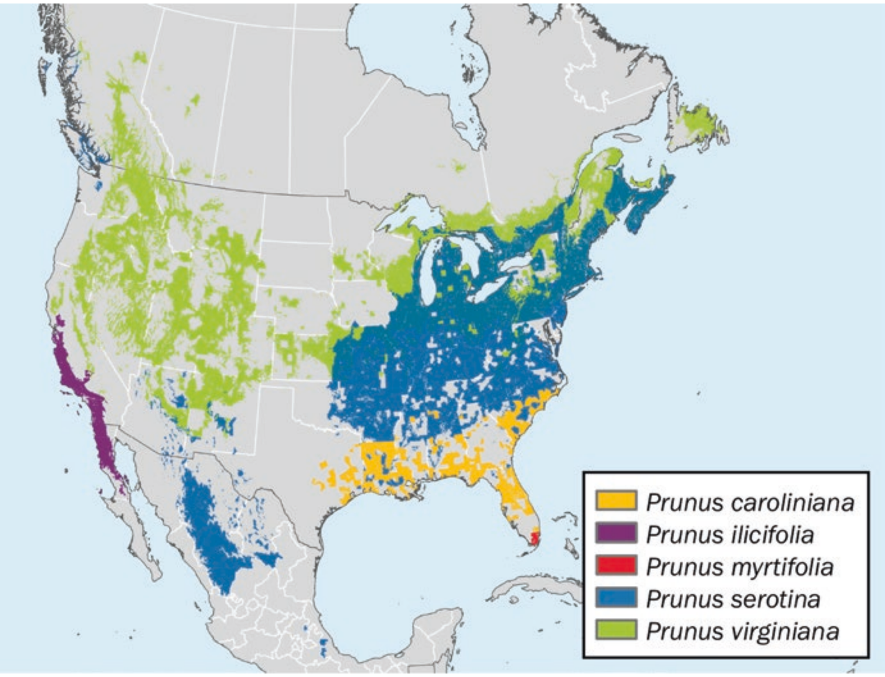


Fig. 11.14 Species distributions map of North American wild *Prunus* species in the racemose flower clade for which geographic distribution data were available including *P. caroliniana* (Mill.) Aiton, *P. ilicifolia* (Nutt. ex Hook. & Arn.) D. Dietr., *P. myrtifolia* (L.) Urb., *P. serotina* Ehrh., and *P. virginiana* L. Potential distribution models are based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are given in Appendix 1

domestica, 71 accessions; *P. dulcis*, 172 accessions; *P. persica*, 319 accessions; *P. salicina*, 40 accessions) as well as representatives of wild species (Table 11.2). *Prunus* accessions in the NPGS genebanks are currently conserved as field-grown trees, and 33 *P. cerasus* accessions are backed up at the NLGRP as dormant bud scions. *Prunus* seeds are considered to be orthodox (although they may require some modified handling procedures, SID 2017; Walters et al. Chapter 10), and *Prunus* pollen can also be conserved (Parfitt and Almehdi 1984). Seeds and pollen could conserve diversity of CWR in a cost-effective manner. Accessions of wild *Prunus* species conserved in botanic gardens are listed in Table 11.2.

Some North American *Prunus* species are listed by the IUCN, including critically endangered *P. murrayana*, near threatened *P. minutiflora* and *P. texana*, and data deficient P. *havardii*, *P. maritima*, and *P. rivularis* (IUCN 2017). In addition, *P. geniculata* has a global distribution of four counties in Central Florida and is listed as federally endangered by the US Endangered Species Act (Shaw and Small 2004; USDA Plants 2017). Many other North American *Prunus* species are listed as endangered, threatened, or of special concern in specific states (Table 11.2) (USDA Plants 2017).

11.4 *Diospyros* Genetic Resources Native to North America

11.4.1 Introduction

Asian persimmons (*Diospyros kaki* Thunb.) are large, sweet fruit often marketed in grocery stores (Fig. 11.15). *Diospyros kaki* are cultivated in the United States in hardiness zones 7–10 and are produced in the San Joaquin Valley of California. North American persimmons (*Diospyros virginiana* L.) are also edible, but they are smaller, astringent when unripe, and limited to the eastern regions of the United States (hardiness zones 5–9) (Fig. 11.15). Development of American persimmons as a commercial crop (other than local markets) has been challenged by the need for long seasons for ripening, the small fruit size, nonuniform fruit quality, many seeds, and poor storage, shipping, and processing traits. Despite these challenges, cultivars of American persimmons have been selected and bred since the 1880s. *D. virginiana* can also serve as a rootstock to impart cold resistance to *D. kaki* (Briand 2005).

Diospyros species are economically valued as fresh fruit but are also recognized as a source of ebony (decorative wood) and for their ethnobotanical uses (Mallavadhani et al. 1998). Studies have identified *Diospyros canaliculata* DeWild. and *Diospyros crassiflora* Hiern extracts as having antimicrobial activities against tuberculosis and gonorrhea (Kuete et al. 2009). In addition, persimmon leaves, con-

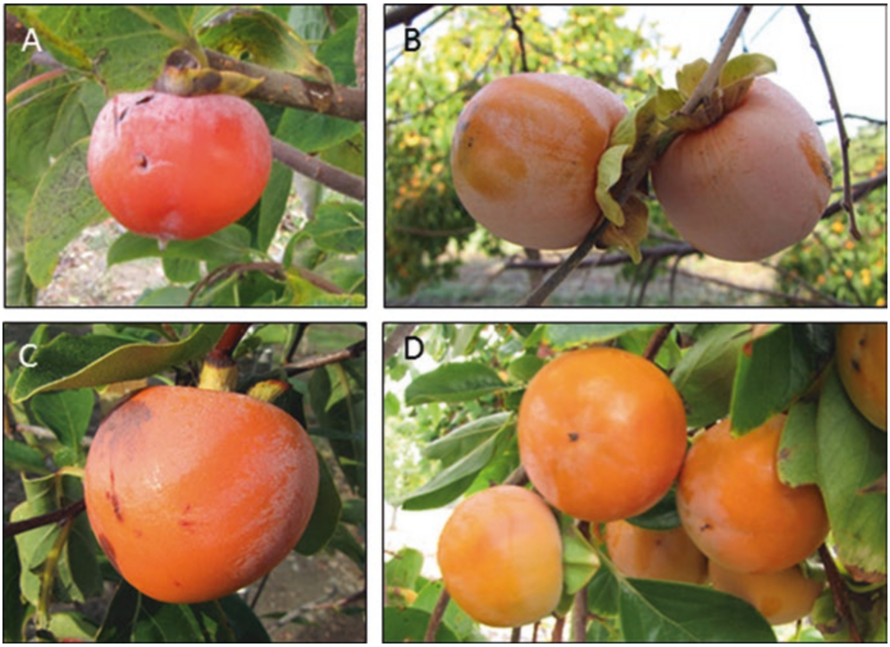


Fig. 11.15 Fruit images of *Diospyros virginiana* L. ((**a**) DDIO 92; (**b**) DDIO 69) and *Diospyros kaki* Thunb. ((**c**) DDIO 109 “Nuui Nai”; (**d**) DDIO 36 “Fuyu”). Identification numbers refer to accessions in the USDA-ARS National Plant Germplasm System. Images were taken by Jenny Smith and downloaded from GRIN-Global (USDA 2017)

sumed as beverages in Chinese folk medicine, have high levels of flavonoids, resulting in antioxidant and free radical scavenging activities (Sun et al. 2011). Extracts of *Diospyros* species exhibit insecticidal, insect growth regulator, piscicidal, molluscicidal, and fungicidal activities (Mallavadhani et al. 1998).

Diospyros virginiana has been consumed by Native Americans for centuries. Colonists used *D. virginiana* to make dried pulp, puddings, pies, syrups, and beverages (Briand 2005). In addition, persimmon fruits were used to make ink, seeds into buttons, and the bark as antiseptics as well as contra diarrhea, dysentery, diphtheria, dropsy, fevers, gonorrhea, hemorrhoids, syphilis, and thrush (Briand 2005).

There are 67 wild species of *Diospyros*, distributed in Africa, temperate Asia, tropical Asia, northern America, southern America, and the Pacific islands (USDA 2017). Of the 67 wild *Diospyros* species, eight are native to North America, including Mexico (*Diospyros conzattii* Standl., *Diospyros juruensis* A. C. Sm., *Diospyros rosei* Standl., *Diospyros sonorae* Standl., *Diospyros sphaerantha* Standl., and *Diospyros texana* Scheele) and the United States (*D. texana, D. virginiana*, and *Diospyros sandwicensis* (A. DC.) Fosberg). Within the United States, *D. texana*, the black persimmon, is native to Texas, *D. sandwicensis* is native to Hawaii, and *D. virginiana* is native to the north central, northeastern, southeastern, and south central regions (Fig. 11.16). *Diospyros digyna* Jacq. (black sapote) is a species native to Mexico and Central America and serves as an important food source (USDA 2017).

11.4.2 Speciation and Taxonomic Relationships

Diospyros species inhabit both temperate and tropical zones, and those in temperate zones (including *D. kaki* and *D. virginiana*) are less genetically diverse than tropical species (Yonemori et al. 2008). Although *D. kaki* and *D. virginiana* are both hexaploid and temperate-range, *D. kaki* is more closely related to diploid species *Diospyros oleifera* W. C. Cheng and *Diospyros glandulosa* Lace than it is to *D. virginiana* (Yonemori et al. 2008). It is possible that the ancestor of *D. virginiana* migrated from Asia to North America before the last ice age (Yonemori et al. 2008). *D. texana* is more closely related to South American species *Diospyros cayennensis* A. DC., *Diospyros longifolia* (Spruce ex Engl.) Sleumer & F. White, *Diospyros guianensis* (Aubl.) Gürke, and *Diospyros tetrandra* Hiern and is also associated with North American species *Diospyros crassinervis* (Krug & Urb.) Standl. (Cuba), *Diospyros tetrasperma* Sw., and *Diospyros yatesiana* Standl. Ex Lundell.

According to GRIN-Global, the primary economic species of *Diospyros* is *D. kaki*, whose tertiary species include *Diospyros glandulosa* Lace, *Diospyros glaucifolia* F.P Metcalf, *Diospyros lotus* L., and *Diospyros oleifera* and whose graft stocks include *D. glaucifolia*, *Diospyros japonica*, *D. lotus*, *D. oleifera*, and *D. virginiana* (USDA 2017; Wiersema et al. 2012).

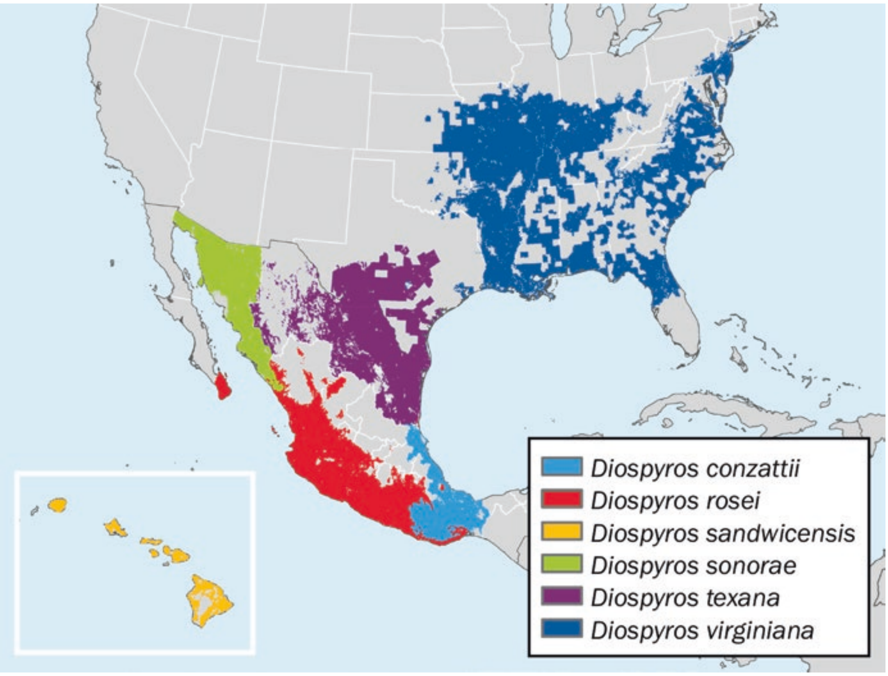


Fig. 11.16 Species distributions map of North American wild *Diospyros* species for which geographic distribution data were available including *D. conzattii* Standl., *D. rosei* Standl., *D. sandwicensis* (A. DC.) Fosberg, *D. sonorae* Standl., *D. texana* Scheele, and *D. virginiana* L. Potential distribution models are based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are given in Appendix 1

11.4.3 Conservation

Ex situ collections of *Diospyros* are traditionally conserved as field-grown trees in field genebanks. According to the Seed Information Database, *Diospyros* seeds are considered orthodox, intermediate, recalcitrant, or uncertain, depending on the species (SID 2017). *D. virginiana* seeds are desiccation tolerant and can survive overnight in liquid nitrogen (Pence 1991), and *D. texana* seeds are desiccation tolerant and can be stored for at least 2 years at ambient temperatures (Everitt 1984). In contrast, *D. sandwicensis* seeds cannot be dried or stored without significant loss of viability (Hawaiian Native Plant Propagation Database 2017).

Being the primary consumed species of persimmon, *D. kaki* has been the primary focus of genebanking efforts. The USDA-ARS NPGS *Diospyros* collection is maintained at the USDA-ARS National Clonal Germplasm Repository for Tree Fruit and Nut crops and Grapes in Davis, California. The collection has 55 *D. kaki* accessions and 3 *D. virginiana* accessions available for distribution (Table 11.3; USDA 2017). Additional North American native species of *Diospyros* are listed in the BGCI database (160 accessions of *D. virginiana* and 24 accessions of *D. texana*; Table 11.3; BCGI 2017).

Table 11.3 *Diospyros* (persimmon) species that are native to North America

Taxon	Common name	NPGS	BGCI	IUCN
Diospyros conzattii Standl.		0	0	n/a
Diospyros juruensis A. C. Sm.		0	0	n/a
Diospyros rosei Standl.		0	0	n/a
Diospyros sonorae Standl.		0	1	n/a
Diospyros sphaerantha Standl.		0	0	n/a
Diospyros texana Scheele	Black persimmon	0	24	n/a
Diospyros virginiana L.	American persimmon	6	160	n/a

Common name, number of accessions in the USDA-ARS National Plant Germplasm System (NPGS), number of accessions in the Botanic Gardens Conservation International (BCGI 2017), number of accessions in the Genesys database (Genesys 2017), and Red list status according to the International Union for Conservation of Nature (IUCN 2017) are provided

As a crop with great historical, cultural, and economic importance in Asia, *D. kaki* genetic resources are conserved in Japanese (343 accessions; NARO 2017) and Chinese (650 accessions; Ruan et al. 2009; Yang et al. 2013) national genebanks. The Chinese genebank field collection in Yangling, Shaanxi, has primarily *D. kaki* but also includes *D. lotus*, *D. glaucifolia*, *D. oleifera* (2n = 2x = 30), *D. rhombifolia* (2n = 2x = 60), *D. cathayensis*, and *D. virginiana* (2n = 2x = 90) which are valued as potential rootstocks. A multinational European project (GENRES 29) inventoried, characterized, and evaluated collections of *Diospyros* in Europe (Bellini and Giordani 2005). Four European collections in Italy and Spain had a total of 160 accessions. As part of this project, a *Diospyros* core collection was established with 25 accessions, including 23 *D. kaki* cultivars, and 1 accession each of *D. lotus* and *D. virginiana* (Bellini and Giordani 2005). Other countries that were developing persimmon collections include Romania (11 accessions), Czech Republic (28 accessions), Turkey (74 accessions), and Israel (Bellini and Giordani 2005).

Diospyros virginiana is protected in New York (threatened) and Connecticut (special concern) (USDA Plants 2017).

11.5 *Asimina* Genetic Resources Native to North America

11.5.1 Introduction

Pawpaws (*Asimina triloba* (L.) Dunal) are the largest native North American tree fruit (Fig. 11.17). Pawpaw fruits are high in vitamin C, potassium, magnesium, iron, copper, and manganese (Huang et al. 1998). Pawpaw fruits are not commercially produced in orchard settings, but can be found at farmers' markets in regions where trees produce fruit in the wild. The uneven ripening of fruit on trees and the short shelf life (2–4 days) have limited the commercial distribution of pawpaws (Archibold et al. 2003). A limited number of breeding programs have selected and named superior clones from the wild and have made some crosses to improve production and fruit quality traits (Peterson 2003).

Fig. 11.17 Fruit images of *Asimina triloba* (L.) Dunal (**a**, **b**) and a comparison of the relative fruit and seed size of *Asimina triloba* and *Asimina parviflora* (Michx.) Dunal (**c**). Images provided by John Ray

A. triloba are understory trees that are well adapted to low light conditions, reaching a maximum height of about 10 m (Hosaka et al. 2008; Slater and Anderson 2014). Trees produce root suckers, resulting in large stands of clonal trees. They also sexually reproduce and make seeds when grown in high light environments (Hosaka et al. 2016). Resulting seeds are distributed by raccoon, bear, coyote,

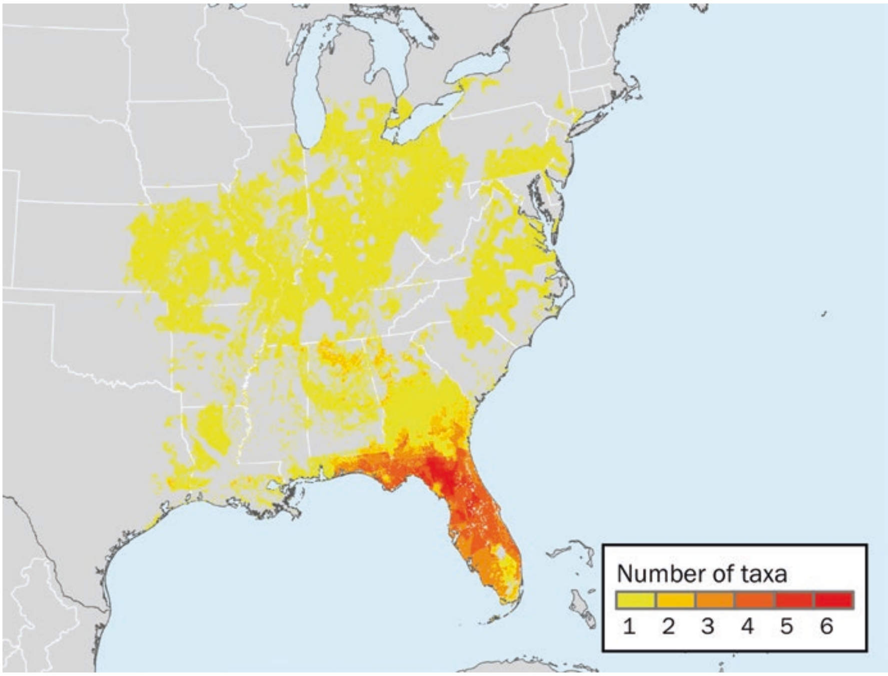


Fig. 11.18 Species richness map of modeled potential distributions of *Asimina* taxa, based on climatic and edaphic similarities with herbarium and genebank reference localities. Warmer colors indicate areas where greater numbers of taxa potentially occur in the same geographic localities. Full methods for generation of maps and occurrence data providers are given in Appendix 1

turkey, and white-tailed deer, who consume the fruit (Murphy 2001). Compounds in twigs, unripe fruit, seeds, roots, bark, and fruit are cytotoxic but also exhibit in vivo antitumor, pesticidal, antimalarial, antiviral, and antimicrobial properties (McLaughlin 2008; Pomper et al. 2009). Current commercialized products include shampoos to eliminate head lice, pesticidal sprays, oral herpes ointment, and an extract used as a botanical supplement for cancer patients (McCage et al. 2002; McLaughlin 2008).

There are nine wild species of *Asimina*, distributed exclusively in Northern America (USDA 2017). *A. triloba* is more widely distributed in the North Central, Northeastern, South Central, and Southeastern United States and Eastern Canada (Fig. 11.18). Southeastern United States *Asimina* species include *Asimina incana* (W. Bartram) Exell, *Asimina longifolia* Kral, *Asimina obovata* (Willd.) Nash, *Asimina parviflora* (Michx.) Dunal, *Asimina pygmaea* (W. Bartram) Dunal, *Asimina reticulata* Shuttlew. Ex Chapm., *Asimina tetramera* Small, and *Asimina* × *nashii* Kral. Some hybridization between *A. triloba* (found in river flood plains and stream bottoms) and *A. parviflora*, the dwarf pawpaw (found in the lower regions of well-drained slopes), was identified in South Carolina (Horn 2015) (Fig. 11.18).

11.5.2 Speciation and Taxonomic Relationships

Genetic diversity analyses have revealed high levels of diversity among populations of *A. triloba* (Huang et al. 1998). Based on assessments of geography, climate, and ecological conditions, 11 regions were identified for capturing the diversity of *A. triloba* (Huang et al. 1998). All the described *Asimina* species are diploid, except for *A. pygmaea*.

11.5.3 Conservation

The NPGS *Asimina* collection is at Kentucky State University as a satellite repository of the National Clonal Germplasm Repository in Corvallis, Oregon (Peterson 2003). This collection is maintained almost entirely as a field collection. According to the Seed Information Database, the seed storage behavior is "uncertain" (SID 2017); however there are reports that seed germination rates are low due to desiccation sensitivity (Pomper et al. 2010).

The NPGS *Asimina* collection includes 1000 *A. triloba* accessions, with about 850 seedlings from its native range, 25 cultivars, and 125 crosses and advanced selections (Table 11.4). The collection also has one *A. longifolia* maintained in the greenhouse, three *A. triloba* × *A. obovata* hybrids, and ten *A. triloba* × *A. reticulata* hybrids (Sheri Crabtree, personal communication). Two other large *A. triloba* collections are maintained by the University of Maryland (900 seedling trees planted in 1981) and by Neal Peterson (400 specimens of F3 hybrids between *A. triloba*, *A. reticulata*, and *A. obovata*) (Neal Peterson, personal communication). The BGCI lists 172 accessions of *A. triloba*, 15 accessions of *A. parviflora*, 7 accessions of

Table 11.4 *Asimina* (pawpaw) species that are native to North America

Taxon	Common name	NPGS	BGCI	IUCN
Asimina incana (W. Bartram) Exell	Flag pawpaw	0	0	n/a
Asimina longifolia Kral		1	1	n/a
Asimina x *nashii* Kral		0	1	n/a
Asimina obovata (Willd.) Nash	Flag pawpaw	0	2	n/a
Asimina parviflora (Michx.) Dunal	Dwarf pawpaw	0	15	n/a
Asimina pygmaea (W. Bartram) Dunal	Dwarf pawpaw	0	1	n/a
Asimina reticulata Shuttlew. ex Chapm.	Flag pawpaw	0	0	n/a
Asimina tetramera Small	Four-petal pawpaw	0	7	Endangered
Asimina triloba (L.) Dunal[a]	Pawpaw	1000	172	n/a

Common name, number of accessions in the USDA-ARS National Plant Germplasm System (NPGS), number of accessions in the Botanic Gardens Conservation International (BCGI 2017), number of accessions in the Genesys (2017) database, and Red list status according to the International Union for Conservation of Nature (IUCN 2017) are provided

[a] 850 seedlings from the *Asimina triloba* native range, 25 cultivars, 125 crosses and advanced selections

A. tetramera, 2 accessions of *A. obovata*, and 1 accession each of *A. longifolia*, *A.* × *nashi*, and *A. pygmaea* (BCGI 2017) (Table 11.4).

Asimina tetramera is listed as endangered in Florida, and *Asimina triloba* is listed as endangered in New Jersey and threatened in New York (USDA Plants 2017).

11.6 Conclusions

Native North American tree fruit species have been important to humankind for millennia. The importance of these species will likely increase as researchers develop a better understanding of the genetic potential of North American CWR. Most of the North American temperate tree fruit CWR are poorly represented within genebanks and unexplored with respect to their value to plant breeding, horticulture, and restoration. This underscores the need to identify and document the spatial distributions of wild populations, particularly for *Prunus* and *Diospyros* species. With this information, plans could be developed for complimentary ex situ and in situ conservation efforts to ensure the long-term protection of CWR species, particularly those that have poorly described or very limited geographic distributions (such as *P. havardii*, *P. rivularis*, *P. hortulana*, *P. geniculata*, *P. murrayana*, *P. minutiflora*, *P. salasii*, *P. texana*, *P. myrtifolia*, and *P. rivularis*). Genetic diversity assessments within and among species across their distribution ranges will reveal localized diversity, and key population target for conservation, as well as evidence of hybridization. Given the expense of field collections, it may be preferable to conserve seeds that represent wild species populations and maintain only selected numbers of species exemplars in field collections for phenotypic assessments and distribution.

New breeding methods will facilitate the incorporation of specific genes (such as those that may provide abiotic or biotic stress resistance) from wild species into cultivars that have desirable production traits. Genebanks will play a key role in ensuring long-term access to genetic resources for future generations.

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Chapter 12
Crop Wild Relatives of Avocado, Mamey Sapote, and Cherimoya

C. H. Avendaño-Arrazate, E. Campos-Rojas, J. Andres Agustin, S. Espinosa-Zaragoza, and G. Sandoval Cancino

Abstract Avocado, mamey sapote, and cherimoya are tropical fruits widely distributed in Mexico. These fruit species have played very important roles in the different cultures of Mexico, as food, medicine, cosmetics, and for rituals. Therefore, this chapter presents the economic, social, cultural, and environmental importance, risks, and threats each one of them has faced for hundreds of years and how cultures have maintained them through a series of strategies that have allowed them to be among the most important fruit trees in Mexico today. In addition, the strategies of conservation (in situ and ex situ), the advances in their use, and the challenges and expectations to continue maintaining their genetic diversity are presented here.

Keywords Tropical fruits · Diversity · Uses · Conservation ex situ · In situ · *Persea* · *Pouteria* · *Anona*

C. H. Avendaño-Arrazate (✉)
Cocoa Program, Experimental Station Rosario Izapa-INIFAP, Tuxtla chico, Chiapas, Mexico
e-mail: avendano.carlos@inifap.gob.mx

E. Campos-Rojas
Department of Phytotechnology, Universidad Autónoma Chapingo, Chapingo, Mexico

J. Andres Agustin
Chirimoya Centro Universitario de Oriente (CRUCO) Universidad Autónoma Chapingo, Chapingo, Mexico

S. Espinosa-Zaragoza
Faculty of Agricultural Sciences, Universidad Autónoma de Chiapas, Huehuetán, Chiapas, Mexico

G. Sandoval Cancino
National Genetic Resources Center, INIFAP, Tepatitlán de Morelos, Jalisco, Mexico
e-mail: sandoval.gabriela@inifap.gob.mx

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12.1 Avocado (*Persea americana* Mill.)

12.1.1 Origin of the Crop and Brief History of Use Worldwide

Avocado belongs to the genus *Persea*, which contains 85 species found between Southern United States and Chile. There are a few geographic exceptions, such as *Persea indica* (L.) Spreng. found in the Canary Islands and several recently described *Persea* (Chanderbali et al. 2001). Avocado is native to Mexico (Zentmyer 1985), with the oldest known remains (~8000 years old) found in Tehuacan, Puebla (Barrientos-Priego and López-López 2000). Ancient American cultures had substantial knowledge of avocado, as evidenced from the Florentine codex descriptions of three types of avocado: "aoacatl" may be *Persea americana* var. *drymifolia* (Cham. & Schltdl.) S.F. Blake (Mexican race), "tlacacolaocatl" may be *Persea americana* var. *American* Mill. (Antillean), and "quilaoacatl" may be *Persea americana* var. *guatemalensis* L.O. Williams (Guatemalan race) (Barrientos-Priego and López-López 2000). The *Codex Mendoza* also mentions avocado in the context tribute (Smith 1966). Specifically, the *Codex Mendoza* mentions the "Ahuacatla" tribe which is represented by a tree, and its root "ahuacatl" means "avocado or avocado tree." Therefore, Ahuacatla translates as "place of avocado tree"; there are still two villages with this name from ancient Mexico, Ahuacatlan in the state of Nayarit and Aguacatlan in Northern Guatemala.

The first Latin document that talks about avocado was written by Martín Fernández de Enciso (Suma de Geografía, published in 1519 in Sevilla, Spain) who found avocado in the village of Yaharo near Santa Marta in Colombia in 1519. Popenoe and Zentmyer (1997) wrote of Fernandez de Oviedo, historian of the conquistadors, who described avocado in 1526 as:

> a big tree with broad leaves similar to laurel but bigger and greener. They produce pears that weigh a pound or more, although some weigh less, and its color and shape is like pears, but the shell is somewhat thicker but softer, and in the center of fruit is a seed like a peeled chestnut ... and between this and the shell is the eatable part which is abundant and is very similar to butter paste and has exquisite flavor, and those who have these fruits saved it with great esteem and trees are wild as the others I mentioned, since the master gardener is God, and the Indians did not work it at all. These pears are excellent when eaten with cheese, and harvested and stored before they ripen, and when so treated mature perfectly to eat, but after they have reached this state rot quickly if allowed. ("Sumario de la Natural Historia de las Indias" mentioned by Popenoe 1963)

There are other references to avocado from the sixteenth century including those written by Cervantes de Salazar (Crónica de la nueva España), Fray Bernardino de Sahagún (History Historia de las cosas de la Nueva España), and Acosta (Historia Natural y Normal de las Indias). Pedro de Cieza described his experiences from 1532 to 1550 and reported the occurrence of avocados in several countries. The first record of avocado in Europe is Clusius (Rariorum Plantarum Historia) in 1601, who describes Mexican trees grown in Valencia, Spain. Fray Bernabé Cobo (Historia Del Nuevo Mundo, 1653) describes:

> "three different kinds of Aguacate". The fruit "is commonly the size of a quince, in some regions is as large as a small pumpkin or a large citron, varieties of the province of Yucatan in New Spain (Mexico) are of this kind. The avocado has a thin shell, softer and more flexible than lemon, green on the outside, and when the fruit is ripe; it is easily peeled. It has the largest seed I've seen in any fruit of the Indies or Europe. The second type is large, round and produced in the province of Guatemala, which does not have such smooth skin as the first. The third is a small avocado found in Mexico which resembles a fig in size, color and shape; some are round, others elongated, and the shell is so thin and smooth like a plum ... The name Aguacate is used in the language of Peru. In most of India is called avocado, which is the name given by the Indians to the Spanish. This was an accurate description of the three types of avocados now known: Antillean, Guatemalan and Mexican."

There is little precise data about the center of origin of avocado. Avocado distribution spans much of Mexico (Fig. 12.1), the states of Chiapas, Oaxaca, Quintana Roo, San Luis Potosi, Tabasco, Veracruz, and Yucatan (Rojas et al. 2007). Vegetation where the Mexican avocado race predominates is the pine-oak forest, while the Guatemalan race is in the cloud forests, and Antillean is in tropical rain forest, but there are only a few examples of the latter (Barrientos-Priego et al. 1992).

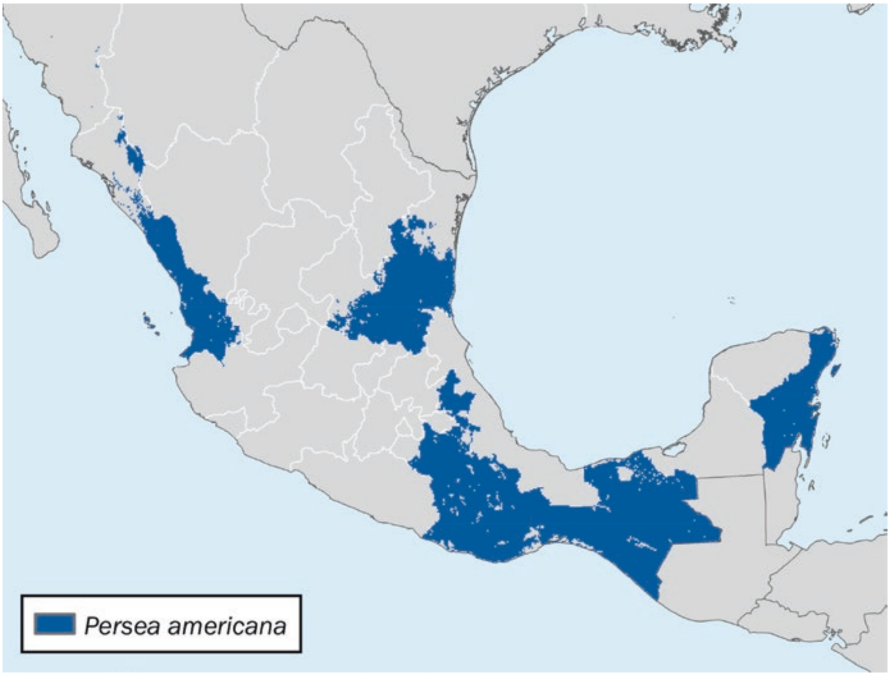

Fig. 12.1 Modeled potential distribution of *Persea americana* Mill. (avocado), based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

12.1.2 Current Use

The socioeconomic importance of avocado is large. Orchards create jobs in a wide range of fields. The importance of avocado in the international market has grown steadily, ceasing to be an exotic fruit and becoming a dietary staple of many countries. In 2010, the major avocado importing countries were the United States (47.1%), France (12.8%), Japan (6.1%), and Canada (4.9%). In addition to a large consumer market for fresh fruit, avocado oil is used for making cosmetics, soaps, and shampoos, and avocado fruit is used for processed foods, such as guacamole and pasta. The major exporting countries are Mexico (51.4% market share), followed by Israel (11.6%), Peru (9.4%), and South Africa (8.0%). Avocado is considered a healthy food, containing large amounts of vitamin E, folic acid, and glutathione, as well as ten essential minerals. Also, avocado contains important fatty acids, including mono- and polyunsaturated, especially the omega-9, omega-7, omega-6, and omega-3 (a chemopreventive; Cabrera 1996). Avocado also contains β-sitosterol, which prevents the accumulation of cholesterol. Avocado also contains ten essential amino acids (arginine, phenylalanine, histidine, isoleucine, leucine, lysine, methionine, threonine, tryptophan, and valine) which are required in protein synthesis and for better cellular metabolism (Werman and Neeman 1987). Pharmacological properties are attributed to avocado seed due to the presence of fatty acids (Werman and Neeman 1986), polyphenolic compounds (Valeri and Gimeno 1953), and sterols (Werman and Neeman 1987). Avocado has been used since antiquity against conditions such as muscle aches, parasites, and mycosis (Cabrera 1996; Argueta et al. 1994; Atzin 1990). Its leaves are also used as expectorants. Typical consumption includes salads, soups, stews, desserts, and drinks. The cosmetics industry uses avocado oils in lotions, soaps, creams, and shampoos (Argueta et al. 1994; Atzin 1990).

12.1.3 Challenges in Cultivation

The variety “Hass” is 90% of avocado production in Mexico and has been introduced into areas that traditionally cultivate other types such as San Cristobal de las Casas, Chiapas. The prevalence of “Hass” has led to a decrease in local cultivars. For example, in 1990 “Hass” avocado was rarely present in indigenous markets. Today local types are no longer found in markets. Undoubtedly, the abundance of “Hass” in markets has discouraged the sale of local avocados, and therefore it is likely that the local fruit trees are neglected. In fact, we’ve found that people in the area around Motozintla in South Chiapas planted seeds of avocados that they liked for decades, and this has generated great variability and an opportunity for biodiversity conservation. However, during an inspection in 2004, it was found that people are establishing “Hass” seeds, thus threatening avocado genetic diversity (Barrientos et al. 1995).

Another limitation is the interaction of climatic factors at farm sites. Despite its tropical origin, plantations are found in subtropical and Mediterranean locations. This wide adaptation is explained mainly by genetic diversity, marked by three horticultural races: West Indian (favored in equatorial zones), Mexican (has cold tolerance), and Guatemalan (intermediate) (Table 12.1). Ideal conditions are daytime temperatures between 25 and 30 °C and nights between 15 and 20 °C. Temperatures above 36 ° C cause serious damage, particularly in fertilization and curdling, and it is important that a cold period (around 10 °C) occurs in winter to stimulate floral induction. A spring and summer not very hot can lengthen the fruiting phase of some late cultivars, which allows to extend the collection period. In general, it is recommended to choose frost-free zones.

12.1.4 Crop Wild Relatives and Wild Utilized Species

Approximately 80–85 species are recorded in the Americas, and possibly 10–12 are native to Mexico (Storey et al. 1986, 1987; Zentmyer 1991; Rojas et al. 2007). Many of these species are moderately managed and harvested in the field. Important species that are often wild harvested include *Persea americana*, *P. floccosa* Mez., *P. nubigena* (Williams) (Kopp 1966), *P. steyermarkii*, *P. americana* var. *costaricensis* (Ben-Ya'acov et al. 2003), *P. americana var. americana* (Scora and Berg 1992; Scora et al. Mexicana, *P. americana* var. *Drymifolia* (Schlecht. & Blake)), and *P. americana* var. *Guatemalensis* Williams. Wild avocado and *P. schiedeana* (chinini) as shade trees on coffee plantations in Mexico (Soto-Pinto et al. 2000), with fruits and wood harvested. *Persea* species are frequently cut for charcoal or for timber or firewood. This is also a source of conservation (Moguel and Toledo 1999; Birnbaum et al. 2003).

Three races of avocado are recognized, Mexican, Guatemalan, and Antillean, and these are recognized as landraces. The botanical classification of these three races has been varied, some suggesting the Mexican race as a separate species, *Persea drymifolia* (Schltdl. & Cham.) S.F. Blake, while others classify the Guatemalan race as *Persea nubigena* var. *guatemalensis*. In 1987 Bergh and Ellstrand classified three races of avocado: the Mexican strain as *Persea americana* var. *drymifolia*, the Guatemalan race as *Persea americana* var. *guatemalensis*, and the Antillean race as *Persea americana* var. *americana*. Although Bergh (1992) later found the three races genetically separate, they are now generally grouped (Barrientos-Priego and López-López 2000). Many *Persea* are found throughout North America as can be seen from the species distribution (Fig. 12.2).

Currently, no institution has a program to monitor the diversity of avocado and related species in Mexico. In the most important production areas, native avocado and wild relatives have been decreasing due to the prevalence of the variety "Hass." Wild-type trees are being eliminated, as they are hosts of pests and pathogens that create phytosanitary barriers for export. These actions are eroding existing avocado germplasm in Mexico. Further, the introduction of *Phytophthora cinnamomi* Rand

Table 12.1 Principal morphological differences between races of avocado

Character	Mexican race	Guatemalan race	Costaricensis race	American race
Weather	Semitropic to temperate	Semitropic	Semitropic	Tropic
Altitude above sea level	Over 2000 m	1000–2000 m	800–1500 m	Less to 1000 m
Resistance to salinity	Less	Less	NA	More
Resistance to cold	More	Medium	Less	Less
Leaf				
Size	Less	Medium	Less	More
Color	Dark green	Dark green	Dark green	Pale green
Smell	Anise odor	Without anise odor	Without anise odor	Without anise odor
Flower				
Pubescence	More	Less	NA	Less
Stem				
Young bud	Pale green	Reddish	Pale green	Pale green
Trunk bark	No grooved	No grooved	No grooved	Grooved
Fruit				
Size	Variable, usually small	Medium size	Small	Variable, usually large
Pedicel	Cylindrical and medium	Conical and bulky	Cylindrical and regular	Nail head shape, and medium and high thickness
Perianto persistence	Higher	Higher	Higher	Less
Shell	Thin, smooth, and soft	Thick, brittle, and rough	Medium thickness, flexible, and smooth	Medium thickness, flexible, and soft
Seed	Adhered or loose and smooth or slightly rough cotyledons	Adhered and smooth cotyledons	Adhered and smooth cotyledons	Loose with rough cotyledons
Seed cover	Thin	Thin	Thin	Medium thick and membranous
Oil	High containment	Medium content	NA	Low content
Flavor	Usually aniseed	Lightly, occasionally nut	Light, no specific flavor	Light, often sweet; with a bitter taste at the end
Fiber in pulp	Common	No common	No common	No common
Period of flower to fruit (months)	6–9	10–16	NA	5–9
Relative size of the tree and growth habit	Medium open	High erect	Medium open	Medium open and high erect

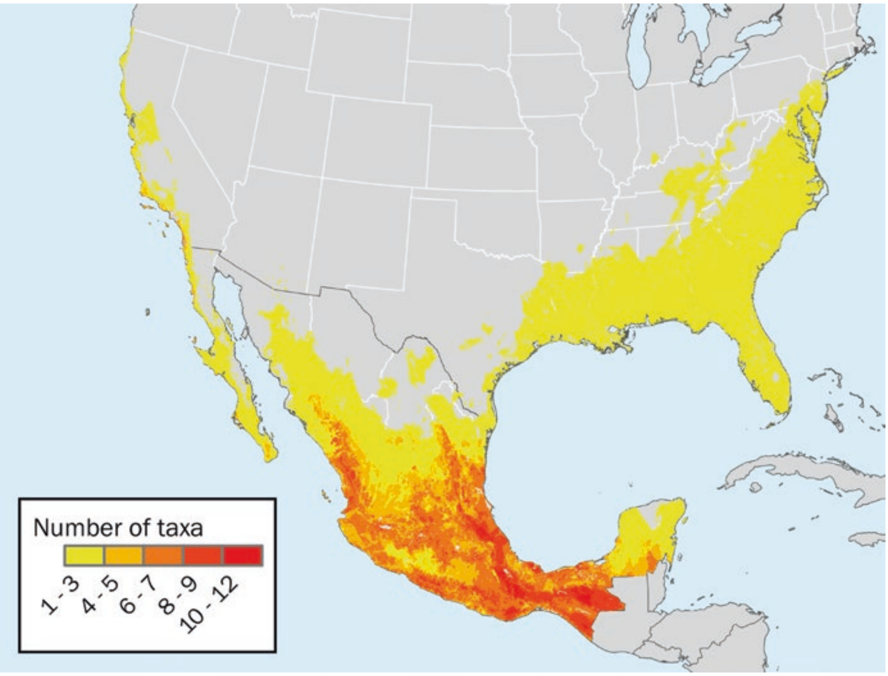

Fig. 12.2 Species richness map of modeled potential distributions of North American *Persea* taxa, based on climatic and edaphic similarities with herbarium and genebank reference localities. Warmer colors indicate areas where greater numbers of taxa potentially occur in the same geographic localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

has devastated native avocado tree and wild relatives (Anderson 1950). The number of species recognized for the subgenus fluctuates according to the author to be consulted: two (van der Werff 2002), three (Lavi et al. 2003), and seven (Kopp 1966; Williams 1977). Here we present the results obtained by Scora and Berg (1992), and Rojas et al. (2007) (Table 12.2).

Persea is divided into two subgenera: *Persea* and *Eriodaphne* (Koop 1966), differentiable by the sepals. Avocado, *Persea americana* Mill., belongs to the subgenus *Persea*, which has larger fruits than the subgenus *Eriodaphne* (fruits called aguacatillos). Koop (1966) classified the Mexican avocado as *P. americana* var. *drymifolia*, the Guatemalan and Antillean (West Indian) kinds as *P. americana* var. *americana*, and a wild-type avocado as *P. americana* var. *nubigena* L.O. Williams and includes in this subgenre *P. schiedeana* Nees, *P. steyermarkii* Allen, and *P. floccosa* Mez.

Persea americana Mill*:* It is the most widely dispersed species in Mexico, and collections from Mexico, Central America, and Chile are preserved.

Table 12.2 Species that are grouped in the subgenus *Persea*, according to the main recognized taxa

Taxon	Kopp (1966)	Williams (1977)	Bergh and Ellstrand (1986), Bergh (1993)	Scora and Berg (1992)	van der Werff (2002)
P. americana	var. *americana*	var. *americana*	var. *americana*	var. *americana*	*P. americana*
P. guatemalensis	var. *guatemalensis*	var. *guatemalensis*	var. *guatemalensis*	var. *guatemalensis*	
P. drymifolia	var. *drymifolia*	var. *drymifolia*	var. *drymifolia*	var. *drymifolia*	
P. nubigena	var. *nubigena*	var. *nubigena*	*P. nubigena*	var. *nubigena*	var. *nubigena*
P. costaricensis			var. *costaricensis*		
P. parvifolia		*P. parvifolia*			
P. floccose	*P. floccosa*	*P. floccosa*	*P. floccose*	var. *floccosa*	
P. parviflora				*P. parviflora*	
P. primatogena		*P. primatogena*		*P. primatogena*	
P. schiedeana	*P. schiedeana*	*P. schiedeana*	*P. schiedeana*	*P. schiedeana*	*P. schiedeana*
P. steyermarkii	*P. steyermarkii*	*P. steyermarkii*	*P. steyermarkii*	var. *steyermarkii*	var. *steyermarkii*
P. tolimanensis			*P. tolimanensis*	*P. tolimanensis*	
P. zentmeyerii			*P. zentmeyerii*	*P. zentmeyerii*	

Persea nubigena L.O. Williams*:* Characterized by small leaves and do not smell like anise when rubbed. The flower structure is similar to the common avocado, but the clusters are more consistent, larger, and longer. Fruit diameter varies from 1.5 to 3 inches, its shape is oval to circular, and seed is large in proportion to the size of the fruit, which has a thick skin. It is considered a progenitor of the Guatemalan avocado (Schroeder 1951). The genebank of CICTAMEX preserves genotypes collected in Mexico, and some hybrids from Israel.

Persea steyermarkii C.K. Allen*:* It is a very rare taxon from Guatemala, El Salvador, and Venezuela. Inflorescence, flowers, and fruits indicate a very close relationship with *P. americana*. It is considered an ancestor of the Guatemalan variety (Schieber and Zentmyer 1978). Genotypes are conserved in the Mexican genebank.

Persea schiedeana Nees*:* This species is native to the tropics of Southern Mexico and Central America. In Mexico specimens are known as “chinini” or “chinine.” In Guatemala, specimens are described as reaching more than 20 m tall, seed is large, the epicarp is clear, green, thick, but flexible, and therefore easy to peel. The flesh color varies from white to pale brown and tends to exude a milky juice. *P. schiedeana* has a close relationship with the common botanical avocado *P. americana*, with the main difference found is its pronounced pubescence (Schroeder 1974). Genebank collections preserve individuals from Honduras, Guatemala, and Mexico.

Persea cinerascens S.F. Blake *:* This species is known by the name of canelillo in the region of Tacambaro, Michoacan, where specimens up to 20 m high are found. It has a characteristic smell of cinnamon in the wood and leaves. The stem of the infructescence is 7–10 cm. in length, with 20–30 fruits per plant. Perianth segments are persistent to maturity and easily observable; the fruits are baciform and slightly elliptical with a fleshy and lightly flavored avocado mesocarp. The epicarp is violet at maturity and the embryo is very small. It is incompatible with the varieties Fuerte and Hass. In the genebanks, the preserved genotypes are from Tacambaro, Michoacan.

Persea hintonii C.K. Allen (subgenus Eriodaphne): Preserved genotypes were collected in Tejupilco and Otzoloapan, State of Mexico, and seedlings are developed at the nursery.

Persea longipes (Schltdl.) Meisn.*:* A species of the subgenus *Persea*, with small fruits 3–5 cm in diameter. Preserved genotypes were collected in the mountain range of Tantima, Veracruz, Mexico.

Persea parvifolia L.O. Williams*:* This species has a small obovoid fruit, 3.5–2.5 cm in diameter, with seed 1.7 cm in diameter, and a 4 mm thin shell. It is found in mountain forests in Chocaman, Tetla, Veracruz, where it is an endangered plant. Genotypes were collected in Zongolica, Veracruz, and Chocaman.

Persea floccosa Mez*:* This taxon is related and similar to *P. americana*. Corresponding to rare genotypes found in Aquila, Veracruz (Schroeder 1951; Williams 1977), this species is distinguished by the dense pubescence of its new shoots, leaves, and fruits. Its fruits are small ovoids of about 5 cm long. Some authors regard it as the probable ancestor of *P. americana* var. *drymifolia*, the Mexican race of avocado (Barrientos and López 2000). Genotypes collected in Veracruz, Mexico, are preserved.

Persea meyeniana Nees*:* Endemic to Chile, this species belongs to the group of aguacatillos, and a genotype brought from Chile is preserved by seed.

Beilschmiedia spp.: The genus *Beilschmiedia* is represented in Mexico by *B. americana*, *B. anay* (S.F. Blake) Kosterm, *B. ovalis* (S.F. Blake) C.K. Allen, *B. pendula* (Sw.) Nees, *B. schiedeana* (chinene), and *B. steyermarkii* C.K. Allen. The fruit of *Beilschmiedia anay* is ovate in shape and green and black in color; the epidermis of green is relatively thick (0.4 mm) and the black has thin skin, preventing separation of the pulp; both produce fruits of similar size, which have shiny and attractive skin (Borys et al. 1993). Conservation has been done through seed; genotypes preserved in the collections are originally from Mexico and Chile. *Beilschmiedia anay* was found in Puebla, Mexico, but collected by seed at Huatusco, Veracruz.

While the systematic efforts to monitor diversity are limited, there are several wild *Persea* species that are currently used in the development of new cultivars and rootstocks. Currently two institutions are conducting breeding; the INIFAP (National Institute of Forestry, Agriculture, and Livestock) in Nayarit is performing selection of rootstocks tolerant to drought and disease. This program has released drought-tolerant and *Phytophthora cinnamomi* Rands-resistant rootstocks. The development of *Phytophthora*-resistant rootstocks is also an objective of the Salvador Sánchez Colín CICTAMEX Foundation breeding program (Sánchez Colín and Barrientos Priego 1987), in conjunction with the Autonomous University of Chapingo. There are also efforts to crossbreed the Mexican and Guatemalan races in order to find varieties with better fruit quality and that produce off-season. There are also plans to improve avocado for industrial uses, for example, more oleic acid (high-quality fatty acid). However, the majority of breeding is conducted with landraces rather than wild relatives.

12.1.5 Conservation of Avocado Genetic Resources

Ex situ conservation is based on the spread of accessions by new cuttings entering the center via exploration, exchanges, or donations from foreign collections. In Mexico there are about 21 *Persea* species, including *Persea americana*, preserved in the CICTAMEX genebank (Tables 12.3 and 12.4). Germplasm banks in Mexico were first established in the 1950s in Tacambaro, Michoacan, the first formal aguacate germplasm bank in Mexico, to preserve local types, such as the "Basaldúa," "Tucuata," "Cerezo," "Lopez," "Epigmenio," and "Moreno." However, these efforts were abandoned after a few years. During the 1970s, Dr. Armando García (García and Ichikawa 1979) and the INIA researchers revived these efforts (Ireta Ojeda 1977). Further collection efforts were made in the 1990s by a group of researchers

Table 12.3 Genotype by subgenus and species preserved in CICTAMEX S.C

Subgenre	Species
Persea	*Persea americana* Mill. (races: Mexican, Antillean, Guatemalan, and Costaricensis) *Persea steyermarkii* C. K. Allen *Persea nubigena* L. O. Williams *Persea floccosa* Mez *Persea schiedeana* Nees *Persea parvifolia* L. O. Williams + *Persea meyeniana* Nees + *Persea tolimanensis* Zentmyer & Schieber +
Eriodaphne	*Persea cinerascens* S. F. Blake *Persea lingue* (Ruiz & Pav.) Nees *Persea longipes* (Schltdl.) Meisn. *(Tantima III)* *Persea hintonni* +
Other related species	Nectandra "San Simón el Alto, Malinalco" + *Beilschmiedia anay* *Beilschmiedia miersii* (Gay) Kosterm. "Persea rare" ++

+ Only nursery preserved, recent
++ not well identified yet

Table 12.4 Distribution of *Persea* in Mexico

Species	State of Mexico where it is located
Persea americana Mill var. *drymifolia* (Mexican race)	States of North and Central Zone as Nuevo Leon, Tamaulipas, San Luis Potosi, Queretaro, Hidalgo, Mexico, Tlaxcala, Puebla, Michoacan, Oaxaca, Queretaro, Guanajuato, etc.
Persea americana var. *americana* Mill (Antillean race)	Tamaulipas, Veracruz, Tabasco, Campeche, Quintana Roo, Yucatan, Chiapas, Oaxaca, Guerrero, etc.
Persea americana Mill var. *guatemalensis* (Guatemalan race)	Veracruz, Oaxaca, Guerrero, Chiapas, Tabasco, etc.
Persea bourgeauviana Mez	Chiapas
Persea brevipetiolata Van der Werff	Oaxaca, Veracruz
Persea chamissonis Mez	Queretaro, Hidalgo
Persea cinerascens Blake	Veracruz
Persea donnell-smithii Mez	Chiapas
Persea flavifolia Lundell	Colima, Durango
Persea floccosa Mez	Michoacan, Oaxaca
Persea hintonii C.K. Allen	Jalisco, Guanajuato, Michoacan, Nayarit, Mexico
Persea longipes (Schltdl.) Meisn.	Veracruz, Oaxaca
Persea pachypoda Nees	Oaxaca, Chiapas
Persea palustris (Raf.) Sarg.	San Luis Potosi, Guanajuato, Queretaro
Persea parvifolia L.O. Williams	Oaxaca and Puebla
Persea podadenia S.F. Blake	Sonora, Chihuahua
Persea podadenia S.F. Blake	Sinaloa
Persea purpussi L.E. Kopp	San Luis Potosi, Queretaro, Hidalgo
Persea rufescens Lundell	Oaxaca, Chiapas
Persea sp.	Tamaulipas and Nuevo Leon
Persea standleyi C.K. Allen	Veracruz
Persea steyermarkii C.K. Allen	Chiapas
Persea nubigena L.O. Williams	Chiapas

from Salvador Sánchez Colín-CICTAMEX Foundation and the Autonomous University of Chapingo (UACh) (Ben-Ya'acov et al. 1992). Additionally, the University Regional Center West (CRUO) also performed collections in Veracruz (Escamilla-Prado et al. 1992), and in the later 1990s, INIFAP followed (Sanchez-Perez 1999). A collaboration between the National Council of Avocado Producers (Conapa) and Avocado Net of the National Plant Genetic Resources for Food and

Agriculture (Sinarefi) resulted in a proposal to certify the regional wild-type avocado from Michoacan as a source for the production of avocado plants.

As part of the actions of the Avocado Net of SINAREFI, an agreement between the INIFAP and Salvador Sánchez Colín-CICTAMEX Foundation established the National Germplasm Repository for Aguacate, which houses 500 accessions and is planning future collections. Within the collection's diversity are *Persea americana* var. *drymifolia*, *Persea americana* var. *guatemalensis*, *Persea americana* var. *americana*, *Persea americana* var. *costaricensis*, *Persea schiedeana*, *Persea nubigena*, *Persea tolimanensis*, *Persea steyermarkii*, *Persea indica*, *Persea cinerascens*, *Persea gigantea*, *Persea floccosa*, *Persea lingue*, *Persea vesticula*, *Beilschmiedia anay*, and *Beilschmiedia tova.* The germplasm originated a wide variety of countries. The collection will be replicated in Celaya, Guanajuato, and Coatepec Harinas with at least three replicates per genotype in a nursery garden system which can be maintained with pruning for about 10 years. Efforts for ex situ diversity conservation require an institutional commitment and funding source; here SAGARPA through SINAREFI and specifically Avocado Net have provided resources for partial maintenance of three genebanks over the last 5 years. Accessions that make up this collection have been characterized according to UPOV guidelines and IPGRI (Barrientos-Priego et al. (1992), IPGRI (1995), and UPOV (1991)). Information has been integrated in a descriptive manual of conserved accessions. Many species can be stored for long periods of time at low temperatures and humidity; however, there are species whose seeds cannot be preserved in this way because they produce "recalcitrant" seeds and cannot be stored; the genus *Persea* is an example of this.

Avocado and several related species, such as *Persea americana* var. *guatemalensis*, *Persea steyermarkii*, *Persea nubigena*, and *Persea schiedeana*, grow wild in forests and jungles (Barrientos-Priego et al. 1992). In fact, *Persea* is considered to be an indicator of the cloud forest ecological zone (Cayuela et al. 2006). These forests are subject to the system of slash-and-burn agriculture, and there is a need to increase preservation of these areas (Ochoa-Gaona and González-Espinosa 2000; Ochoa-Gaona 2001). In situ conservation is being carried out in some areas of the country, where protected areas host the *Persea*, such as Sierra Manantlán Biosphere Reserve, where *Persea hintonii* grows (Figueroa-Rangel and Olvera-Vargas 2000). Within protected areas, there are also other *Persea*, like those of the Pico de Orizaba (Veracruz), Los Tuxtlas (Veracruz), Benito Juárez (Oaxaca), El Triunfo (Chiapas), Palenque (Chiapas), Lagunas de Montebello (Chiapas), and Lacan-Tul (Chiapas). However, only Tuxtlas and El Triunfo are cloud forest (Lorea-Hernández 2002), where *Persea americana* is housed, so it is important that other areas are considered for protection in the country, like Oaxaca, Puebla, or Guerrero presenting such forests, or some more in the highlands of Chiapas. Forest farms are also making efforts, led by the ECOSUR Chiapas (De Jong et al. 2006), where they already have demonstration plots for indigenous people to take a conservationist model. The ECOSUR has extensive experience in reforestation and management of areas requiring regeneration, in order to reintroduce species in the area including avocado; many of these studies have been funded by CONABIO.

12.1.6 Challenges to Conservation

There is a need for in situ farm conservation; to do this a farmer needs to be integrated into the National System of Conservation of Plant Genetic Resources due to their experience in specific regions. Integration can be handled in several ways, including (1) considering farmers as partners in maintaining germplasm; (2) establishing a national dialogue on agro-biodiversity conservation, sustainable use, and equitable sharing of benefits among farmers, genebanks, and other partners; (3) helping the exchange of information among participants; and (4) developing systems that facilitate easy access to material. There needs to be more general conservation of ecosystems, as there is a loss due to many activities. A benefit of this partnership in conservation programs in situ may mean an improvement in the living standards of farmers in a region. The farm conservation programs can combine development of local infrastructure and increase farmers access to useful germplasm deposited in national genebanks. Farmers benefit from agricultural diversity and ecosystem health. Natural resources grown in localities can be the basis for initiatives to increase the production of crops or provide new market opportunities. The farm conservation also serves to empower farmers on genetic resources in their fields. On-farm conservation recognizes that farmers and communities are curators of local genetic diversity and indigenous knowledge to which it is linked. Therefore, farmers are best placed to perceive any benefit from the genetic material they retain. The importance of the conservation of agricultural biodiversity for the future of world food security is based on the ability of the initiative to supply germplasm to plants breeders and other future users. Socioeconomic benefits could be considered the power that rural communities would. For farmers, farm conservation would serve to support cultural tradition, efficient use of labor in the family, and your budget constraints and mitigate the effect of pests, diseases, and other environmental pressures, and representing insurance, new genetic material meet future environmental and economic changes.

12.2 Mamey Sapote (*Pouteria sapota* (Jacq.) H.E. Moore & Stearn)

12.2.1 Origin of the Crop and Brief History of Use Worldwide

Mamey sapote [*P. sapota* (Jacq.) H.E. Moore & Stearn] is originally from the lowlands of Central America (Morera 1992). Occurrences have been reported in Venezuela (Manzano 2001), Brazil (Donadio and Duringan 1995), Mexico, Belize, Guatemala, El Salvador, Honduras, Costa Rica, Cuba, Puerto Rico, Dominican Republic, Nicaragua (Campbell et al. 1998), and the United States (Popenoe 1948; Lamberts and Crane 1996; Mossler and Nesheim 2002). The most likely center of origin is located in Guatemala, Honduras, Costa Rica, and Southern Mexico (Toral-Jarquin 1988). This species has been used since prehistoric times with archeo-botanical remains having been found in many areas across Mexico. Mamey was an important plant species consumed along with cocoa, pumpkin, and corn, as shown in engravings from the tomb of Paca'al, a legendary Mayan king (Espinosa-Zaragoza et al. 2012). The tree is part of the jungle high perennifolia, cultivated in monoculture or with other fruit trees in agroforestry systems. Mamey is relatively unknown outside its native range.

12.2.2 Modern Use

Mamey is distributed widely in Mexico, Central America, and South America (Fig. 12.3) but is mostly cultivated in association with other crops in agroforestry systems. In Guerrero, Mexico, production has increased in the last decade, due to collaboration between producers, the Colegio de Postgraduados and the Mexican Government. Conservation efforts have begun by selecting trees with fruits of red pulp, a higher proportion of pulp, and out-of-season production. In agroforestry systems associated with crops, such as coffee, cocoa, and ornamentals, mamey trees are vigorous and vary widely in their characteristics which limit orchard management and marketing (Espinosa-Zaragoza et al. 2009). This scheme of cultivation is common in Mexico and

Fig. 12.3 Modeled potential distribution of mamey sapote (*Pouteria sapota* (Jacq.) H.E. Moore & Stearn), based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

Central America. The potential for crop establishment is large in the tropics, although the level of knowledge of the species and the limited information available regarding postharvest handling of fresh fruit may limit market potential.

Fruits are mainly consumed fresh (Morera 1992; Pennington and Sarukhan 1998), but the pulp can be used to make jellies, ice cream, and juices. It is a nutritious fruit providing vitamins, salts, and carbohydrates, which promote digestion (Casas-Alencaster 1977). The seed is used to prepare skin tonic, a revitalizing tonic that prevents hair loss (popular usage). The oil extracted from the seeds can be used for biodiesel production through alkaline transesterification (Laiz-Saldaña et al. 2009). There are areas with high productive potential; for example, plantations in the Yucatan Peninsula are ripe for expansion. However, crop establishment must be accompanied by market development and research on postharvest handling. El Salvador, Costa Rica, Nicaragua, Guatemala, and Florida (USA) have small but stable industries that produce and sell frozen/dehydrated pulp (Morera 1992; Balerdi et al. 1996). Currently the market in Florida, where it was introduced 100 years ago, has recently increased in importance there in the Cuban and Central American communities (Morera 1992; Pennington and Sarukhan 1998).

12.2.3 Challenges in Cultivation

Mamey occurs in a wide variety of agroclimatic conditions; it is found from sea level to 2100 m with rainfall from 550 mm under irrigation up to 2500 mm. Average temperatures in production areas range from 15 to 33 °C, usually over 25 °C. Today, mamey is regarded as a tropical plant with ample opportunities for orchard development. The predominant characteristics of mamey plants in production are variable, which limits marketable yield. Toral-Jarquín (1988) found that fruits with excess fiber and unacceptable taste were common. Also, there is a limited disease resistance, with damage from *Botryodiplodia theobromae* Pat, *Lasiodiplodia theobromae*, *Pestaliotopsis paeoniicola*, and *Pestalotia sp.* being common (Martínez-Carrillo et al. 1996; Bautista-Baños et al. 2002; Gómez-Jaimes et al. 2009; Gómez 2008). *Penicillium olsonii* Bainier G. and *Alternaria alternata* (Fr.) Keissl. were identified as causative agents of necrosis floral mamey (*P. sapota*) in Alpoyeca, Guerrero, Mexico. In Mexico, Vásquez-López et al. (2012b) determined *Lasiodiplodia theobromae* as a causative agent of dieback of mamey (*P. sapota*). *Anastrepha serpentina* (Wiedemann), known as the sapodilla fly, is reported as a major postharvest pest in fruits of mamey (Aluja 1993).

12.2.4 Wild Relatives of the Crop

The family Sapotaceae consists of trees and shrubs of the tropical forest, including ~540 species, distributed from Southern United States, Mexico, Central America to Paraguay, Chile, and Uruguay (Pennington 1990). There are 11 genera recognized, among which the most important, because they produce edible fruits, are *Manilkara*, *Pouteria*, and *Chrysophyllum*. The commercial value of the wood and latex highlights the genera *Pouteria*, *Manilkara*, and *Ecclinusa*. Within genus *Pouteria* (188 species), there are several species that are very important, including *P. sapota* (mamey), *P. campechiana* Baehni (canistel), *P. viridis* Ruiz & Pav. (green sapote), *P. lucuma* (Ruiz & Pav.) Kuntze (lucuma), and *P. fossicola* Cronquist (sapote). The genus *Chrysophyllum* has 43 species, among which *C. cainito* L. is most important. Genus *Manilkara* has 30 species, including *M. zapota* (L.) P. Royen (sapodilla). There is tremendous species richness in Mexico (Fig. 12.4). The distribution and characteristics of the materials and their ecological niches may be subject to study, generating information of potential production areas and areas with high probability of natural populations in which to make collections.

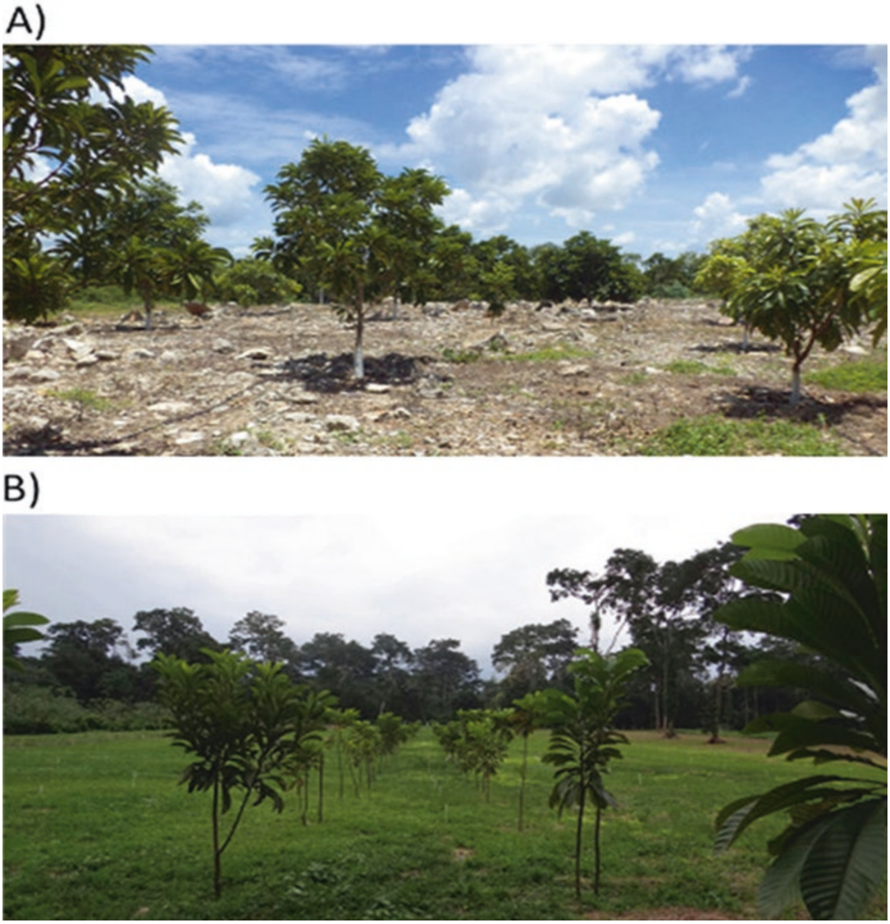

Fig. 12.4 (**a**) Collection work of mamey. Conkal, Yucatán, México. (**b**) Germplasm bank. Experimental Station Rosario Izapa/INIFAP. Tuxtla Chico, Chiapas, México

12.2.5 CWR and Their Genepool Classifications

There is limited breeding and classification of crossing between species. The most developed breeding program led by Mr. Carlos Magaña, a producer who identified superior trees from his farm (the largest area of cultivated mamey in the world). Individual selection has prospered to the extent that asexual reproduction has been tested, with grafting being favored, although the success rate is very variable (0–100%). Favored traits include high productivity (kg/tree, fruit/tree), red pulp without fiber, high percentage of pulp >75%, fruit weight <1000 g, and fruit maturity from September to March. Due to these limitations, mamey materials in germplasm collections are classified according to individual characteristics, shape, size, and color of the fruit first, and occasionally they have names linked to families, farms, or their productive characteristics, such as "El Regalo," "El Conejo," "El Mexicano," or "La Piedra." For example, "El Regalo" is a tree that produces lots of fruits. There is preference for red fruit, weight between 600 and 1000 g and fiber-free pulp. Other classifications are associated with collection site and harvest time. Attempts at molecular characterization have been made. Rodríguez-Rojas et al. (2012) characterized mamey sapote trees using 10 RAPD primers (165 fragments, 82.4% polymorphic), which allowed 10 of the 15 trees studied to be uniquely characterized.

12.2.6 Conservation Status of CWR and WUS

In situ conservation of mamey is associated with agroforestry systems; these systems can be maintained for over 100 years if landowners are aware of trees with desirable characteristics and are part of the conservation effort. However, currently there are no programs that favor conservation in situ. Mexico has invested in conservation, use, and the institutions (Autonomous University of Chiapas, Autonomous University of Nayarit, INIFAP, Colegio de Postgraduados) that do this work. The goal of these programs is to provide a source diversity to adapt to new production conditions or uses. As mamey seed is recalcitrant to germination, there has been limited diversity preserved by genebanks where seed collections are established and maintained. However, there are collections maintained at Conkal, Yucatan, Mexico (Fig. 12.4), and at the germplasm bank of Rosario Izapa Experimental Station of INIFAP, both by the System of Plant Genetic Resources SAGARPA in Mexico. Collections are also maintained in Costa Rica, promoted by the government of that country. In the United States, a collection is maintained at the Fairchild Tropical Botanic Garden (FTBG) and the University of Florida's Tropical Research and Education Center. The last collection is maintained at the Technological Innovation Center of El Salvador (52 accessions).

Despite collections in four countries, there is still a need to increase the number of accessions; therefore, collections are continuing to be made looking mainly for quality characteristics, performance, and short time of flower to fruit. The most recent collections (2009–2015) were made with the support of SAGARPA (Ministry of Agriculture, Rural Development, Fisheries and Food, Mexico), following an action plan from RFAA FAO, and were made in areas considered extreme for growth, including those outside the altitudinal range or beyond the ecological limit. It is expected that these accessions are a reservoir of genes with wide adaptability to climate change.

There is a need to validate performance in different environments for producers. In the near future, crop diversification may help local and regional food security, reducing costs for postharvest handling and transportation. The current material in germplasm repositories needs to be phenotyped. Currently, data on the first varietal assays in Mexico are being collected, and descriptors for this purpose have been proposed from previous experience in crops like cocoa. Similarly, the materials that have been collected could be analyzed from other points of view, such as nutraceutical content

12.2.7 Suggestions on Ways to Improve Conservation

The integration of the value chain or value networks of mamey is an important producer and consumer awareness of the potential of this fruit strategy. It is also a convenient network to integrate plant material and financial and human resources for the use and conservation available. Likewise, the promotion of including new accessions to the germplasm banks will help facilitate use.

12.3 Cherimoya (*Annona cherimola* Mill)

12.3.1 Origin of the Crop and Brief History of Use Worldwide

Members of the family *Annonaceae* are distributed in tropical regions of Mexico (Table 12.5). According to the Global Biodiversity Information Network (REMIB), there are 14 genera in several states of the Mexican Republic and 62 species (Table 12.5). Cherimoya (*Annona cherimola* Mill) is the only species of the family *Annonaceae* distributed in subtropical regions of the states of Chiapas, Veracruz, Michoacan, Oaxaca, State of Mexico, Morelos, Puebla, Guanajuato, and Jalisco at altitudes ranging from 700 to 2600 m above sea level (Fig. 12.5). Cherimoya is consumed fresh, usually in fruit salads, or adding its pulp to juices. Rich in soluble sugars and vitamin C, the pulp is white, creamy, soft, aromatic, and sweet, with a barely noticeable acidity. The Haenke naturalist (Díaz Robledo 1981) considered it "the masterpiece of nature." The cherimoya is a fruit tree that has great potential for development in the subtropical regions of the world. There are increased efforts in varietal selection, breeding, and technological development. There is also market development investment, in order to introduce this crop in the European Union. Until very recently, cherimoya has been supplied to Chile and Spain; in addition,

Table 12.5 Family *Annonaceae*, genus and species in Mexico, according to Herbal REMIB (CONABIO)

Genus	Species	Distribution (federal entities)
Anaxagorea	*A. guatemalensis* Standl.	Ver., Oax.
Annona	*A. globiflora* Schltdl	Ver., Hgo., Chis., Tamps., Gto.
	A. testudinea Saff.	Chis.
	A. cherimola Mill.	Ver., Mich., Chis., Oaxaca., Mor., Pue., Qro., Jal., Gto.,
	A. longiflora S. Watson	Mex.
	A. macrophyllata Donn. Sm	Jal., Ver.
	A. reticulata L.	Camp., Q.Roo., Yuc.
	A. glabra L.	Yuc., Jal., Mich., Pue., Q.Roo, Nay., Tab.
	A. purpurea Moc. & Sessé ex Dunal	Ver., Q.Roo, Yuc., Camp., Tab., Jal., Oax., Nay., Gro.
	A. diversifolia Saff.	Ver., Mich., Chis., Yuc., Jal.
	A. lutescens Saff.	Mich., Gro., Yuc., Ver., Mex.
	A. longipes Saff.	Pue.
	A. scleroderma Lam.	Chis.
	A. muricata L.	Ver., Chis., Tab., Yuc., Col., Gro., Q. Roo, Nay., Mich.
	A. squamosa L.	Yuc., Mich.Q.Roo, Camp., Ver., Oax., Jal., Nay.
Desmopsis	*D. trunciflora* (Schltdl. & Cham.)	Jal.
	D. lanceolata Lundell	Chis.
	D. trunciflora var. glabra G.E. Schatz.	Ver., Oaxaca., Chis.
	D. galeottiana (Baill.) Saff.	Jal., Gro., Chis.
	D. panapensis (Rob.) Saff.	Chis., Ver.
	D. mexicana R.E.Fr.	Mich. (Aquila, Coalcoman)
	D. schippii Standl.	Tab.
	D. bibracteata (B.L.Rob.) Saff.	
Cymbopetalum	*C. hintonii* Lundell	Mich. (Aquila)
	C. mayanum Lundell	Chis.
	C. galeottiana (Sessé & Moç. ex Dunal) Baill.	Ver., Jal., Chis.
	C. penduliflorum (Sessé & Moç. ex Dunal) Baill.	Ver., Chis
	C. baillonii R.E. Fr.	See.
Guamia	*G. Mexicana* G.E. Schatz	See.

(continued)

Table 12.5 (continued)

Genus	Species	Distribution (federal entities)
Guatteria	*G. anomala* R.E. Fr.	Chis., Ver.
	G. amplifolia Triana & Planch.	Chis., Ver., Tab., Jal.
	G. depressa (Baill.) Saff.	Ver., Chis.
	G. dolichopoda Donn. Sm.	See.
	G. bibracteata (Hook.) Hemsl.	See.
	G. diospyroide Baill.	Ver., Oaxaca.
	G. grandiflora Donn. Sm.	Chis.
	G. oliviformis Donn. Sm.	Chis.
	G. galeottiana Baill.	Ver., Oaxaca.
	Guatteria sp.	See.
Malmea	*M. depressa* (Baill.) R.E.Fr.	Chis., Ver., Camp., Mich., Tab., Oaxaca., Q.Roo, Yuc.
	M. gaumeri (Greenm.) Lundell	Ver., Chis.
Oxandra	*O. lanceolata* (Sw.) Baill.	Mich., Gro., Jal., Q.Roo
	O. lanceolata spp. macrocarpa R.E.Fr.	Gro. (José Azueta)
	O. laurifolia (Sw.) A. Rich.	Null
Tridimeris	*T. hahniana* Baill.	See.
	T. tuxtlensis G.E. Schatz	See.
	T. uxpanapensis G.E. Schatz	Oax.
Rollinia	*R. jimenezii* Saff.	Ver., Chis.
	R .mucosa (Jacq.) Baill.	See.
	R. rensoniana Standl.	Ver., Oax.
Sapranthus	*S. humilis* Miranda.	See.
	S. campechianus (Kunth) Standl.	Yuc., Camp., Q.Roo
	S. foetidus (Rose) Saff.	Jal.
	S. microcarpus (Donn. Sm.) R.E. Fr.	Ver., Chis., Jal., Oax.
	Sapranthus sp.	Nay., Oax.
Xylopia	*X. sericophylla* Standl. & L.O. Williams	See.
	X. frutescens Aubl.	Tab., Chis., Ver., Oax.
Mosannona	*M. depressa* (Baill.) Chatrou	See.
	M. depressa spp. depressa (Baill.) Chatrou	Ver., Q.Roo
Stenannona	*S. humilis* (Miranda) G.E. Schatz	Tab., Ver.

Source: CONABIO-REMIB. *Tab* Tabasco, *Ver* Veracruz, *Q.Roo* Quintana Roo, *Ny.* Nayarit, *Oax* Oaxaca, *Pe.* Puebla, *Mex* México, *Gro.* Guerrero, *Yuc.* Yucatan, *Cam.* Campeche, *Jal* Jalisco, *Mich.* Michoacan, *Gto.* Guanajuato, *Tamps.* Tamaulipas, *Chis.* Chiapas, *Hgo.* Hidalgo, *Qro.* Queretaro

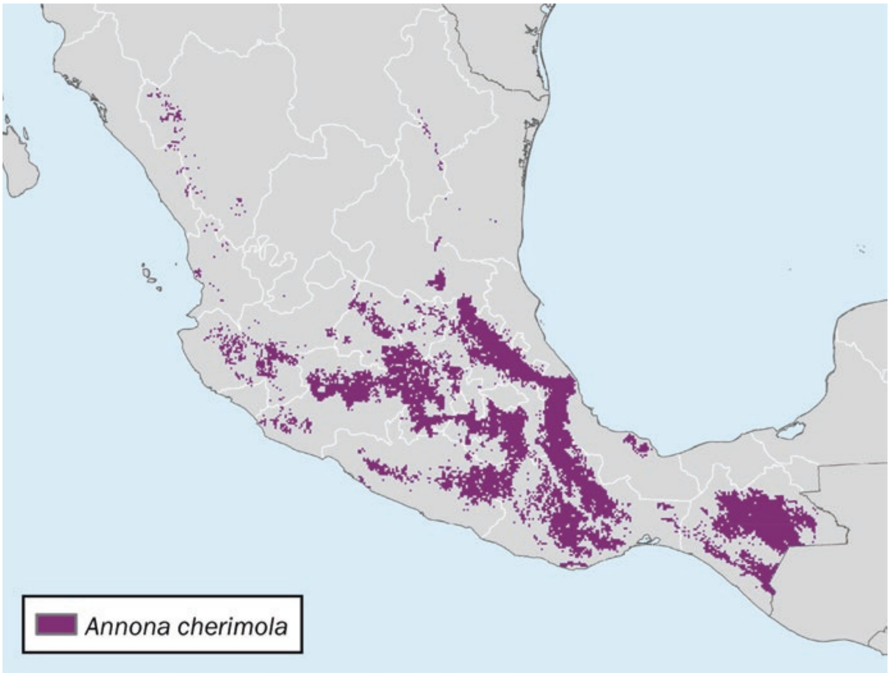

Fig. 12.5 Modeled potential distribution of *Annona cherimola* Mill, based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

the Government of Chiapas is currently promoting fruit projects, including some anonas, and promoting organic markets to encourage job creation based on nontraditional products.

12.3.2 Utilization of Crop Wild Relatives

Some species in the family have aromatic oils that are used for perfumes or spices. The bark is used for transporting cargo in the Amazon jungle and for making wooden implements, such as tool handles and plugs. The wood is used also as fuel, and some species are also grown for ornamental purposes (ICUC 2002). In the case of *Annonaceae* in Mexico, there has been a series of collection, characterization, selection, and conservation works in species of major economic importance, such as cherimoya (*A. cherimola*), ilama (*A. diversifolia*), saramuyo (*A. squamosa*), and guanabana (*A. muricata*). In addition, collections and characterizations of the red anona (*A. reticulata*) were started in Yucatan. The characters used vary according to the species, although in general the following were used: fruit weight, number of seeds, percentage of pulp, percentage of shell, total soluble solids (Brix degrees), shell type, and shape of the fruit (roundness) among the most frequent variables (Abadie and Berretta 2003). In general, the species of *Annonaceae* are marginally cultivated in Mexico. The largest areas cultivated for commercial purposes are guanabana and cherimoya. Saramuyo, ilama, red anona, sincuya or blackhead, and atemoya (interspecific hybrid between *A. cherimola* and *A. squamosa*) are anonas that are grown in the backyard and are scattered along roadsides, terrain-cultivated or grazing areas, or between natural vegetation or in preliminary crop trials and their fruits are harvested for local markets. The biribá or anoma cimarrón (Ro-llinia mucosa) is native to South America and is grown on a small scale in the United States. Cultivation potential has been evaluated in the La Chontalpa area, but production potential has been variable (Sol-Sánchez 2006). In the case of *A. pupurea*, Luna-Cázares et al. (2006) conclude that this species in Chiapas is grown to obtain its fruits, almost always in season, that are marketed in local markets and have not been thought of as a natural resource feasible to study and take advantage of a sustainable management plan. The remaining species are semi-cultivated in backyards or are harvested seasonally for subsistence consumption and local sale. External quality is determined by the size, shape or symmetry, color, and lack of physical damage. However, producers are often unaware of the proper management technologies that could help maximize yields. Other limitations are related to high production costs, the incidence of pests and diseases, the lack of adequate natural pollination, the poor postharvest handling, the market problems, the need for mechanization, and the lack of support for farmers.

The medicinal uses include antitumor, antifungal, anti-tryanosomics, and antibacterial, among others. Historically, the bark, leaves, and roots are used in folk medicines. Pharmaceutical research has found antifungal, bacteriostatic, cytostatic properties. A large number of chemical compounds, including flavonoids, alkaloids, and acetogenins, have been extracted from these plants. Flavonoids and alkaloids have shown antibacterial properties and have been used to treat skin diseases, roundworms, and eye inflammation. Acetogenins are believed to have anti-HIV and anticancer properties. Consequently, a wide variety of products are available for the treatment of cancer (ICUC 2002). Flavonoids and alkaloids in the bark, seeds, and leaves of several species of the family *Annonaceae* have shown insecticidal properties (ICUC 2002). In the Yucatan Peninsula, insecticide use of seed extracts is widely recognized to combat parasites in humans.

In Mexico, many endemic species with highly restricted distribution are likely to be affected by the factors (i.e., fires, housing, roads, livestock, forestry, agriculture). In Mexico there is some experiences of commercial use, mainly fruit such as cherimoya and soursop. However, the use that people make of these species is very wide, taking advantage of the fruit for consumption and sale [e.g., saramuyo, ilama (papausa), head (soncoya), and red anone], for medical use (leaves and bark), for use as an insecticide, for ceremonial purposes, and for ornamental purposes. Economic potential has not been valued for these species, and it is unacceptable that small traditional farmers live in extreme poverty, yet they have a great diversity of genetic resources of anonas, due to the many environmental and growth types that they are found in. These areas are missing economic opportunities, as anonas fruits are considered exotic and reach very high prices in export and national markets. Additionally, farmers also receive little public and private support for the production, commercialization, and industrialization.

12.3.3 Potential for Expanded Use

Annonaceae species are grown minimally in Mexico with the largest cultivated areas for commercial purposes which are soursop and cherimoya. The largest market is currently present for soursop, and there is potential to expand to other tropical areas across the world. The second most cultivated species of *Annona* is cherimoya. Although this species' cultivated area is much smaller than the soursop, it is an important anona in Mexico and elsewhere in the world. Its cultivation stands out in Michoacan state, followed by Morelos and Hidalgo. Unlike most species of *Annona*, being grown under tropical climatic conditions, cherimoya is adapted to a subtropical climate, which creates a large number of potential growth locals. The main constraint for the cultivation of cherimoya is the lack of markets, because although a little is exported to Japan, mainly from the State of Morelos, that market is open to only the highest-quality fruit, which is determined by its shape, size, color, and blemish-free appearance. For export, agricultural management practices, such as artificial pollination, pruning, and control of pests and diseases, such as seed borers (*Talponia batessi*) and the disease known as anthracnose, are required.

12.3.4 Conservation Status of CWR and WUS

The species of the family *Annonaceae* are mainly distributed in tropical regions of Mexico (Table 12.6), with cherimoya (*A. cherimola*) being the only species in subtropical regions. In Mexico, in situ conservation depends on the species, if wild, semi-cultivated, or cultivated. Conservation in situ of *Annonaceae* occurs mainly in traditional agroecosystems commonly referred to as home gardens or backyards. However, the vast majority of species of the family *Annonaceae* are wild type, and greater diversity is found in the natural vegetation of tropical forests, where conservation through protecting natural areas becomes important. Although there are no accurate inventories, some species, such as an unnamed *Guatteria*, are threatened by the destruction of the natural vegetation and require urgent action to rescue and protect these regions.

Cherimoya collections have been made in the subtropical regions of the Mexican states of Michoacan, Oaxaca, State of Mexico, Morelos, Guanajuato, and Hidalgo, and about 150 accessions have been evaluated to reach a core collection of 70 accessions consisting of 55 Mexican selections and about 15 varieties that are introduced under exchange agreements, mainly from Spain. This collection is propagated by grafting varieties. These collections are kept in the Germplasm Bank of Salvador

Table 12.6 Accessions of cherimoya available at the germplasm bank of CICTAMEX, S.C.

Accession number	Cultivar/selection	Accession number	Cultivar/selection
1–5	Segregante	158	Mich 04–40
6–10	Campas	159	Mich 04–06
11–14	Bronceada	161–162	196
16–17	Fino de Jete	163	Mich 04–15
18–20	Burtons favorite	164	Mich 04–17
21–25	White	165	196
26	Delicia	167–170	Selene
28–30	Fino de Jete	171–176	Cumbe
31–39	Concha Lisa	178–182	Amarilla
40–41	97–52	183	Mich 04–44
43	Oax 04–34	186–187	262
44	Oox 04–21	189	Mich 04–06
45	Oax 04–52	190	Segregante
46	Oax 04–07	191	262
47	Oax 04–18	192	Selene
48–52	Bonita	193–196	Segregante
53–57	94–33	197–203	156
58	Segregante	204–208	Amarilla
59–61	Chiuna 3	210	Mich 04–39
65	Oax 04–49	213	Mich 04–03
67	Oax 04–33	214	Mich 04–38
68	Oax 04–16	215–217	258
69	Oax 04–46	218–225	257
70	Oax 04–50	226	Segregante
71	Oax 04–32	227	257
72	Oax 04–07	228–234	261
73	Oax 04–21	236	8 M Morelos
74–75	Chiuna 1	237–238	Bonita
76	94–28	239	Segregante
81	White	240	Criollo D4
82	Pazicas	242	Segregante
85	Concha	243–245	Raquel 1
88	OAX 04–33	246	Segregante
89	OAX 04–18	247–248	Campas
90–97	Pazicas	249	Segregante
98–106	Cortez	250	Chiuna 4
108	Raquel	251–253	261
109	Mich 04–39	254	8 M Morelos
110	Mich 04–03	257	Bonita
111	Mich 04–17	258	Campas
112	Mich 04–44	259	Bonita
113	Mich 04–08	262	Raquel 1

(continued)

Table 12.6 (continued)

Accession number	Cultivar/selection	Accession number	Cultivar/selection
114	Mich 04–38	263–264	Cumbe
115	Mich 04–15	267	Segregante
116	Mich 04–42	268–269	Campas
117	256	271	9H Morelos
118–128	Bays	272–273	Campas
129	Segregante	274	Bays
130–132	Alvaro	277–278	Bays
134	Mich 04–16	279–280	Chiuna 4
138–145	Cruz Verde O San Simon de G	282–283	Cumbe
146–150	Chaffey	284	Campas
152–157	Alvaro	285-	Duraznos

Sánchez Colín Foundation (CICTAMEX, SC). This collection is one of the most representatives of the anonas of Mexico and is home to the greatest diversity of cherimoya in Mexico. Collections need still to be made particularly in Veracruz, Chiapas, and Puebla. In this collection, molecular genetic diversity has not been studied nor has work on genetic improvement begun. The collections have only been characterized for morphological data.

According to the definition of species and subspecies of flora endemic to Mexico that are endangered, threatened, rare, or subject to special protection under the Mexican official standard NOM-059-ECOL-1994, *Guatteria anomala* is the only species found in the category of threatened (A). This species is a wild type and is distributed in the high evergreen forest in the states of Chiapas, Veracruz, and Oaxaca, mainly areas where the destruction of the rainforest is serious and known by all to have endangered this species and others. All species of *Annonaceae* sheltered in situ present some risks of loss, due to the construction of housing, roads, and other public works, as well as opening up new areas of pastures and crops. In the Yucatan Peninsula, besides construction and change in land use, the biggest risk is damage from hurricanes. For many wild species that have no agricultural base, risks are mainly adverse environmental factors, forest fires, and aggressive and uncontrolled deforestation.

12.3.5 Challenges to Conservation

It is necessary to emphasize that the cultivation of cherimoya in particular, and in general for anonas, requires official promotion from state institutions to develop more and less demanding markets (local and international), as well as financial support for the establishment of orchards. In addition to markets, pulp processing facilities need to utilize the below-grade fruit culled from export packing houses; this could be an economically attractive by-product. Therefore, in addition to technology and varieties, available in Mexico through the Autonomous Chapingo University and Salvador Sánchez Colin (CICTAMEX) Foundation, more effort needs to be placed in collection of new genetic resources that can be placed in new markets. Finally, postharvest handling must be refined, including the use of frozen pulp and conservation of external quality through the protection needed to transport over long distances.

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Chapter 13
Temperate Nut Crops: Chestnut, Hazelnut, Pecan, Pistachio, and Walnut

John E. Preece and Mallikarjuna Aradhya

Abstract Pecan is the only major nut crop native to North America; however, many important wild relative species of nut crops, including chestnut, hazelnut, pecan, pistachio, and walnut, are native to North America and are important sources of useful genes. This chapter briefly covers the history and use of temperate nut crops and more thoroughly discusses the occurrence, potential usefulness, and conservation status of North American crop wild species that have potential value in nut crop improvement.

Keywords Chestnut · Nuts · Pecans · North America · Hazelnut · Pistachio · Walnut

13.1 Introduction

Nut crops are grown for their high calorie, nutritious seeds that humans have consumed over millennia, beginning with the gathering of wild nuts. For some ancient peoples, these nuts served as meat substitutes especially in isolated areas, such as islands that had limited numbers of animals to use as protein. Today, nuts, their oils, flours, and other edible products are popular worldwide. In addition to their culinary uses, tannins from the bark can be used for tanning and dyes, and the hard, finely grained wood has high value for woodworking and veneer, with some, such as chestnut having good rot resistance for fence posts and other uses requiring ground contact. Cultivation of these nut crops contributes greatly to local and national economies, and they sell well because they are tasty and are an important part of a healthy diet.

Pecan is the only endemic North American nut crop with a wide and important international market. The most economically important species of chestnut, hazelnut, pistachio, and walnut originate from Europe into Asia. However, wild nut crops

J. E. Preece (✉) · M. Aradhya
USDA-ARS National Clonal Germplasm Repository, University of California,
Davis, CA, USA
e-mail: John.Preece@ars.usda.gov; Malli.Aradhya@ars.usda.gov

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in North America are important sources of genes for improving their cultivated relatives and may have primary uses other than food, such as their valuable wood.

North American wild nut relatives are used for disease resistance of both the scion and rootstock portions of these nut trees. Conversely, relatives from foreign nut crops are also used to impart disease resistance into North American endemic species, such as overcoming the susceptibility of American chestnut to chestnut blight.

13.2 Chestnut (*Castanea* Mill.)

13.2.1 Introduction to Chestnut

Castanea is a tertiary genus with disjunct distribution in eastern Asia and eastern North America. The genus comprises three sections and seven species (Johnson 1988). Section *Castanea* (Eucastanon of Dode, Dode 1908) comprises five species, *C. mollissima* Blume, *C. seguinii* Dode from China, *C. crenata* Siebold & Zucc. from Japan, *C. dentata* (Marshall) Borkh. from North America, and *C. sativa* Mill. from Europe, all with typical three nuts per involucre. Section *Balanocastanon* has two species, *C. pumila* (L.) Mill. and *Castanea ozarkensis* Ashe that are exclusively found in the southeastern USA. Both are characterized by one nut per involucre (Pereira-Lorenzo et al. 2012). *C. pumila*, the Allegheny chinkapin, has a wide distribution from southern New Jersey and Pennsylvania, west to Indiana and Missouri, and south to Florida and Texas. *C. ozarkensis*, the Ozark chinkapin, has limited and fragmented distribution in the Ozark Mountains of eastern Oklahoma, southwest Missouri, and north-central Arkansas (Johnson 1988). Chinkapins are shrubby and are not economically important. *Castanea henryi* (Skan) Rehd. & E.H. Wils. is found in a restricted area in southeast China and is sometimes called the Chinese chinkapin because it is characterized by a single nut per cupule (Lang and Huang 1999); it is valued for its timber and is grouped under section Hypocastanon.

North American chestnuts occur in eastern North America (Appalachia), from Florida to southern Ontario, and as far west as Illinois. They include *Castanea dentata* (American chestnut) and *C. pumila* (chinkapin). The American chestnut was a dominant canopy tree in eastern North America before populations were devastated by the introduced fungus, *Cryphonectria parasitica* causing chestnut blight. By the 1950s, the American chestnut had been devastated throughout its native range. In the USA and Canada, it is a very minor crop, accounting for less than 1% of the world's production.

13.2.2 Origin of Chestnuts and Production Worldwide

The sweet or European chestnut (*C. sativa*) was probably domesticated in north Turkey and the Caucasus region perhaps as far back as the Iron Age and certainly from the Roman times (Zohary et al. 2012). Chestnut blight and ink root disease introduced from abroad reduced yields in the late 1800s and early 1900s by about 90% (Zohary et al. 2012). Most commercial sales of chestnuts are *C. sativa* (Missouri Botanical Garden 2016).

In Asia, *C. crenata*, *C. mollissima*, and *C. sequinii* are cultivated and found in the wild (Pereira-Lorenzo et al. 2012). *C. mollissima* (Chinese chestnut) is the most commercially important of these Asian species. In Asia, chestnuts were domesticated very early and over 5000 years ago were mentioned in ancient Chinese poetry (Hochmuth et al. 2012). Chinese chestnut is a source of resistance to chestnut blight (Missouri Botanical Garden 2016).

The American chestnut (*C. dentata*) was harvested from the wild and contributed to the Appalachian economy. Not only were the nuts harvested for use and sale in large eastern cities, but the light, strong, and rot-resistant wood was also important for furniture, posts, and other uses (Anon 2016a). Chestnut was a major eastern deciduous forest tree in the late nineteenth and early twentieth centuries. The American chestnut and much of the industry were destroyed after the introduction of *Cryphonectria parasitica* (Murr.) Barro in Japanese- and Chinese-origin chestnut trees that were brought into the USA by the Bronx Zoological Park, New York City (Anon 2016a). By the 1940s, chestnut blight had spread throughout the range of *C. dentata* and decimated the population. Root suckers develop from existing root systems that are not infected by the fungus (Anon 2016a); however, once the new shoots grow for a few years, they become infected and die, and more suckers form. This had a major adverse effect on *Castanea* biodiversity in eastern North American forests (Anon 2016a). Pre-blight range of chestnut extended from central Alabama north into southern Ontario and in the west through Tennessee and Kentucky, southern Indiana, and Ohio (Sargent 1905; Fernald 1950), and by the end of nineteenth century, the range contracted from the blight epidemic (Woods 1953). However, chestnut still persists across most of its range in small isolated stands, with trees seldom reaching appreciable size (Burnham 1990). Since 1909, efforts have been made to develop blight-resistant cultivars by hybridizing with Chinese chestnut, *C. mollissima*, and Japanese chestnut, *C. crenata* (Clapper 1954; Huang 1996), but the progress is slow.

In 2012 world production was on approximately 349,000 Ha (Pereira-Lorenzo et al. 2012). The top five countries had the following production of chestnuts (metric tons, MT) on area harvested (Ha) in 2012 (FAOSTAT 2016a): China (1,650,000 MT on 305,000 Ha), Republic of Korea (70,000 MT on 36,500 Ha), Turkey (59,789 MT on 3878 Ha), Bolivia (57,000 MT on 44,000 Ha), and Italy (52,000 MT on 25,000 Ha). These numbers reflect worldwide growth of chestnut production because averaged over 2000–2007, 1,140,332 MT of chestnuts were produced worldwide (Pereira-Lorenzo et al. 2012), and by 2012, China alone surpassed that total.

The USA is a small producer of chestnuts with its 919 producers growing the crop on approximately 1500 Ha, accounting for less than 1% of total world production in 2015 (Romero 2015a). Within the USA, Michigan is the top producer of sweet chestnuts (*C. sativa*), with the most growers and area of land planted to this crop (Michigan State University Extension 2016). In 2012 the top five states were as follows (number of farms – Ha): Michigan (115–250), Florida (111–592), California (59–240), Oregon (70–145), and Ohio (41–97, USDA Census of Agriculture 2012).

13.2.3 Challenges in Cultivation: Pests, Diseases, and Edaphic and Climatic Limitations

The top challenge to production, particularly in North America and Europe, is chestnut blight. Chestnut blight was first discovered in 1904 in a stand of chestnut nursery stocks introduced from Japan in New York's Bronx Zoological Park, but later work determined that it actually arrived in the USA in the late nineteenth century. It quickly spread to New Jersey, Maryland, and Virginia and continued to spread rapidly reaching Pennsylvania and North Carolina by the early twentieth century. All efforts to control its spread failed, and by 1940, the entire range of American chestnut was infected. The blight killed some 4 billion trees and was one of the greatest natural disasters in American history (Wheeler and Sederoff 2009). *Phytophthora* root rot caused by *Phytophthora cinnamomi* Rands is a problem especially on Chinese chestnuts (Michigan State University Extension 2016). Chestnuts are susceptible to nut rots caused by *Sclerotinia pseudotuberosa* (Rehm) Rehm, which is a troublesome pathogen in Europe, or *Phomopsis castanea* (Sacc.) Petr. in New Zeeland and Australia (Michigan State University Extension 2016).

Chestnuts require deep well-drained soils with a gentle slope and a pH of 4.5–6.5 and grow best in full sunlight (Anon 2006). Wet areas, compact soils, and low-lying frost pockets are not suitable for chestnut (Anon 2006; Barkley 2007). *Castanea dentata*, American chestnut, is endemic to regions in USDA plant cold hardiness zones 4–8 (Barkley), indicating a chilling requirement and good cold hardiness. Climate change could result in less cold injury in production areas, such as Michigan, and also enable farmers to move the crop northward in the Northern Hemisphere offering an additional crop for northern farmers. Many of these new areas have acidic soils that may be well adapted for chestnut production if winter injury no longer precludes a crop.

The American Chestnut Foundation is committed to restoring chestnut trees to its native ecosystems. Successful reforestation programs for chestnut should consider progeny testing to identify blight-tolerant genotypes to establish seedling and clonal seed orchards to produce genetically superior seeds for reforestation.

13.2.4 Nutritional and Functional Use

Fresh chestnuts are rarely consumed. Roasting and boiling increases available protein, sugars, and total dietary fiber content. Chestnut is rich in mono- and polyunsaturated fatty acids, which help to protect cardiovascular health. European chestnuts are lower in calories and fats than other seeds and nuts in part because of their higher starch content (Rudrappa 2016a). They are also high in fiber, vitamin A, B vitamins, vitamin C, folates, oleic acid, palmitoleic acid, and minerals (Rudrappa 2016a). Because of the high starch content, chestnut flour is used as a wheat substitute in bread, and mashed chestnuts are used as a potato substitute. Chestnuts are also used as vegetables and made into porridge, and a glazed sweet treat known as *marrons glacé* is also popular (Rosengarten 1984).

American chestnut is valued for its wood with up to a 20% tannin content that imparts rot resistance (Chestnut Hill Farm 2016). Therefore, it makes good posts or fences because it will hold up with ground contact. It has also been used for building ships, doors, window trim, floors, and siding, where it may be exposed to water (Chestnut Hill Farm 2016). The wood also makes beautiful furniture. The tannin is extracted and used for dying silk, tanning leather, and varnish (Chestnut Hill Farm 2016).

13.2.5 North American Crop Wild Relatives

There are three wild *Castanea* species in North America (Bailey and Bailey 1976): *Castanea dentata* (American chestnut), *C. pumila* (chinkapin), and *C. ozarkensis* (Ozark chinkapin). These native North American chestnuts are all highly susceptible to chestnut blight.

13.2.5.1 Distribution/Habitat/Abundance

The genus *Castanea* (Fagaceae) is widely distributed in the deciduous forests of the Northern Hemisphere. The modern distribution shows disjunctions with different biogeographic histories. *Castanea dentata* and *C. pumila* are found naturally in the eastern USA, along the Allegheny Mountain range into Ontario provenance in Canada. American chestnut occurs where it is moist and well-drained, along lower slopes and sometimes on rocky ridges (Faison and Foster 2014). Chinkapin occurs in oak, oak–hickory, oak–hickory–pine, southern mixed forest, and sand pine scrub (Sullivan 1994). *Castanea ozarkensis* ranges from Arkansas to Louisiana and from Oklahoma to Mississippi, USA, and grows in upland deciduous forests, open woodlands, and sandy soils that are dry. These species now exist as primarily understory trees that grow as coppice, in that they sprout from the roots, grow a few years, and then die from chestnut blight. This is the biggest impediment to utilization and the biggest challenge to increased use of these species.

13.2.5.2 Utilization of North American Chestnut Wild Relatives

Breeding efforts to restore the American chestnut to its former place of prominence are largely associated with nonprofit organizations including the American Chestnut Foundation (www.acf.org) and the Canadian Chestnut Council (www.canadianchestnutcouncil.ca). This breeding effort began by making crosses between Chinese or other blight-resistant chestnuts (*C. crenata* and *C. seguinii* Dode.) and American chestnut. The two blight resistance alleles are partially dominant, making selection for resistance possible (Steiner et al. 2017).

The plan for incorporating these disease resistance genes into American chestnut was presented by Burnham et al. (1986). The plan was to cross *C. dentata* with *C. mollissima* and other blight-resistant chestnut species and then backcross the progeny to *C. dentata*. The first progeny from the third backcross was planted in 2002 (The American Chestnut Foundation 2016). This third backcross generation was intercrossed to create a third-generation backcross, F_2 population, and then produce an F_3 population (Steiner et al. 2017). The backcross generations were assumed to be heterozygous for the resistance alleles, and the intercrossing is designed to allow for selection of plants that are homozygous for the resistance alleles.

The third-generation backcross was shown to be morphologically more similar to American chestnuts than Chinese chestnuts, and some had intermediate blight resistance (Cipollini et al. 2017). There is therefore promise that the American chestnut can be restored in North America.

13.2.5.3 Conservation Status of North American Chestnut

The American chestnut has been greatly reduced by chestnut blight (Fitzsimmons 2016). The estimated number of 464 million stems, based on the US Forest Service Inventory and Analysis, is only about 0.1% of the over 4 billion chestnut trees in eastern North America that existed before the introduction of chestnut blight (Scrivani 2010). Although it is not designated as a threatened species in the USA, it is listed as an endangered species under Ontario's Endangered Species Act, 2007. Substantial efforts are being made to maintain conservation orchards in the USA and Canada through programs to collect and conserve diverse chestnut trees in mother tree orchards. Ex situ storage of seed is difficult due to desiccation sensitivity, and *C. dentata* and its wild relative species are currently considered recalcitrant, in terms of ability to endure conventional seed storage (Hong et al. 1998). Most of the *C. dentata* germplasm (along with its wild relative species) currently exists in a coppice condition in situ throughout its distribution range.

13.3 Hazelnut or Filbert (*Corylus* L.)

13.3.1 Introduction to Hazelnut

Corylus L. (Betulaceae), hazel, is a tertiary disjunct genus consisting of about 15 to 20 taxa with Old and New World distributions. There are at least three species in Europe and the Mediterranean, three in North America, one in the Himalayas, and about ten in eastern Asia, but species delimitation is controversial.

The current revision based on morphological and molecular criteria recognizes four subsections (Erdogan 1999; Erdogan and Mehlenbacher 2000) within the genus *Corylus*. The subsection *Corylus* includes three species with leafy overlapping involucres covering the nuts (*C. avellana* L., *C. Americana* Marshall, and *C. heterophylla* Fisch. ex Trautv). The subsection Siphonochlamys comprises three species with tubular, bristle-covered involucres (*C. cornuta* Marshall, *C. californica* (A. DC.) Rose, and *C. sieboldiana* Blume). The subsection Columnaea is comprised of three single trunk tree species (*C. colurna* L., *C. chinensis* Franch, and *C. jacquemontii* Decne.). The subsection *Acanthochlamys* has one species that is characterized by a chestnut-like spiny involucre bract (*C. ferox* Wall.).

Corylus is hazel and its nut is commonly known as a filbert or hazelnut. It is a monoecious and wind-pollinated multi-stemmed deciduous shrub native to mild temperate regions of Asia, Europe, and North America. The main cultivated species in the world is *C. avellana*. This species is threatened by eastern filbert blight.

The North American wild hazels have been used in breeding programs with *C. avellana* to introduce resistance to eastern filbert blight and to enhance cold hardiness. The breeding efforts have been going on since the early twentieth century.

13.3.2 Origin of Hazelnuts and Use Worldwide

Corylus avellana (European hazel or filbert, Figs. 13.5 and 13.6) has been enjoyed by humans since the Mesolithic Age as evidenced by a discovery of a 9000-year-old large nut processing pit dating to 7000 BCE on the Hebridean island of Colonsay, Scotland, containing thousands of burnt hazelnut shells (Denison 1995).

It is likely that the Hebridean pit was processing nuts collected from the wild. People first began cultivation by planting seeds from superior trees; however, by Roman times, clonal trees were being propagated by layering of branches. This allowed horticulturists to select superior phenotypes and avoid the unevenness of seedlings that can exhibit great variation in nut size and shape (Zohary et al. 2012).

Hazelnuts were historically important in China according to a manuscript dated 2838 BCE (Tulum 2001). In the Pacific Northwestern USA, the earliest people arrived up to 14,000 BCE and likely gathered fruits and nuts (Hummer 2001). *C. californica* is indigenous to the western USA and likely served as a food source for early native people (Hummer 2001).

13.3.3 Challenges in Cultivation: Pests, Diseases, and Edaphic and Climatic Limitations

The most important insect pests of hazelnut orchards in the USA are aphids (*Myzocallis coryli* (Goetze) and *Corylobium avellanae* Shrank), filbert worms (*Cydia latiferreana* (Wlsm.), and leafrollers (*Archips rosanus* L. and *Choristoneura rosaceana* Harris), with filbert worm being the most significant insect pest (Olsen et al. 2013). Filbert worm damages the developing nut kernel, and aphids suck the tree's juices and sap vigor and may result in black sooty mold as a secondary problem. The filbert leafroller was introduced into the USA from Europe in 1915 (Olsen et al. 2013). Filbert leafroller larvae eat leaves and the developing nut shell within the husk, and they can be controlled by spraying.

The most common diseases in the USA are eastern filbert blight and bacterial blight (Olsen et al. 2013). The fungus that causes eastern filbert blight (*Anisogramma anomala* (Peck) E. Müll) had always been in the eastern part of North America but, in 1970, was discovered in a hazelnut orchard near Vancouver, WA (Olsen et al. 2013). It has now spread to Oregon and to British Columbia, Canada. Infected trees die slowly; however, fungicides are available as well as disease-resistant cultivars.

Bacterial blight is caused by *Xanthomonas arboricola* pv. *corylina* and is worse during wet years with heavy rains (Olsen et al. 2013). It can girdle the trunk and kill trees up to 5 years old. Infected branches can be removed by pruning, new trees should not be stressed or allowed to become sunburned, and copper sprays can be used to control this disease.

Hazelnuts are not tolerant of soils that remain wet and saturated for long times in the winter (Olsen et al. 2013). They are susceptible to *Phytophthora* root rot, often associated with wet soils, and to *Armillaria* (oak root fungus).

The production areas for *C. avellana* are limited by low temperatures (Molnar et al. 2005). Woody stem tissues suffer midwinter damage by extreme low temperatures, and staminate flowers are even less cold hardy than woody stems. The catkins are formed by autumn, so they are formed and exposed all winter and can be injured by low air temperatures, desiccation, and wind or by a frost or freeze during bloom (Molnar et al. 2005). Because it can grow and produce nuts in USDA hardiness zone 9 with no major problems (personal observation), it is unlikely that lack of chilling will become a major problem in production areas.

13.3.4 Nutritional, Functional Use

Hazelnuts are mainly used for their nuts and wood; however, all other parts of the plant are utilized including bark, leaves, roots, shells, and husks (Sullivan et al. 2014). The nuts are eaten raw, blanched, roasted, or made into flour. Hazelnuts are used in pralines, Nutella, tortes, ice cream (Gelato di Nocciola), and other dessert products (Sullivan et al. 2014). *C. avellana* seedlings are the most common species inoculated with *Tuber melanosporum* Vitt., the Périgord black truffle (Lefevre and Hall 2001). The European hazelnut is used because of its well-developed root system that forms a mycorrhizal association with the fungus. Successful inoculations have also been made with *C. colurna* and *C. heterophylla* (Lefevre and Hall 2001).

Hazelnut kernels contain over 60% oil by weight and some up to 70% with 15–18% carbohydrate and 10–16% protein. Hazelnuts are nutritious because of their high protein content, fiber, iron, calcium, vitamins B and E, and antioxidants and that more than 80% of their fat is monounsaturated with 75–80% oleic acid and to a lesser extent linoleic acid similar to olive oil (Hazelnut Growers of Oregon 2016; Sullivan et al. 2014). The good fats and nutrients accompanied by no cholesterol testify to hazelnuts being part of a healthy diet. The kernel is rich in potassium and fat-soluble vitamins A, E, and K and water-soluble vitamins thiamin, riboflavin, niacin, pantothenic acid, folate, and biotin, contributing to the health-promoting effects.

13.3.5 North American Crop Wild Relatives

There are three wild *Corylus* species native to North America: *C. americana* (American filbert or American hazel), *C. cornuta* (beaked filbert or beaked hazel), and *C. californica* (California hazel or western beaked hazel, Fig. 13.1), which has hairier young stems, and the involucral tube is shorter than var. *cornuta*.

13.3.5.1 Distribution/Habitat/Abundance

Corylus americana grows naturally from Oklahoma to Georgia and from Saskatchewan to Maine in eastern North America (Coladonato 1993). In nature, American hazelnut is a dominant or codominant shrub that can occur in forests that may contain maples, basswoods, jack pines, paper birches, trembling aspens, and oaks (Coladonato 1993).

Corylus cornuta grows naturally across the northern USA and southern Canada (Fryer 2007). *C. cornuta* occurs across much of the same distribution area as described for *C. americana*. *C. californica* occurs from southern California into British Columbia (Young-Mathews 2011). Beaked hazelnut is a dominant understory shrubby species in aspen, pine, birch, and mixed hardwood forests (Fryer 2007).

Fig. 13.1 *Corylus californica* (A. DC.) Rose (California hazel or western beaked hazel) growing at approximately 2000 m elevation in forest of the Sierra Nevada Mountains of California. The long involucral tube gives the fruit a beaked appearance. Both of the photographs of the fruit depict a set fruit and a fruit that did not set. There were very few fruits on these understory shrubs

13.3.5.2 Utilization of North American Hazelnut Wild Relatives

All *Corylus* species produce edible nuts and interspecific hybridization within subsections are generally possible with limited crossibility between different subsections (Erdogan and Mehlenbacher 2000). Sporophytic incompatibility has been reported in *Corylus*, but economically useful traits can be accessed through interspecific hybridization circumventing incompatibility.

Corylus maxima (giant filbert) grows naturally in the Balkans, Caucasia, and north Turkey and generally has larger nuts than *C. avellana*, with which it is fully fertile (Zohary et al. 2012). The larger nuts and better yields are causing some European farmers to replace European filberts with giant filberts. However, not everyone thinks that *C. maxima* is a separate species, and some believe that because all nine *Corylus* species freely intercross, they should all be in one large species: *C. avellana* (Mehlenbacher 1991).

The pathogen *Anisogramma anomala* that causes eastern filbert blight occurs naturally on *C. americana* in the wild and does not cause much damage (Muehlbauer et al. 2014). Eastern filbert blight is a serious disease on the commercially important *C. avellana* and is a threat to the industry. The first eastern filbert blight-resistant cultivar identified was the *C. avellana* low-yielding cultivar “Gasaway” which has a dominant resistance allele (Muehlbauer et al. 2014; Colburn et al. 2015).

Capik and Molnar (2012) inoculated 190 clonal *Corylus* accessions with *Anisogramma anomala* to assess resistance to eastern filbert blight, including *C. avellana*, *C. americana*, *C. heterophylla*, *C. colurna*, and *C. fargesii*. Eastern filbert blight did not occur on most accessions of *C. americana* and not on any *C. heterophylla* tested. When these two species were crossed with *C. avellana,* the hybrids ranged from none to severe symptoms, indicating that these species are sources of resistance to be exploited. It is not surprising that *C. americana* is a source of resistance, but *C. heterophylla* is from Asia where the pathogen is not present yet has good resistance.

Corylus americana has been crossed with *C. avellana* for decades to bring eastern filbert blight resistance and enhanced cold hardiness into cultivated hazel (Molnar et al. 2005). *Corylus cornuta* was also used for its cold hardiness. These old eastern USA breeding programs did not develop cultivars that were widely adopted (Molnar et al. 2005). However, the hazelnut breeding program at Oregon State University is producing new cultivars, including some with eastern filbert blight resistance.

13.3.5.3 Conservation Status of North American Hazelnut Wild Relatives

These species are not federally endangered or threatened; however, *C. cornuta* no longer exists in the wild in Ohio and in Illinois is rare (Fryer 2007), so there may be some cause of concern for loss of genetics. In the USA, the *Corylus* collection is managed by the National Clonal Germplasm Repository in Corvallis, OR, where 444 accessions are listed on GRIN-Global (https://npgsweb.ars-grin.gov/

gringlobal/search.aspx). Their collection includes the 8 major species and lists 444 accessions; 70 accessions of *C. avellana* accessions are backed up in tissue culture (Joseph Postman, personal communication 2017).

13.4 Pecan (*Carya illinoinensis* (Wangenh.) K. Koch)

13.4.1 Introduction to Pecan

Carya, commonly known as hickory, is an economically important genus in the walnut family, Juglandaceae, with approximately 18 extant species of deciduous trees adapted to temperate and subtropical regions of the Northern Hemisphere. The genus exhibits an intercontinental disjunction in its distribution between East Asia and eastern North America (Stone and Flora of North America Editorial Committee 1997). Five to six species are native to southern China, northeastern India, Laos, and northern Vietnam (Chang and Lu 1979), while 12 species are endemic to eastern and southeastern USA and Mexico (Manning 1949, 1978; Stone et al. 1969). The most economically important *Carya* species is *C. illinoinensis* (Wangenh.) K. Koch, pecan (Fig. 13.2).

Fig. 13.2 Left, *Carya illinoinensis* (Wangenh.) K. Koch (pecan) tree. Right, nut cluster, dehiscent fruit cracking, and split open to reveal the nut

13.4.2 Origin of Pecan and Use Worldwide

Pecan is native to North America and is the only major nut crop from this continent. Unlike other nut crops, it does not have a long written history. The name "pecan" is from the Algonquin word "paccan" meaning "all nuts requiring a stone to crack" (McWilliams 2013; National Pecan Shellers Association 2016; Rosengarten 1984). This also indicates that Native Americans were utilizing the nut and taught the name to Europeans and others. It is believed that Native Americans ate pecans in the autumn and used them to make a fermented, alcoholic drink known as powcohicora (National Pecan Shellers Association 2016). These original Americans mainly consumed the crop as whole nuts but also ate it as a flour or meal mixed with bread, corn gruel, and bison meat (McWilliams 2013). McWilliams (2013) further writes that there is evidence that the Native Americans purposefully spread the seeds, thus extending the range of this nut crop. These were the first domestication events. The current distribution of *C. illinoinensis* may therefore overrepresent the original natural distribution because of these early anthropomorphic activities.

Native peoples sold or bartered pecans with early Spanish settlers in the sixteenth century (McWilliams 2013), thus introducing the delicious nut to the Europeans. In the 1800s, settlers in the southeastern USA thinned natural forests to leave pecan trees with grazing grasses below (Ree 2006). The earliest planting of pecan trees was on Long Island, NY, USA, in 1772 (Wood et al. 1994). These were propagated by seeds. By 1822, Abner Landrum from South Carolina had published a successful budding technique to propagate elite pecan clones (Wood et al. 1994). The problem was that this information was lost, not well communicated, or ignored. In 1846, Antoine (a slave gardener owned by Governor Telesphore J. Roman, Oak Alley Plantation, Louisiana) was successful in grafting a superior genotype, eventually named "Centennial" to 16 native pecan seedlings (Rosengarten 1984; Wood et al. 1994). By the late 1800s and early 1900s, grafting became more common; Bordeaux spray was introduced to control scab, and by the 1930s shelling machinery was available (Ree 2006). Patch budding and inlay bark grafting are now commonly used on pecan (Rosengarten 1984).

Today in the USA, commercial production of pecans is from naturally occurring, non-grafted trees (managed natural stands) and from orchards planted with grafted improved cultivars (Grauke et al. 2016). These two sources result in the USA being, by far, the world's largest pecan producer, with about 75%, and Mexico second with about 20% of world production (Hadigeorgalis et al. 2005). South Africa and Australia produce about 5% of the world's pecans (Grauke et al. 2016). By 2014, the USA pecan crop was valued at $517 million and was 119,816 metric tons from 14 states with Georgia, New Mexico, Texas, and Arizona having the largest production (Marzolo 2015).

13.4.3 Challenges in Cultivation: Pests, Diseases, and Edaphic and Climatic Limitations

Because pecan trees can survive for more than 200 years, and old, native trees continue to produce nuts, scientists consider the genetic diversity in *C. illinoinensis* to be robust (Grauke et al. 2016). Scab caused by *Cladosporium caryigenum* (Ellis & Langl.) Gottwald is the most serious disease of pecans (Von Broembsen 2013). This is controllable with sanitation and fungicides. *Xylella fastidiosa* (Wells et al.), which is spread to pecan by the glassy-winged sharpshooter (*Homalodisca vitripennis* (Germar)), Johnson-grass sharpshooter (*Homalodisca insolita* (Walker)), or pecan spittlebug (*Clastoptera achatina* (Germar)), is an emerging pathogen on pecan and causes pecan bacterial leaf scorch (PBLS) (Grauke et al. 2016). Other pecan diseases include vein spot (*Gnomonia nerviseda* Cole), liver spot (*Gnomonia caryae* (Ell. and Ev.) var. *pacanae*), powdery mildew (*Microsphaera alni* (DC.) G. Winter), Rosette (zinc deficiency), bunch disease (phytoplasma), hypoxylon canker (*Hypoxylon atropunctatum* (Schwein.) Cooke, Grevillea), twig dieback (*Botryosphaeria berengeriana* De Not), crown gall (*Agrobacterium tumefaciens* Smith et al.), and nematodes (Von Broembsen 2013).

There are a number of insect pests of pecan, including pecan nut casebearer (*Acrobasis nuxvorella* Neunzig), hickory shuckworm (*Cydia caryana* (Fitch)), hickory nut curculio (*Conotrachelus affinis* Boheman), pecan spittlebug, kernel-feeding bugs, weevils, phylloxera, aphids, and scorch mites (*Eotetranychus hicoriae* McGregor), with phylloxera, shuckworm, hickory nut curculio, and weevils being the most serious pests (Hudson 2013). There are effective sprays for these pests.

Late spring and early autumnal frosts can reduce production, as can too much rain during the pollination period, drought, or too much cloud cover (Grauke et al. 2016).

13.4.4 Nutritional, Functional Use

The fresh nuts are eaten, or baked into various products, including pies, cakes, candies, and cookies. In addition, the shells are used as mulch, a gravel substitute, and fuel. The tree is an attractive landscape specimen, and the wood is used for veneer, fine furniture, paneling, and hardwood flooring (Rosengarten 1984).

Pecans have high monounsaturated fatty acids, such as oleic acid, and are good energy sources with 690 calories in 100 g of nut meat (Rudrappa 2016b). They are also high in antioxidants, such as ellagic acid, vitamin B complex, vitamin E, beta-carotene, lutein, and minerals, including calcium, iron, and magnesium (Rudrappa 2016b).

13.4.5 North American Crop Wild Relatives

Grauke et al. (2016) list 12 species and 2 sections (*Apocarya* and *Carya*) in North America. Section *Apocarya* (pecan hickories) members are diploids and include pecan (C. *illinoinensis*), *C. aquatica* (F. Michx.) Nutt., *C. cordiformis* (Wangenh.) K. Koch, and *C. palmeri* Manning. Section *Carya* (true hickories) members are tetraploids and include *C. floridana* Sarg., *C. glabra* (Mill.), *C. laciniosa* (F. Michx.) Loudon, *C. myristiciformis* (F. Michx.) Nutt., *C. ovata* (Mill.) K. Koch, *C. pallida* (Ashe) Engl. & Graebn., *C. texana* Buckley, and *C. tomentosa* (Poir.) Nutt. (Grauke and Thompson 1996; Grauke et al. 2016). Species with the same ploidy level are interfertile and interspecific hybrids are listed in Grauke et al. (2016).

13.4.5.1 Distribution/Habitat/Abundance

Carya illinoinensis is distributed along the lower Mississippi Valley, from Louisiana into Illinois and Indiana, westward to Kansas and central Texas. It is generally a bottomland species in the Mississippi Valley where it can occur in pine, oak-pine, and mixed hardwood forests (Coladonato 1992). It grows best on loamy soils with good drainage and is associated with silver maple, box elder, pawpaw, pokeweed, and giant cane.

Carya cordiformis ranges from Texas into southern New England, into southern Ontario and Quebec provenances, and into Minnesota. *Carya aquatica* ranges from Texas into southern Illinois and in the southeastern USA. *Carya palmeri* occurs naturally in Mexico. *Carya laciniosa* ranges from Nebraska eastward into southern Ontario province and into New York with scattered stands in the southeastern USA. *Carya myristiciformis* occurs in scattered stands in Mexico, Texas, Louisiana, and eastward as far as North Carolina. *Carya ovata* is wide ranging from Texas to Maine and from Quebec and Ontario provinces to Minnesota and Iowa. There are some disjunct natural stands in Mexico. *Carya tomentosa* ranges from Texas to Florida to New Hampshire and into Quebec and Ontario provinces to Iowa. *Carya glabra* ranges from Louisiana to Florida and north into New Hampshire and west into Illinois. *Carya pallida* occurs from Louisiana into Virginia. *Carya floridana* grows naturally in Florida. *Carya texana* occurs in Texas to Illinois and south to Louisiana.

13.4.5.2 Utilization of North American Pecan Wild Relatives

Because *C. illinoinensis* is native to North America, its genepool exists in its native, in situ population and at the National Collection of Genetic Resources for Pecans and Hickories, Somerville, TX, USA. Although none of the hickories are cultivated or the nuts sold, nuts of *C. laciniosa* (Shellbark hickory) and *C. ovata* (Shagbark hickory) are harvested from the wild and eaten (Grauke et al. 2016).

Some of the *Carya* wild relatives have been crossed with pecan to bring in new traits. For example, the smallest hickory trees are *C. floridana* which is being crossed with pecan to reduce tree size (Grauke et al. 2016). This can be for scion and rootstock breeding. Interspecific hybrids between pecan and *C. ovata* from Mexico have been made to bring in the traits of low chilling and early maturing nuts (Grauke et al. 2016).

13.4.5.3 Conservation Status of North American Carya Genetic Resources

Two *Carya* species, *C. floridana* (scrub hickory) and *C. myristiciformis* (nutmeg hickory), are the most threatened because of scrub hickory being restricted to central Florida, USA, and nutmeg hickory being present only in scattered, disjunct populations (Grauke et al. 2016). In 2009, collections of *C. floridana* were made across its range and preserved in the USDA-ARS National Collection of Genetic Resources for Pecans and Hickories, Somerville, TX, USA. This Repository also lists 40 accessions of *C. myristiciformis*. Most of the North American *Carya* exist in abundant numbers in the wild. The area occupied by natural stands of pecans has been reduced, especially in Arkansas (Grauke et al. 2016). Cattle grazing under trees has limited production in wild stands and has resulted in conversion of land to grafted, cultivated cultivars (Grauke et al. 2016).

13.5 Pistachio (*Pistacia vera* L.)

13.5.1 Introduction to Pistachio

The genus *Pistacia* is a member of the Anacardiaceae family and includes at least 11 extant dioecious tree species grouped into 4 sections (Zohary 1952) with both Old and New World distributions. The section *Lentiscella* Zoh. contains the two New World taxa, *P. mexicana* Kunth and *P. texana* Swingle, distributed in South Central USA, Northern Mexico, and Guatemala. The section *Eu Lentiscus* Zoh. contains *P. lentiscus* L., *P. saporte* Burnat., and *P. weinmannifolia* Poiss. ex Franch with distributions in North Africa, southern Europe, West Asia, China, and Indo-China. The section *Butmela* Zoh. includes a single taxon, *P. atlantica* Desf., with distributions in North Africa, West Asia including northern India, Pakistan, the Caucuses, and Eastern and Southeastern Europe. The section *Eu Terebinthus* contains *P. vera* L. from West and Central Asia; *P. khinjuk* from Northeastern Africa, West Asia, and northern states of the Indian subcontinent; *P. terebinthus* L. from North Africa, West Asia, and Southern Europe; *P. chinensis* Bunge from China, Taiwan, and the Philippines; and *P. palaestina* Bois. from the Palestinian territories, Syria, and Israel.

Fig. 13.3 Row of *Pistacia texana* Swingle at the National Clonal Germplasm Repository, Davis, CA, USA. Inset, close-up of fruit along a branch of a female tree

The two *Pistacia* wild relatives in North America, *P. mexicana* and *P. texana*, are secondary gene sources for *P. vera*, and the leaves of these two species are used as goat feed, and the plants can be handsome landscape plants. The female *P. texana* have beautiful, red fruit along the stem (Fig. 13.3).

13.5.2 Origin of Pistachio and Brief Use Worldwide

Pistacia vera is indigenous to an area from northeastern Iran through north Afghanistan and up to Tajikistan, Kyrgyzstan, Turkmenistan, Uzbekistan, and Kazakhstan (Zohary et al. 2012). It has been used by humans for more than 9000 years. Much of this early utilization was from collection from the wild; in fact, people continue to harvest pistachio nuts from wild forests in countries, such as Afghanistan (L. Ferguson personal communication, Rosengarten 1984), following a tradition that dates back millennia.

Formal cultivation of the crop did not begin until about 1900 when selections began to be made of superior phenotypes from the wild (Rosengarten 1984). These early orchards were mainly in Iran and Turkey.

Today the following countries are top producers of pistachio nuts (metric tons, MT) on area harvested (Ha) in 2012 (FAOSTAT 2016b): Iran (472,097 MT on

257,925 Ha), the USA (231,000 MT on 72,000 Ha), Turkey (150,000 MT on 53,071 Ha), China (74,000 MT on 25,000 Ha), and Greece (10,000 MT on 5400 Ha).

Yield and harvest data, other than area harvested, can be misleading when considering only 1 year because pistachio is a strongly alternate bearing crop and yield depends on whether it is an "on" year or "off" year in that particular region. During 2012, Iran had by far the biggest yield, followed by the USA and Turkey. These three countries consistently are the largest producers of pistachio nuts and have the most land devoted to the crop.

13.5.3 Challenges in Cultivation: Pests, Diseases, and Edaphic and Climatic Limitations

The following are diseases and pests of pistachios: *Verticillium* wilt (*Verticillium dahliae* Kleb.); *Armillaria* root rot (oak root fungus, *Armillaria mellea* (Vahl) Quel.); late blight *(Alternaria alternata* (Fr.) Keissler); Blossom, shoot, and fruit blight (*Botrytis cinerea* Pers.: Fr.); panicle and shoot blight (*Botryosphaeria dothidea* (Moug. ex Fr.) Ces. de Not.); navel orangeworm (*Amyelois transitella* Walker); citrus flat mite (*Brevipalpus cuneatus* Canestrini and Fanzago); leaffooted plant bugs (*Leptoglossus clypealis* Heidemann, and *Leptoglossus zonatus* (Dallas)); and various species of small plant bugs (Ferguson et al. 2016). *Verticillium* wilt is the disease that has caused the most economic loss to growers and is best managed by grafting onto rootstocks containing *P. integerrima* Stew ex Brandis genetics, such as "Pioneer Gold I" or "UCB-1" (Holtz 2002; Ferguson et al. 2016).

A recent report describes a new pistachio disease "Bushy Top" that is caused by *Rhodococcus* (Stamler et al. 2015). It appears to be associated with some nurseries producing clonal "UCB-1" rootstock and causes unacceptable stunting in grafted trees. An alternative hypothesis is that these are clonal variants produced in long-term micropropagated shoot cultures and not a result of an infection (Preece 2017, unpublished).

Pistacia vera is very drought tolerant and grows naturally in dry climates (Rosengarten 1984). It has the most salt tolerance of any nut tree grown in the USA (Miyamoto 1993). Because of this, growers will plant pistachio on marginal lands with soil salinity levels too high for almonds or grapes (Sanden et al. 2013).

13.5.4 Nutritional, Functional Use

When pistachios are compared to almonds and walnuts, they are lower in fat and calories but higher in potassium, vitamin K, phenols, phytosterols, and lutein plus zeaxanthin (Dreher 2012). Also, when compared to other nuts, pistachios also have high levels of Cu, Mg, and Mn and vitamins A, B, and C, with the exception of vitamin B_{12}, which they are lacking (Bulló et al. 2015).

Pistachios are primarily sold as in-shell nuts and are mainly consumed after roasting and salting (Boriss 2015). Nuts that have not split, or are stained, are used in candies and confections or cooked in casseroles and other recipes (Boriss 2015).

The beautiful wood of pistachio is not widely used but has been used for carvings, turned objects, musical instruments, and inlays (Meier 2013a). Interestingly, when a black light is shined on the heartwood, the wood fluoresces a vibrant yellow/green color.

13.5.5 North American Crop Wild Relatives

Since 1952 there have been two *Pistacia* species recognized as native to North America, *P. mexicana* (Mexican pistache, Fig. 13.4) and *P. texana* (Texas pistache, American pistachio, wild pistachio, Lentisco) (Zohary 1952) (Figs. 13.3 and 13.4). However, there is not universal agreement that these are two species, and some believe that the native North American *Pistacia* are all *P. mexicana* (Al-Saghir and Porter 2012). In this chapter, while acknowledging that there could be a single species, P. *mexicana*, we follow GRIN taxonomy and discuss *P. mexicana* and *P. texana* as separate species. Based on interspecific hybridization, both of these species are considered to be in the secondary gene pool of *P. vera* (Hormaza and Wünsch 2011).

Fig. 13.4 Male *Pistacia mexicana* Kunth tree within the collection at the National Clonal Germplasm Repository, Davis, CA, USA, with a close-up of the leaves

13.5.5.1 Distribution/Habitat/Abundance

Pistacia mexicana occurs in northern Mexico in the states of Coahuila, Nuevo Leon, San Luis Potosi, and Tamaulipas and extends through southern Mexico, occurring in the states of Chiapas, Guanajuato, Guerrero, Hidalgo, Michoacan, Oaxaca, Puebla, Queretaro, Veracruz, and the country of Guatemala.

Pistacia texana grows on the Edwards Plateau and in Rio Grande canyons of Texas on hard limestone (Anon 2016b). It has good drought, salt, and heat tolerance, adapts to different soil pH values, and is hardy in USDA hardiness zone 8. The species is cultivated for use in landscapes and appears to be secure.

13.5.5.2 Utilization of Pistachio Wild Relatives

Although these species are in the secondary gene pool, they are not utilized as breeding material, nor are they used as rootstocks, as are other crop wild relatives of *P. vera*. *Pistacia mexicana* and *P. texana* seeds are unimportant for wildlife or human food; however goats eat the leaves (Lady Bird Johnson Wildflower Center 2015). They are used as landscape plants and are available commercially for this use.

Pistacia wild relatives (*P. atlantica*, *P. integerrima*, and *P. terebinthus*) have been used historically and continue to be used as rootstocks. Internationally, *Pistacia vera* scions are often grafted onto *P. atlantica* or *P. terebinthus* (Rosengarten 1984). In California, these two rootstocks have been used, as well as *P. integerrima* (“Pioneer Gold I”), and the interspecific hybrid rootstocks: “Pioneer Gold II” (*P. integerrima* X *P. atlantica*) and “UCB-1” (*P. atlantica* X *P. integerrima*) (Ferguson et al. 2005; Beede et al. 2010). Growers tend to use rootstocks with *P. integerrima* genetics because this species offers resistance to *Verticillium*.

13.5.5.3 Conservation Status of North American Pistachio Wild Relatives

Pistacia mexicana is considered a “Near Threatened” species according to the IUCN Red List (Maxted and Rhodes 2016). This likely relates to its restricted distribution and altitudinal range. It grows in dry mountain scrub or pine-oak mixtures (Ramirez-Marcial and González-Espinosa 1998) from 500 to 2000 m elevation. It is facing habitat loss from grazing and agricultural activities (Maxted and Rhodes 2016).

Pistacia mexicana and *P. texana* accessions are maintained and curated by the National Clonal Germplasm Repository, Davis, CA. The Repository currently has three *P. mexicana*, and all are male. There are eight *P. texana* accessions at the Repository: five females and three males. Because of the vulnerability of *P. mexicana*, the ex situ collection should be strengthened.

13.6 Walnut (*Juglans* L.)

13.6.1 Introduction to Walnut

The section *Rhysocaryon* (black walnuts) is endemic to the Americas and comprises five North American temperate taxa, *J. californica* S. Wats., *J. hindsii* (Jeps.) Rehder, *J. nigra* L., *J. major* (Torr. ex Sitgr.) Heller, and *J. microcarpa* Berl.; four Central American subtropical taxa, *J. hirsuta* Manning, *J. mollis* Engelm., *J. olanchana* Stadl. et I. O. Williams, *J. guatemalensis* Mann.; and two South American tropical taxa, *J. neotropica* Diels and *J. australis* Griesb, mainly occurring in the highlands. They typically bear nuts that are four-chambered at the base with thick nutshells and septa. Although the nuts are eaten on many of these, none are important major nut crops. However, the beautiful wood of some of the species, especially *J. nigra*, has great economic value as veneer, furniture, gunstocks, and other uses.

The Persian or English walnut (*Juglans regia* L.) belongs to the section *Juglans* within the genus *Juglans* of the family Juglandaceae. It is native to the region in Eurasia extending from the Near East through the Central Asia to the Himalayas and on to Western China. (Zohary and Hopf 1993). The thin-shelled cultivated walnut (*Juglans regia*) belongs to the section *Juglans* within the genus *Juglans* of the family Juglandaceae.

Juglans regia is the primary culinary walnut species and is grown worldwide for its large, sweet, and easy to crack nuts. *Juglans regia* means royal nut of the Gods, or of Jupiter, because *Juglans* is from the Latin *Jovis glans* or nut of the God Jupiter and regia means royal (Rosengarten 1984). People have been gathering and cultivating this delicious nut for millennia, and it is now produced worldwide. *J. regia* has a natural range from the Balkan Mountains to the Himalayan Mountains.

13.6.2 Origin of Walnut and Use Worldwide

Although the origin of walnut (*J. regia*) is obscure, based on the historical biogeography and the probable locations of the Quaternary glacial refugia, it can be speculated that walnut has multiple centers of origin in the Carpathians, the Balkans, the Caucasus, the Near East, and the western Tian Shan mountainous region comprising the Transcaucasia, northeastern Turkey, the western Tien Shan Mountains, and southwestern China (Aradhya et al. 2017). However, Zohary et al. 2012 believe northeastern Turkey and the southern Caucasus regions are the plausible centers of domestication of walnut. The postglacial wild walnuts in the Balkans and Central Europe represent feral derivatives introduced by humans in the Bronze Age.

Zohary et al. (2012) cite radiocarbon calibrated dating of *J. regia* remains that were discovered in northern Italy, Turkey, and Spain dating back 6450–10,650 BCE, indicating early domestication. However, the exact time of walnut domestication is unknown. Early people likely gathered these nuts from the wild, often in riparian areas. The process of selecting trees with large, sweet nuts with sufficiently thin shells for easy cracking is thought to have begun in or around Persia many 1000 years ago (Rosengarten 1984). Seeds from these elite trees were moved and planted. Some areas of the world continue to rely on seed-propagated walnuts for their crop, even though seedling walnuts segregate for various traits.

The following five countries are top producers of walnuts (metric tons, MT) on area harvested (Ha) in 2012 (FAOSTAT 2016c): China (1,700,000 MT on 425,000 Ha), Iran (450,000 MT on 64,000 Ha), the USA (425,820 MT on 98,980 Ha), Turkey (194,298 MT on 99,617 Ha), and Mexico (110,605 MT on 69,796 Ha).

13.6.3 Challenges in Cultivation: Pests, Diseases, and Edaphic and Climatic Limitations

Juglans regia requires from 700 to 1000 h of chilling below 7 °C for normal bud break and growth (McGranahan and Leslie 2012). During the winters preceding the 2014 and 2015 growing seasons, chilling was less than adequate in California for walnuts. This causes unusual bud break patterns in that the buds on the northern sides of vertical shoots grew in the spring, whereas those on the southwestern side did not grow and remained dormant. Therefore, if chilling hours continue to decrease in walnut-growing regions, production might have to shift to locations with adequate chilling. McGranahan and Leslie (2012) believe that the commercial production range for walnuts could probably expand by exploiting genetic diversity in the germplasm.

There is a variety of walnut pathogens and pests. Pathogens include *Agrobacterium tumefaciens* that causes crown gall; *Armillaria mellea* (oak root fungus) that causes *Armillaria* root rot; *Erwinia nigrifluens* Wilson et al. that causes shallow bark canker; *Brenneria rubrifaciens* Wilson et al. that causes deep bark canker; cherry leaf roll virus that causes blackline, which is a failure at the Persian walnut/black walnut graft union; *Geosmithia morbi*da Kolařik that causes thousand canker disease; *Phytophthora* spp. that cause *Phytophthora* root and crown rot; and *Xanthomonas campestris* pv. *juglandis* (Pierce) Dye that causes walnut blight (UC IPM 2016). They are susceptible to three nematodes: *Meloidogyne* spp., root-knot nematodes; *Mesocriconema xenoplax* (Raski) Luc and Raski, ring nematode; and *Pratylenchus vulnus* Allen & Jenson, lesion nematode (UC IPM 2016). Insect pests include *Amyelois transitella* Walker, navel orangeworm; *Archips argyrospila* Walker, fruit-tree leafroller; *Chromaphis juglandicola* (Kaltenbach) and *Callaphis juglandis* (Goeze), aphids; *Chrysobothris mali* Horn, Pacific flatheaded borer; *Cydia pomonella* (L.), codling moth; *Diaspidiotus perniciosus* (Comstock), San Jose scale; *Epidiaspis leperii* Sign., Italian pear scale; *Hyphantria cunea* Drury, fall webworm; *Nysius raphanus* (Howard), false chinch bug; *Parthenolecanium corni* (Bouché), European fruit lecanium; *Parthenolecanium pruinosum Cocquillet*, frosted scale; *Pityophthorus juglandis* Blackman, walnut twig beetle; *Quadraspidiotus juglansregiae* (Comstock), walnut scale; *Rhagoletis complete* Cresson, walnut husk fly; *Schizura concinna* JE Smith, redhumped caterpillar; and

Solenopsis xyloni McCook, southern fire ant (UC IPM 2016). Mite pests include *Eriophyes erinea* (Nalepa), walnut blister mite; *Panonychus ulmi* (Koch), European red mite; *Tetranychus pacificus*, Pacific spider mite; and *Tetranychus urticae* Koch, twospotted spider mite (UC IPM 2016).

Diseases, such as walnut blight, can be controlled genetically by breeding for late leafing in the spring. Early leafing tends to be more synchronous with wet periods creating an environment that favors infection by the bacterial pathogen, *Xanthomonas campestris* pv. *juglandis*. Additionally, genes are available for rootstocks to provide resistance to soil-borne pathogens, such as *Agrobacterium tumefaciens*, *Phytophthora*, and nematodes.

13.6.4 Nutritional, Functional Use

Walnuts have a low glycemic index and are high in omega-3 fats, including monounsaturated fat and polyunsaturated fat, and are high in alpha-linolenic acid with very little saturated fat (George Mateljan Foundation 2016). They are good sources of biotin, calcium, copper, iodine, iron, magnesium, manganese, molybdenum, phosphorus, potassium, selenium, and zinc (George Mateljan Foundation 2016). Walnuts have excellent antioxidant activity and are high in the gamma-tocopherol form of vitamin E, which has anti-inflammatory activity and defends against nitrogen oxides, cancers, and Alzheimer's disease compared to the alpha-tocopherol form (George Mateljan Foundation 2016; MacWilliam 2006).

Walnuts are generally eaten raw without salt and roasting. They are used in various confectionaries, including cookies, cakes, ice cream, and candy. A negative of being high in monounsaturated and polyunsaturated fat is those easily digestible fats become rancid more quickly than saturated fats. This reduces the popularity of walnuts in some foods because storage life is not as long as with some other nuts, such as pistachios or almonds. Walnut milk can be made from blanched walnuts, or they can be made into flour. Walnut oil is also available commercially. Green walnuts can be pickled, preserved in sweet syrup, made into preserves, or used to prepare a nut brandy (Rosengarten 1984). Walnut wood is beautiful and has been prized for furniture; however, *Juglans nigra* (eastern black walnut) is the walnut most prized for its dark grained wood that is used for furniture, gunstocks, bowls, and other creations. Black walnuts are also used for dyes.

13.6.5 North American Crop Wild Relatives

There are nine *Juglans* species native to North America: *J. californica* (Southern California black walnut, Fig. 13.5), *J. cinerea* (butternut, Fig. 13.6), *J. hindsii* (Northern California black walnut, Fig. 13.7), *J. hirsuta* (Nuevo Leon walnut),

Fig. 13.5 *Juglans californica* S. Watson tree and fruit growing in the collection of the National Clonal Germplasm Repository, Davis, CA, USA

J. major (Arizona black walnut, Fig. 13.8), *J. microcarpa* (Texas black walnut, Fig. 13.9), *J. mollis* (Mexican walnut), *J. nigra* (Eastern black walnut, Fig. 13.10), and *J. olanchana* (nogal, boza, cedar-walnut).

13.6.5.1 Distribution/Habitat/Abundance

North American *Juglans* range throughout the eastern USA into southeastern Canada, and into Colorado, but they are not present throughout the Rocky Mountains. They also range along the Pacific coast of the USA, into Mexico, and across Texas and Arizona. There are nine North American *Juglans* species. *Juglans californica* is native to southern California. In Ventura Co., it is in the southern Santa Inez and Santa Susana Mountains, and in Los Angeles Co., it occurs in the foothills and the Santa Monica Mountains (Keeley 1990). It can occur up to 1000 m elevation in the Santa Susana Mountains (Keeley 1990) and does well along riparian areas with gravelly soils that are moist to dry (Plants for a Future 2016a). *Juglans cinerea* extends from southeastern New Brunswick, Canada, into Ontario and Quebec, south into northern Alabama, Georgia, Mississippi, and Arkansas, up into Minnesota and the New England states (Coladonato 1991). It occurs in riparian areas and the sides of hills on well-drained soils (Rink 1990). *Juglans hindsii* has been planted

Fig. 13.6 *Juglans cinerea* L. trees in the collection of the National Clonal Germplasm Repository, Davis, CA, USA. Inset, cluster of mature fruit

and has naturalized from about Fresno, north into Oregon. However, there may be as few as one viable native stand that remains (CNPS, Rare Plant Program 2016). It is adapted to riparian areas. *Juglans hirsuta* is endemic to a small area in northeastern Mexico (Stone et al. 2009). It grows along riparian areas rather than mountain fog belts (Manning 1957). *Juglans major* has a native range from southwestern New Mexico and central Arizona east to central Texas (Pavek 1993). It can occur as scattered trees or in mixed stands with *Platanus*, *Populus*, and *Fraxinus*, and mixed with pines and oaks (Pavek 1993). *Juglans microcarpa* extends from central New Mexico and Texas into southwestern Kansas and through Oklahoma, and this range includes the Colorado River Valley and the Trans-Pecos Mountains (Tirmenstein 1990). *Juglans mollis* is endemic to eastern central Mexico (Stone et al. 2009). This species can occur at elevations exceeding 1000 m (Manning 1957). *Juglans nigra* ranges throughout the eastern USA, from east Texas, north into South Dakota and Minnesota, and east into New York, and south into the Florida panhandle. It grows best in deep, moist, well-drained soils high in organic matter, such as is found in many riparian areas. *Juglans olanchana* is endemic to southern Mexico, into

Fig. 13.7 *Juglans hindsii* (Jeps.) R. E. Sm. mature trees growing in a riparian area in northern California. Inset, mature fruit

Fig. 13.8 *Juglans major* (Torr.) A. Heller tree in the collection at the National Clonal Germplasm Repository, Davis, CA, USA. Inset, mature fruit and nuts

Fig. 13.9 *Juglans microcarpa* Berland. tree in the collection at the National Clonal Germplasm Repository, Davis, CA, USA. Insets, a mature fruit on the tree and a handful of nuts, showing their small size

Fig. 13.10 Left, *Juglans nigra* L. tree in the collection at the National Clonal Germplasm Repository, Davis, CA, USA. Right, mature fruit being borne terminally on this branch

Guatemala, Honduras, and Nicaragua (Nelson 1998; Stone et al. 2009). It grows in the tropical areas with good rainfall and along riparian areas up into the mountain sides, usually between 400 and 1600 m elevations (Fern et al. 2014).

13.6.5.2 Utilization of North American Walnut Wild Relatives

The nut of *J. californica* can be eaten both raw and cooked into various dishes and confections, the tree has an attractive wood, and it has been used as a rootstock (Plants for a Future 2016a). However, it is not an economically important species. The meat of the nut of *J. cinerea* is difficult to extract but can be eaten raw or ground into a flour for cooking (Plants for a Future 2016b). The fruit husk can yield a yellow to orange dye and the stems, leaves, buds, and unripe fruit and produce a light brown dye, and its wood makes nice furniture and doors (Plants for a Future 2016b). The seeds of *J. hindsii* are eaten raw and the wood can be used for furniture; however, the most important economic use is for rootstocks (Plants for a Future 2016c). The seed of *Juglans major* can be eaten raw or cooked; the wood makes beautiful furniture and is used as a rootstock (Plants for a Future 2016d). The seed of *J. microcarpa* is very small and hard, making extraction of the meat difficult, so it is not eaten very much. An edible oil can be extracted, and the wood is use for veneer, cabinets, and furniture (Plants for a Future 2016e). The nuts of *Juglans mollis* have a thick shell, but are eaten cooked or raw, and the wood is hard and durable and used for making bowls and tubs (Fern et al. 2014). The nut of *J. nigra* is eaten raw or cooked into confections and desserts; however, its economic value is in its beautiful wood, which some think is the most desired from North America for multiple uses including gunstocks, furniture, ships, and veneer (Plants for a Future 2016f).

Of the North American wild relatives, *Juglans nigra* is the most valuable because of its expensive and desired wood. *Juglans hindsii* and *J. microcarpa* have been used in hybrid rootstock development. As mentioned above, *J. hindsii* is used as a rootstock for *J. regia* cultivars. In the late 1800s, Luther Burbank created an interspecific hybrid between *J. hindsii* and *J. regia* and named the resulting seedlings 'Paradox' walnut (Preece and McGranahan 2015). 'Paradox' has hybrid vigor and imparts this vigor to the scion, resulting in a larger tree with good yield, better *Phytophthora* root and crown rot resistance, and better lesion nematode resistance than *J. regia* on its own roots or when *J. hindsii* is the rootstock. A more recent rootstock 'RX1' is a different 'Paradox' as a result of a cross between *J. microcarpa* and *J. regia*. This rootstock has improved *Phytophthora* resistance compared to other walnut rootstocks. At the University of California Davis in conjunction with the National Clonal Germplasm Repository and other scientists, there is an ongoing walnut rootstock breeding and evaluation study focused on the wild genetics in the collection. Crosses between *J. microcarpa* and *J. regia* are resulting in individuals with improved resistance to *Phytophthora*, crown gall caused by *Agrobacterium tumefaciens*, and lesion nematode.

Juglans hindsii has also been hybridized with *J. regia* and then the progeny backcrossed with *J. regia* to restore the superior nut quality of *J. regia*, wild while maintaining hypersensitivity to the blackline virus from the *J. hindsii* genome. Generally, *J. regia* nut quality is considered superior and therefore more desirable than other walnuts, so North American wild walnuts are not used much for hybridization with Persian walnut for walnut scions except to introduce cold hardiness to extend the range and to introduce hypersensitivity for blackline disease.

Several North American walnuts have been used on a limited basis as rootstocks, including *J. californica*, *J. major*, and *J. nigra* (GRIN-Global 2017). *Juglans cinerea* L. has been used as a source of cold hardiness for *J. regia* (GRIN-Global 2017).

13.6.5.3 Conservation Status of North American Walnut Wild Relatives

Juglans californica, *J. hindsii*, *J. major*, *J. microcarpa*, *J. mollis*, and *J. nigra* are maintained and curated by the National Clonal Germplasm Repository, Davis, CA. A small collection of *Juglans cinerea* is maintained by the National Clonal Germplasm Repository, Corvallis, OR. The conservation status of *J. hirsuta* and *J. olanchana* is unknown; however, as mentioned above, *J. olanchana* is an endangered species.

Juglans californica is listed as a vulnerable species (Meier 2013b; World Conservation Monitoring Centre 1998). The World Conservation Monitoring Centre (1998) considers that the vulnerable status applies to both *J. californica* and *J. hindsii* because they state that two or three stands of the original *J. hindsii* remain and most of the genepool is naturalized from these populations. *J. californica* is in decline because of human-made buildings and developments, recreational use, cattle overgrazing (Esser 1993), perhaps poor natural reproduction (World Conservation Monitoring Centre 1998), and thousand cankers disease. The *Juglans cinerea* population is being attacked by the fungus *Sirococcus clavigignenti-juglandacearum* that causes butternut canker, which is a lethal disease. This is reducing the genepool of this species. Butternut is not listed federally as threatened, vulnerable, or endangered, but in Kentucky, it is listed as “special concern,” in New York as “exploitably vulnerable,” and in Tennessee, as “threatened” (USDA Natural Resources Conservation Service 2016). *J. olanchana* is an endangered species (Nelson 1998).

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Part IV

Edible Oils, Industrial Crops, Forages, Ornamentals, Medicinals and Culturally Valuable Plants

Chapter 14
Crop Wild Relatives of Sunflower in North America

Laura Fredrick Marek

Abstract Cultivated sunflower, with seeds valued for oil, snack consumption and bird feed, and flowers popular in gardens and in the ornamental trade, is native to North America, although its development into a global oilseed crop, briefly described here, depended on the international agricultural community. Sunflower crop wild relatives (CWR), all native to North America, are a rich source of genetic diversity for crop improvement and have been used extensively throughout of the history of sunflower breeding. Traits from *Helianthus* wild species have been used to increase disease resistance and abiotic stress tolerance and create a reliable hybrid breeding system; examples are described in this chapter. Despite widespread use of sunflower CWR, there is a critical need to fill significant geographic gaps in ex situ collections and to increase conservation of wild sunflower species in situ. Recent genomic developments have made the use of wild species more feasible in shorter timelines emphasizing the potential value of increased conservation efforts.

Keywords Cultivated sunflower wild relatives · Wild sunflower diversity · Wild sunflower traits of value · Wild sunflower conservation

14.1 Introduction

14.1.1 Origin of the Crop Sunflower and Brief History of Use Worldwide

Helianthus annuus L. (sunflower) was domesticated between 4000 and 5000 years before present from a single event domestication (Blackman et al. 2011; Wills and Burke 2006) in the central eastern USA. The oldest complete carbonized sunflower

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L. F. Marek (✉)
Department of Agronomy/North Central Regional Plant Introduction Station,
Iowa State University, Ames, IA, USA
e-mail: lmarek@iasate.edu

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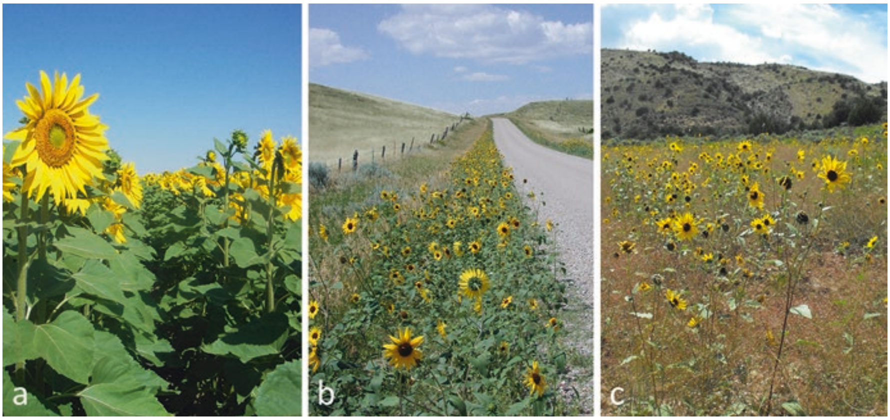

Fig. 14.1 *Helianthus annuus* L. (**a**) Cultivated sunflower field near Seville, Spain, Wild *H. annuus* in typical habitats, (**b**) disturbed roadside southwest of Chugwater, WY, (**c**) disturbed hillside field (possibly previous landslide) southwest of Big Water, UT

seeds within the size range of domesticated seeds analyzed as of this writing were recovered from the Hayes site in Tennessee (Smith 2014). Prehistoric archeological samples from the southwestern USA include only wild *H. annuus*-sized achenes (summarized in Matson 1991). In contrast with its wild progenitor, domesticated sunflower is unbranched, with a single flowering head larger than those on the multi-headed wild plants (Fig. 14.1) and with larger seeds. A critical domestication trait was retention of seed in the head after maturity: loss of the shattering trait. A member of the Asteraceae family, sunflower has composite flowers each with a ring of outer sterile ray flowers with attached brightly colored ligules (perceived as “petals”) and a central disk of up to three thousand small tubular disk flowers which are usually perfect and fertile. The ovaries at the base of the disk flowers develop into the fruit, botanically termed a “cypsela” (previously considered an achene), and with an adhering pericarp termed a “hull”, which will be referred to as seeds herein. A de-hulled seed is commonly referred to as a kernel.

Domesticated sunflower made its way across North America and into Mexico along the same Native American trade routes that brought maize and beans north and east. Sunflower was cultivated in the Hopi culture in the 1200s (Whiting 1966), and sunflower landraces descendent from the earliest domesticated materials were grown in the southwest into modern times, although not as a key food source. No extant landrace materials remain directly from the area of domestication; however, genomic studies have confirmed that southwestern landrace accessions conserved in the 1950s and 1970s are basal in current domesticated sunflower lineages (Baute et al. 2015). Concurrent with domesticated land race development, early explorers observed tribes in the west and in the northern plains using wild sunflowers (Heiser 1951; Putt 1997). Native Americans across the continent ate sunflower seeds, ground them into meal, extracted the oil for use as a hair anointment, produced dye from the hulls, and employed various parts of the plant for medicinal and cultural uses (Heiser 1951; Moerman 1986).

Native Americans were cultivating tall, single-headed sunflowers along with other crops not previously observed by Europeans such as maize and beans, when explorers and settlers first reached North America. The settlers did not adopt sunflower as a food crop, although sunflowers clearly made an impression because explorers took seeds back to Europe probably at different times from various locations (Heiser 1976), although it is likely the first transfer was from Spanish explorers returning to Spain from the southwestern USA and/or Mexico in the early to mid-1500s. Sunflowers were growing in Europe by 1568 as documented by the earliest known published illustration of a typical domesticated sunflower in the herbal of Dodonaeus (Heiser 1976; Peacock 2006). The first documented appearances of sunflower across Europe were in botanic gardens, and it was widely grown in gardens in England by the early 1600s. Seeds were taken to Russia perhaps by Peter the Great from a botanic garden in the Netherlands in the early 1700s and possibly introduced to Russia earlier as well (Pappalardo 2008). Europeans may have been aware of how Native Americans used sunflowers, but one can only imagine that gardeners and others observant in nature would notice birds eating sunflower seeds and would try the seeds for themselves. By the early 1700s, Europeans were experimenting with oil extraction from sunflower seeds as evidenced by English patent No 408 granted to Arthur Bunyan in 1716 for an oil pressing implement for the production of oil for industrial use (Putt 1997), although sunflower did not become a commodity in England or anywhere else in the world until after its development as a crop in Russia.

14.1.2 Modern Crop Development

Development of the modern sunflower crop began in Russia where strict restrictions against uses of common food oils during Lent by the Russian Orthodox Church likely stimulated cultivation of sunflower for production of its unrestricted oil (Pappalardo 2008; Heiser 1955). Prior to the introduction of sunflower to Russia, hemp seed was the alternate, nonrestricted oil source used during Lent, but sunflower was a superior oil and replaced hemp. In Russia, sunflower seed oil was first mentioned in 1779 in the Proceedings of the Russian Academy of Sciences (Putt 1997) which detailed the creation of an oil press for consumable oil, some years after Bunyan's patent of an oil pressing device to source material for industrial applications. Russian farmers grew sunflowers and continued selections initiated by Native Americans to improve the crop; one of the first traits selected for in Europe was earlier maturity (Putt 1997). By the mid-1800s, commercial scale production of oil was underway in Russia as evidenced from the number of sunflower oil mills and from the vast sunflower production areas extrapolated to have existed from documented records of potash production from sunflower stems (Putt 1997). Sunflower became a major crop in Hungary and Romania by the end of the 1800s, and France initiated sunflower production during this time period. Once sunflower became a major crop, formal, organized breeding commenced, and trial stations were established at several locations in Russia and Ukraine by 1913; additional breeding stations were established in the following decade (Tavoljanskiy et al. 2004).

Major breeding objectives were to improve disease resistance, to increase oil concentration and quality and to stabilize yield. Improved cultivars coming out of Russia and Ukraine were responsible for successful crop expansion into other regions including Serbia, Bulgaria, Turkey, Argentina, Canada, India, China, Australia, and Africa which then established breeding programs.

North American developed landrace sunflowers from the southwest were transported to European botanical gardens; improved crop cultivars returned to North America, initially with farmers from Ukraine settling the Canadian prairies in the mid-1870s. In the USA, sunflowers had long been grown for ornamental purposes (Wiley 1901), and several seed companies including Burpee were offering the improved "Mammoth Russian" and other sunflower seeds in the late 1800s (Wiley 1901; Pappalardo 2008). In 1891, the American Consul in St. Petersburg reported on the sunflower industry in Russia (Crawford 1891) and sent sunflower seeds to Washington DC with the suggestion that sunflower could become a new agricultural industry in the USA. There was no infrastructure to support a sunflower oilseed industry and early sunflower use in Canada and the USA was primarily for forage/silage; seed was used as scratch feed for chickens (Wiley 1901, Putt 1997). Sunflower breeding in Canada became focused on oilseeds during the late 1930s as the Canadian government initiated efforts to decrease the county's dependence on imported oil. Forage lines selected for late maturity to maximize biomass yield were inappropriate for oilseed production; the material from Ukraine in the immigrants' gardens and fields was much more useful for initial oilseed breeding stock (Putt 1997). In the late 1950s, the USDA initiated a sunflower breeding program in Texas, and efforts intensified after higher oil lines were introduced from Russia in the 1960s. Europe again fueled a major advance in sunflower production with the discovery and incorporation of a cytoplasmic male breeding system into cultivated sunflower (Leclerq 1969; Kinman 1970) which allowed economical large-scale hybrid seed production. Hybrids were preferred by producers because of improved seed quality, high-yield performance, and crop uniformity for easier harvest and other agronomic management considerations. Farmers quickly adopted hybrid corn when it was developed (from 10% to 90% of production over 4 years in the early 1930s), and in North America, hybrid sunflower was also rapidly accepted after its introduction in the early 1970s. After the development of the hybrid seed process, USDA supported breeding efforts in the USA moved from Texas to Fargo, ND, within the region of primary US production. Targets for modern crop improvement in sunflower include oil quality and quantity, traits related to yield stability and quantity, abiotic and biotic stress resistance, and maintenance of self-fertility.

Sunflower has been one of the top five oilseed crops in the world for a century due to its lightly flavored oil and, in more recent years, the awareness that the oil is naturally low in trans-fat. In 2016–2017, sunflower was the fourth major vegetable oil in production after palm, soybean, and rapeseed oils (USDA, FAS, Oilseeds: World Markets and Trade accessed July 2017). Russia and Ukraine, where sunflower first became a major crop, remain the primary sunflower-producing regions in the world, accounting for around 50% of global production during the past decades; other major producers include the European Union, Argentina, China, Turkey, and the USA. Oil remains the leading sunflower product globally followed by confectionery/snack seeds and birdseed production as well as use of the pressed meal remaining after oil extraction in animal feed rations. Confectionery seed hulls are larger than oil seed hulls and less tightly adhered to the kernel allowing easier shelling and consumption. Confectionary kernels are higher in protein but lower in oil than oilseed kernels. In the USA, roughly 55–60% of the crop is pressed for oil with resulting meal, about 15–20% is confectionery seed used by the snack industry, and about 25% of seed production is used for birdseed (USDA Economic Research Service accessed June 2017). In parallel, there is an ornamental cut flower industry based on *H. annuus* lines bred for flower color, size, ligule arrangement, and other characteristics.

14.1.3 Challenges to Cultivation

Challenges to cultivation faced by sunflower producers are common to many crops and include biotic stresses (diseases and pests); maintenance or incorporation of market priority traits such as oil quantity and quality, seed size and color and cut flower longevity; loss of acreage to crops with less complex agronomic management; and anticipation of climate change effects on production areas and other abiotic stresses.

Many sunflower diseases and pests are environmentally and/or geographically specific and present an ongoing challenge because of the continuing evolution of the pathogens and emergence of new virulent strains. The majority of diseases of significant economic effect on sunflower are caused by fungi (T. Gulya, personal communication 2017). Alternaria leaf blight (*Alternaria helianthi*) is only a serious problem in humid tropical and subtropical production regions such as India and parts of China; Phomopsis brown stem canker (typically *Diaporthe helianthi* but also *Diaporthe gulyae*) is of widespread concern in Europe, Russia, and North America but occurs only occasionally in other production regions. However, Sclerotinia basal stalk rot, mid-stalk, and head rot (three separate diseases caused by the same pathogen, *Sclerotinia sclerotiorum*) and downy mildew (*Plasmopara halstedii*) are prominent diseases in sunflower production areas worldwide (with the exception that downy mildew has not yet been detected in Australia or New Zealand) and the focus of major ongoing research efforts. Rust (*Puccinia helianthi*) is also of great concern in most sunflower-growing regions and was first described by a Russian botanist in the late 1860s (Crawford 1891). Because markets for in-shell confectionery sunflower seeds and ornamental sunflowers are dependent on specific cosmetic appearances, major losses in these crop types can be caused by diseases such as leaf smut (*Entyloma compositarum* fungus) and petal blight (*Itersonilia perplexans*) which have little effect on oilseed production. For complete listing of sunflower diseases, see Harveson et al. (2016).

Orobanche cumana Wallr. (common name, broomrape), an obligatory root parasitic plant, was first observed in Russian sunflower fields in 1866 (Antonova 2014). *O. cumana* routinely devastates production fields in Europe with losses of up to 100%, and it is a serious issue in other production areas including China and now parts of Africa (Shi et al. 2015; Velasco et al. 2016; Nabloussi et al. 2017), but, remarkably, it is unheard of in North America. *O. cumana* has continued to evolve new, more aggressive races since it was first described, similar to a pathogenic response, and efforts to manage and improve resistance are ongoing. There are a number of *Orobanche* species native to North America, and in 2014 *O. ludoviciana* was observed parasitizing about 25% of a sunflower production field in western Nebraska, the first report of an *Orobanche* species attacking sunflowers in the western hemisphere (Harveson et al. 2015). The interaction was of major concern but at the time of this writing has not been observed since despite careful scouting. The severe drought in western Nebraska in 2014 may have promoted the interaction by causing a lack of preferred hosts for the parasitic plant.

Agronomic management issues, including weed and bird control, also present challenges for sunflower production. Unlike other crops, artificial technologies have not been used to develop herbicide-resistant sunflowers; a CWR-derived source is described in 25.3.1.1d. Birds are persistent pests common to all areas of production eating seeds as they begin to mature. Attempts to protect the sunflower seed crop from birds have included a wide range of techniques such as incorporation of bird-resistant morphological traits into production lines including head shape and orientation, spraying fields with bird repellents, planting decoy plots around nesting habitat and/or the primary crop field, cattail control, aerial harassment of predators using unmanned and fixed wing aerial systems, and early harvest (Linz 2015). There is not a consistent, permanent method of dealing with birds, and efforts continue to develop effective control methods.

Climate change is expected to cause significant alterations to weather patterns in traditional sunflower production areas resulting in increased average temperatures, drought, and storm severity (Rosenzweig et al. 2014). Some wild sunflower species grow in extreme environments, tolerating high salt and surviving drought, and the crop has been proposed as a potential model crop for climate change adaptation (Badouin et al. 2017). Abiotic challenges generally evoke complex responses involving many genes. Developing drought tolerance in cultivated sunflower has been of interest for several decades. Cultivated *H. annuus* is considered moderately drought tolerant because the primary root can reach depths of 2 m and more when needed to reach water (Seiler and Jan 2010) allowing plants to reach resources not available to other crops. Access to deep ground water also provides heat tolerance and this deep rooting ability has hampered efforts to assess sunflower germplasm for drought tolerance traits in the field. Increased storm severity may require a renewed emphasis on incorporating traits which prevent plant lodging.

14.2 Crop Wild Relatives (CWR)

14.2.1 CWR: Taxonomic Issues

Wild species in the genus *Helianthus* are restricted to North America. Tables 14.1 and 14.2 list currently determined extant annual and perennial species and subspecies (taxa) in *Helianthus* and the general distribution of wild populations on a state or province basis.

Table 14.1 Extant annual taxa in the genus *Helianthus,* 2017 Taxa list compiled from information in Schilling (2006) and Keil (2010) (Location information from: Rogers et al. (1982); USDA GRIN-Global database curator tool; botanists queried and herbaria searched during preparation for exploration trips including SEINet, VASCAN, Tropicos, Consortium of Pacific Northwest Herbaria, many others)

Taxa	Native populations in these states/provinces
H. agrestis Pollard	FL
H. annuus L.	Found across the continent, see Fig. 14.2
H. anomalus Blake	AZ, NV, UT
H. argophyllus Torr. and A. Gray	TX; naturalized in a few locations in FL, NC
H. bolanderi A. Gray	CA, OR
H. debilis ssp. *cucumerifolius* (Torr. & A. Gray) Heiser	AL, FL, GA, NC, SC, TX
H. debilis ssp. *debilis* Nutt.	FL
H. debilis ssp. *silvestris* Heiser	TX
H. debilis ssp. *tardiflorus* Heiser	FL
H. debilis ssp. *vestitus* (Watson) Heiser	FL
H. deserticola Heiser	AZ, NV, UT
H. exilis A, Gray	CA
H. neglectus Heiser	NM, TX
H. niveus ssp. *niveus* (Benth.) Brandegee	MX-BN
H. niveus ssp. *tephrodes* (Gray) Heiser	CA, MX-SO
H. paradoxus Heiser	NM, TX, MX-CA
H. petiolaris ssp. *canescens* (A. Gray) E.E. Schilling	AZ, CA, NM, TX, UT, MX-CH, MX-SO, see Fig. 14.5
H. petiolaris ssp. *fallax* Heiser	NM, AZ, UT, CO, MX-CH, MX-CA, MX-SO, see Fig. 14.5
H. petiolaris ssp. *petiolaris* Nutt.	CA, CO, IL, IN, KS, MO, MT, ND, NE, NM, OK, SD, TX, WI, WY, SK, MB, AB, see Fig. 14.5
H. porteri (A. Gray) J.F. Pruski	GA; one naturalized location in NC
H. praecox ssp. *hirtus* Heiser	TX
H. praecox ssp. *praecox* Englm. & A. Gray	TX
H. praecox ssp. *runyonii* Heiser	TX

Table 14.2 Extant perennial taxa in the genus *Helianthus,* 2017 Taxa list compiled from information in Schilling (2006) and Stebbins et al. (2013). Location information from: Rogers et al. (1982); USDA GRIN-Global database curator tool; botanists queried and herbaria searched during preparation for exploration trips including, SEINet, VASCAN, Tropicos, Consortium of Pacific Northwest Herbaria, many others

Taxa	Native populations in these states/provinces
H. angustifolius L.	AL, AR, FL, GA, LA, MS, NC, OK, SC, TN, TX, VA
H. arizonensis R. Jackson	AZ, NM
H. atrorubens L.	AL, GA, KY, LA, NC, SC, TN, VA
H. californicus DC.	CA, MX-BN
H. carnosus Small	FL
H. ciliaris[a] DC.	AZ, NM, OK, TX, MX-CA, MX-CH, MX-DU, MX-NL, MX-SL, MX-SO, MX-TM, MX-ZA
H. cusickii A. Gray	CA, ID, NV, OR, WA
H. decapetalus L.	CT, DE, IA, IL, IN, KY, MA, MD, ME, MI, NC, NH, NJ, NY, OH, PA, SC, TN, VA, VT, WI, WV, NB, ON, QC
H. divaricatus L.	AL, AR, CT, DE, GA, IL, IN, MD, NJ, NY, NH, MA, MI, MO, NC, NJ, OH, OK, PA, SC, VA, VT, WI, WV, NB, ON, QC
H. eggertii Small	AL, KY, SC, TN
H. floridanus A, Gray ex Chapman	FL, GA, LA, MS, SC
H. giganteus L.	MN, WI, IL, IN, MI, OH, PA, WV, VA, NC, SC, MD, DE, NJ, CT, ON, NB, QC
H. glaucophyllus Smith	NC, SC, TN
H. gracilentus A. Gray	CA, MX-BN
H. grosseserratus Martens	AR, IA, CT, IL, IN, MA, ME, MI, MN, MO, MS, ND, NE, NH, NY, OH, OK, PA, SD, TX, WI, WV
H. heterophyllus Nutt.	AL, FL, LA, MS, NC, SC, see Fig. 14.7
H. hirsutus Raf.	AL, AR, GA, IA, IL, IN, KS, KY, LA, MD, MI, MN, MO, MS, NC, NE, OH, OK, PA, SC, TN, TX, WI, WV, ON, MX-CA, MX-NL
H. laciniatus A. Gray	AZ, NM, TX, MX-AG, MX-BN, MX-CA, MX-CH, MX-CX, MX-DU, MX-GJ, MX-HI, MX-JA, MX-MX, MX-MC, MX-NL, MX-QE, MX-SL, MX-SO, MX-TN, MX-ZA
H. x laetiflorus Pers.	IA, DE, KS, MA, ME, MO, NC, NE, NH, NJ, NY, OH, PA, SC, TN, VA, WV, AB, BC, MB, ON, SK, QC, NB
H. laevigatus T. & G.	MD, NC, SC, VA, WV
H. longifolius Pursh	AL, GA
H. maximiliani Schrader	AR, CO, IA, ID, IL, IN, KS, MI, MN, MO, MT, NC, ND, NE, NJ, OH, OK, PA, SC, SD, TN, TX, VA, WI, AB, BC, MB, ON, QC, SK, MX-CH, MX-CO, MX-NL
H. microcephalus Torr. & A. Gray	AL, AR, FL, GA, IL, IN, KY, MD, MI, MO, MS, NC, NJ, OH, PA, SC, TN, VA, WV
H. mollis Lam.	AL, AR, GA, IL, IN, KS, KY, LA, MO, MS, ND, NJ, OH, OK, PA, TN, TX, VA, WI, ON
H. nuttallii ssp. *nuttallii* Torr. & A. Gray	AZ, CA, CO, ID, NM, NV, OR, UT, WY, BC, MB, SK

(continued)

Table 14.2 (continued)

Taxa	Native populations in these states/provinces
H. nuttallii ssp. *rydbergii* (Brit.) Long	MT, NE, ND, SD, WA, AB, BC, MB, ON, SK
H. occidentalis ssp. *occidentalis* Riddell	AR, GA, IA, IL, IN, MI, MN, MO, NC, OH, TN, WI, WV
H. occidentalis ssp. *plantagineus* (Torr. & A. Gray) Heiser	AR, TX
H. pauciflorus ssp. *pauciflorus* Nutt.	AR, IA, IL, IN, KS, MI, MO, TX, OK, WI
H. pauciflorus ssp. *subrhomboideus* (Rydb.) O. Spring	CO, MN, MT, ND, NE, NM, SD, WY, BC, SK
H. pumilus Nutt.	CO, WY, see Fig. 14.7
H. radula (Pursh) Torr. and A. Gray	AL, FL, GA, LA, MS, SC
H. resinosus Small	AL, GA, MS, NC, SC
H. salicifolius Dietr.	KS, MO, OK, TX
H. schweinitzii Torr. & A. Gray	NC, SC
H. silphioides Nutt.	AL, AR, KY, LA, MO, MS, OK, TN, see Fig. 14.7
H. simulans E.E. Watson	AL, FL, GA, LA
H. smithii Heiser	AL, GA, NC, SC
H. strumosus L.	AL, AR, FL, GA, IA, IL, IN, LA, MD, MI, MN, MO, MS, NC, NJ, NY, OH, OK, PA, RI, SC, TN, TX, VA, WI, NB, ON, QC
H. tuberosus L.	AL, AR, CT, GA, IA, IL, IN, KS, KY, LA, MA, MD, ME, MI, MN, MO, MS, NC, NE, ND, NH, NJ, NY, OH, OK, PA, SC, SD, TN, TX, VA, VT, WI, WV, AB, BC, MB, NB, ON, QC
H. verticillatus Small	AL, GA, TN
H. winteri J. C. Stebbins	CA

[a] Introduced as an agricultural weed in scattered other locations; populations eradicated and/or not persistent

The Flora of North America (FNA) lists 52 extant species, seven of which are subdivided into 19 subspecies (Schilling 2006). Subspecies *H. niveus* ssp. *niveus* (Benth) Brandegee is endemic to Mexico and is not included in the FNA listing; *H. petiolaris* ssp. *canescens*, now established at the subspecies rank (Keil 2010), previously var. *canescens* and originally *H. niveus* ssp. *canescens* A. Gray, is not included in the FNA listing; and species *H. winteri*, recently described in California (Stebbins et al. 2013), is not listed in FNA; all three are included in Tables 14.1 and 14.2. Therefore, Tables 14.1 and 14.2 indicate 53 species with 20 subspecies, 65 unique taxa of which 23 are considered annual and 42 perennial, although depending on environmental conditions, some of the annuals can persist well beyond 1 year and some of the perennials only survive one growing season. Taxonomy in the genus *Helianthus* has been evolving since Linnaeus first described nine species in 1753 (Seiler and Jan 2010). The most recent major adjustments include a reclassification in 1979 which moved all of what were then South American *Helianthus* species to

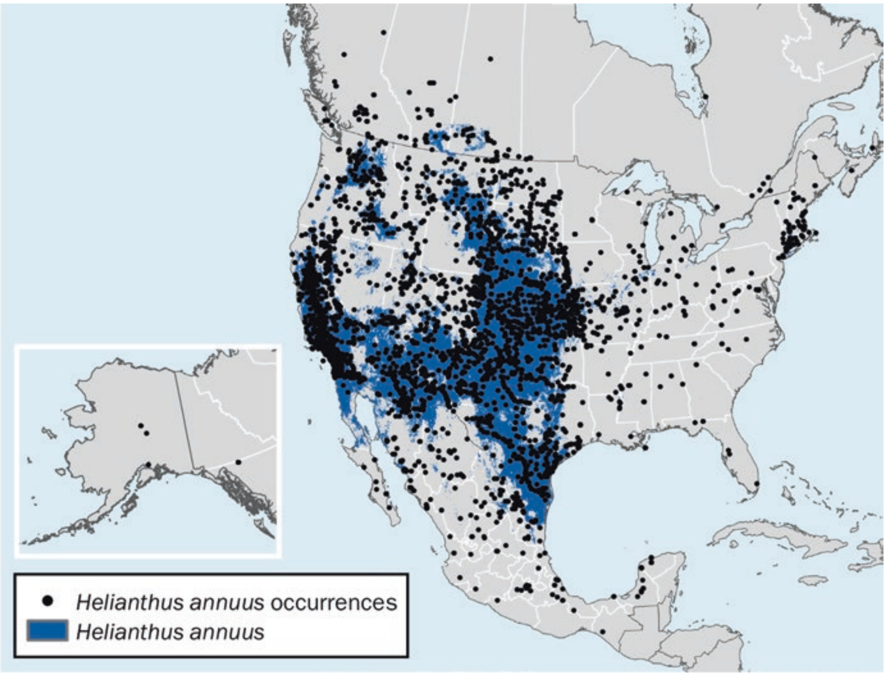

Fig. 14.2 The distribution of wild *H. annuus* L. across North America indicating occurrence points (black circles) and the geographic area of similar climate and soil (blue shading) defined by those occurrence points. The model used to generate the wild *H. annuus* distribution was limited to native areas defined in GRIN taxonomy; occurrence data points extend well outside this defined native area. Full methods for map generation and occurrence data are given in Appendix 1

the new genus *Helianthopsis* (Robinson 1979), amended by Panero (1992) to the genus *Pappobolus*, and the transfer in 1998 of the only eastern North American occurring *Viguiera* species, *Viguiera porteri* to *Helianthus*, now *H. porteri* (A. Gray) J. F. Pruski (Pruski 1998). A potential future modification is the re-inclusion of *H. exilis* A. Gray as an ecotype within *H. bolanderi* A. Gray based on a recent comprehensive genomic and geographic analysis (Owens et al. 2016). Perennials in the southern and eastern USA and Canada are known to hybridize which has made species identification/determination challenging (Heiser et al. 1969).

All of the wild *Helianthus* taxa except *H. agrestis* Pollard are self-incompatible with the result that more than one plant is needed to produce viable seeds. The annual taxa are all diploid with n = 17 chromosomes; the perennials are diploid with n = 17 chromosomes, tetraploid with n = 34, or hexaploid with 51 chromosomes (Seiler and Marek 2011). Interestingly, four perennial species, *H. ciliaris* DC., *H. decapetalus* L., *H. strumosus* L., and *H. smithii* Heiser, have been determined to contain either diploid and tetraploid or diploid and hexaploid populations at least in part depending on geographic origin (Seiler and Jan 2010). Analyses of the results of intraspecific crosses suggest that there is not a single genome common to all diploid and polyploid taxa pointing to a complex origin for some of the members in the genus (Chandler et al. 1986; Kantar et al. 2014; Bock et al. 2014). Relationships of the taxa within the genus remain incompletely determined, hopefully to be resolved with additional sequence and genic analyses (Kane et al. 2013, Vear 2011).

14.2.2 Distribution/Habitat/Abundance

Figure 14.3 is a heat map illustrating the occurrence of wild sunflower taxa across North America clearly demonstrating the wide distribution of the genus *Helianthus*. Map colors are based on the number of species observed/collected from county-based areas, not on the individual species, such that different areas of yellow across the maps probably do not indicate the same two species. For example, the species one would find in central costal CA resulting in the gold and orange colors are not the same species one finds in the gold and orange areas of coastal North and South Carolina.

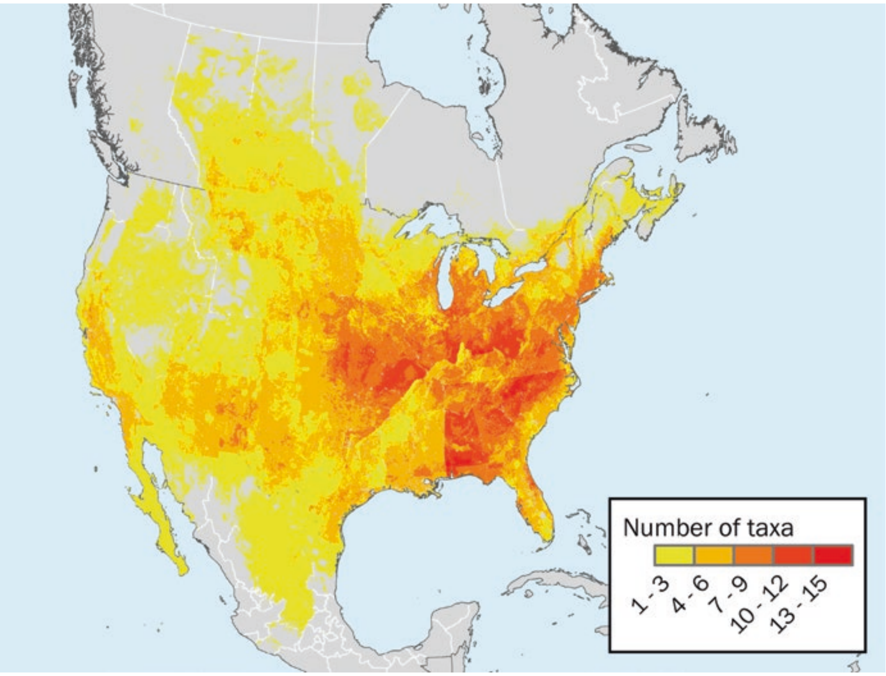

Fig. 14.3 Heat map indicating the spread of all taxa of wild sunflowers across North America. Colors indicate the number of different species/taxa not specific species. Full methods for map generation and occurrence data are given in Appendix 1

The maps in this chapter are based on locations available from herbaria voucher records, genebank accession collection records, and additional observation data and are dependent on there being accurate and significant records to fully assess native ranges. Each map not only reflects where collecting efforts have been directed but also those taxa with accessible online records. Herbaria continue to digitize records and make them web visible with the result that, for some taxa, these maps represent a snapshot. Some *Helianthus* species, including *H. annuus* and *H. ciliaris*, are considered weedy or even invasive, and not always thought to be of value for sampling. In addition, portions of the ranges of several species have not been adequately sampled in Mexico and are therefore not fully represented on the maps. Detailed information about map construction is presented in Appendix 1.

The species in the genus *Helianthus* represent a range of plant structures and growth habits (Figs. 14.1, 14.4, 14.6), flowering time, and colonized habitats. The genus *Helianthus* does not include woody bushes or trees although the recently described continuously flowering *H. winteri* (Fig. 14.4) has stems with more woody characteristics (Stebbins et al. 2013) than its closest relative, *H. annuus* (Fig. 14.1), as well as copious resin production. Some species are single stemmed with one to several flowering heads. *H. radula* (Fig. 14.4) is single stemmed, and, uniquely for

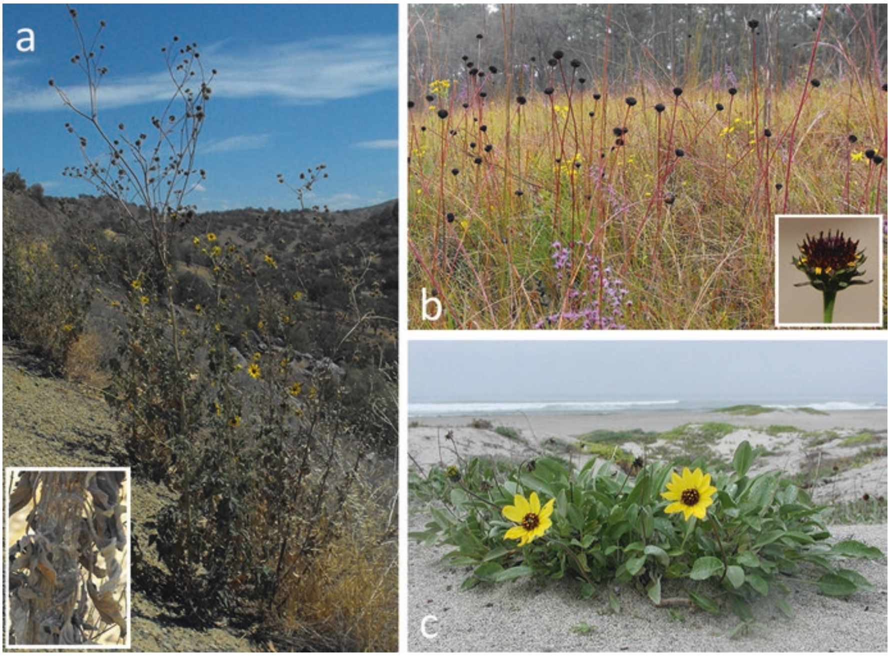

Fig. 14.4 (**a**) *H. winteri* J. C. Stebbins, type locality east of Fresno, CA; insert, older, woody stem with exuded resin drops, (**b**) *H. radula* (Pursh) Torr. & A. Gray longleaf pine habitat, Ft. Stewart, GA; insert, this species typically lacks ray flowers although some plants in some populations produce rudimentary rays, (**c**) *H. niveus* ssp. *niveus* (Benth.) Brandegee, Pacific coast west of Vicente Guerrero, Baja California, MX

Helianthus, the flowering heads do not produce ray flowers; however, there are occasional populations with plants with rudimentary rays. Many taxa are branched small to large bush types with multiple flowering heads, although several of the dune colonizing taxa such as *H. niveus* ssp. *niveus* (Fig. 14.4) are low, spreading, and branched with multiple heads. Some of the perennial species, such as *H. radul*a, begin growing as a ground based rosette of leaves, elongating a single or multi-headed flowering stalk in response to an environmental signal appropriate for reproduction. See Heiser et al. (1969), Rogers et al. (1982), and Schilling (2006) for more complete descriptions of most taxa and Stebbins et al. (2013) for *H. winteri*.

Wild sunflowers most commonly grow in fully open areas with some disturbed ground – deserts, seasonally or permanently wet, marshy areas with saline or fresh water, and open fields and roadsides – although some species grow in moderate to dense shade. Many southwestern taxa grow in extreme habitats including one species endemic to saline cienegas and eight taxa which grow in sandy, typically seasonally droughty ecoregions. Wild *H. annuus*, progenitor of the crop, with the widest distribution of all of the *Helianthus* taxa (Fig. 14.2, Heiser et al. 1969; Rogers et al. 1982), is an opportunistic colonizer of open, disturbed lands across North America. Populations are most common in the central plains of the USA and into Canada and in the southwest into northern Mexico; uncommon in the southern, eastern, and northeastern USA and far eastern and far western Canada. Natural disturbances such as landslides, fires, and the scour prairies that flooding can cause provide excellent habitat as does land disturbed by road and other construction and by agricultural production. Another annual species with a broad distribution is *H. petiolaris* (Fig 14.5); its ranges, which includes two subspecies, completely overlaps with *H. annuus* although the two species occur on different soil types so populations are not often in close proximity. The distribution ranges of several perennials also cover wide geographic regions: for example, *H. maximiliani* Schrader is found from south central Texas north into Canada and east to Ohio with scattered populations across TN and NC and up the eastern seaboard but is not naturally found in the deep southern USA, in New England, nor in significant numbers west of apporximately longitude 108° west (Rogers et al. 1982). Other perennials are much more limited in their native ranges, endemic to more or less specific ecogeographical regions with soil composition being a primary factor in their occurrence. For example, *H. heterophyllus* Nutt. (Figure 14.6) is found in coastal NC; populations largely skip over SC and GA to appear again in northern FL west of Tallahassee and the species continues west into south eastern LA (Fig 14.7). *H. salicifolius* Dietr. (Figure 14.6) is endemic to the Flint Hills/limestone prairies in eastern KS and parts of OK and western MO (Fig. 14.7). *H. pumilus* Nutt. (Figure 14.6) is limited to a region encompassing the foothills and into the Front Range of CO, north of about latitude 37.9° and north into WY (Fig 14.7). The map indicates an area in northwestern WY of climate and soil types currently without occurrence points which is highly similar to the habitat where the known WY occurrences of *H. pumilus* map, suggesting a region with potential for further exploration. Mason et al. (2015) have determined that the very restricted range of *H. carnosus* Small (endemic to five counties in FL) is based on combined soil and environmental characteristics. Among

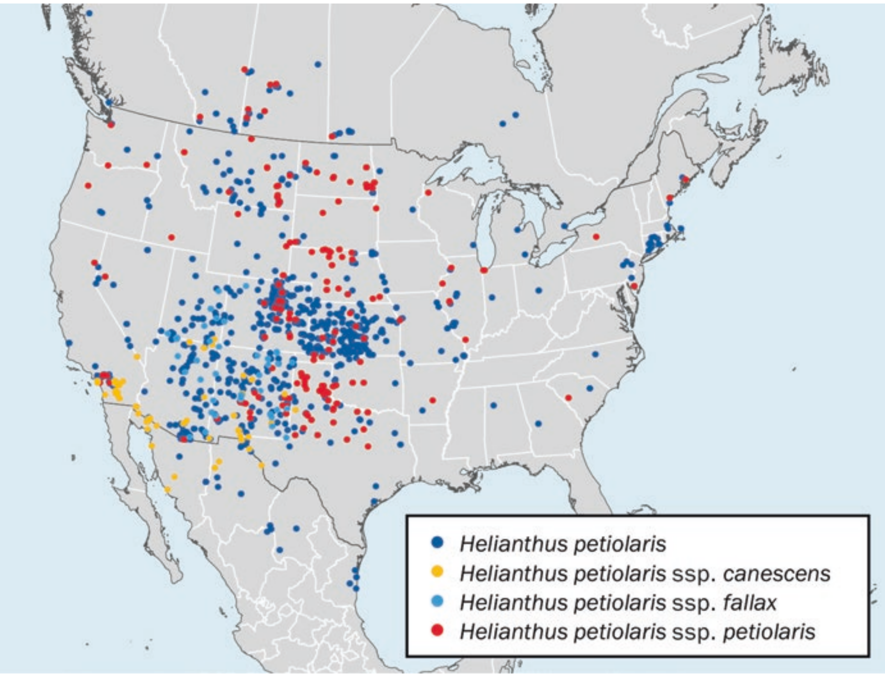

Fig. 14.5 The distribution of *H. petiolaris* Nutt. across North America indicating occurrence points for each of the three subspecies as well as occurrences for which a subspecies was not defined. Full methods for map generation and occurrence data are given in Appendix 1

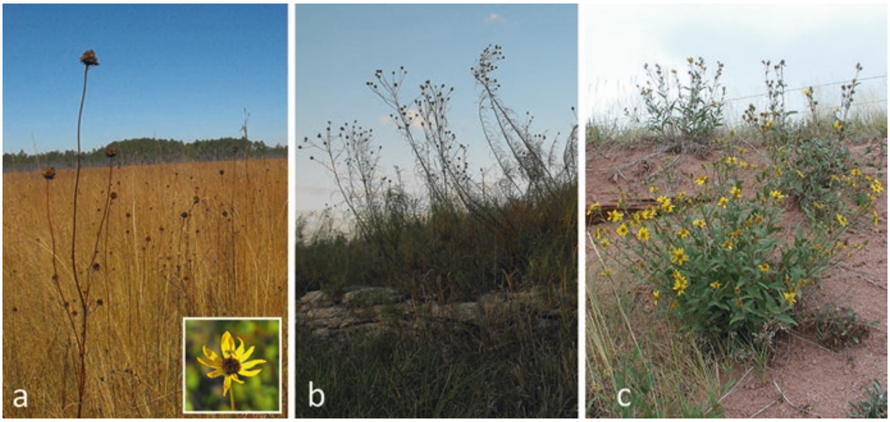

Fig. 14.6 (**a**) *H. heterophyllus* Nutt. expansive population past flowering north of Apalachicola, FL; insert: *H. heterophyllus* flower in MS west of Perkinston, (**b**) *H. salicifolius* A. Dietr., limestone ledge south of Garnett, KS, (**c**) *H. pumilus* Nutt., roadside northwest of Tie Siding, WY

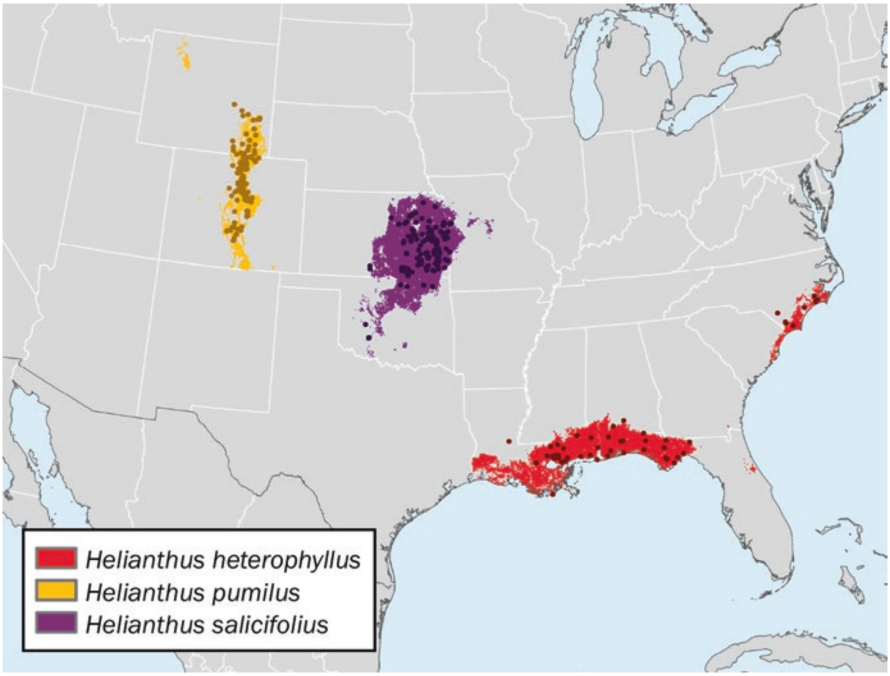

Fig. 14.7 The distribution of three perennial sunflower species (images from sampled populations of these species in Fig. 14.6) indicating occurrence points and the geographic area of similar climate and soil defined by those occurrence points; *H. heterophyllus* (dark red circles and red shading), *H. salicifolius* (dark purple circles and purple shading), and *H. pumilus* (dark yellow circles and yellow shading) illustrating the limited geographic ranges exhibited by many sunflower taxa as compared with wild *H. annuus* (Fig 14.2) and *H. petiolaris* (Fig 14.5). Full methods for map generation and occurrence data are given in Appendix 1

the annual species with limited geographic ranges, *H. agrestis* is found only in peninsular FL between approximately 26.1° and 28.8° north latitude; *H. exilis* is limited to serpentine soils in CA; *H. porteri* is limited to granite outcrops in NC, SC, GA, and AL; *H. paradoxu*s Heiser grows only in saline, cienega habitats in west TX, NM, and one area in Mexico; *H. anomalus* Blake grows only in active dune areas in very northern AZ, southern UT, and the far southeastern corner of NV.

Naturalized populations of wild sunflower species exist around the world (Argentina, Australia, South Africa, Mozambique, Russia, France, and other European locations) which in some areas have been determined to be subpopulations of North American populations (Vischi et al. 2004). Some naturalized wild populations have been evaluated to determine if they could provide genetic diversity useful for crop development (Cantamutto et al. 2010; Ribeiro et al. 2010). Naturalized populations can result from any of several means of introduction. Some introductions occurred from contaminants in seed for cultivation, and some introductions were intentional. For example, *H. annuus* was introduced to central Argentina as a forage crop experiment in the 1950s. *H. tuberosus* L. was introduced in Europe for its tubers in the early 1600s. Plants then escaped cultivation and were ignored. The perennial *H. tuberosus* often does not produce many seeds, but it spreads easily through its rhizomes. Cultivation can serve to spread it further because broken up pieces can root and start new plants. To some extent its initial spread was likely based on a lack of awareness of the invasive potential of the species and the consequences; *H. tuberosus* has become one of the most widespread invasive plants in Europe (Invasive Species Compendium accessed July 2017; European and Mediterranean plant Protection Organization EPPO Global Database).

14.2.3 Utilization

14.2.3.1 Breeding and the Relative Importance of CWR

Sunflower is unique among modern crops because *Helianthus* CWR have been used for crop improvement since the earliest days of formal breeding, and sunflower is ranked as the crop with the greatest confirmed and potential CWR breeding use citations (Dempewolf et al. 2017). Wild species have been critical to the establishment of sunflower as a hybrid crop as well as being key resources for providing disease resistance. As indicated earlier in this chapter, organized sunflower breeding began in Russia in the early 1900s. Very quickly breeders in Russia and Ukraine incorporated *Helianthus* CWR into their programs to improve cultivated *H. annuus*. In 1916, T. Sazyperow described experiments with sunflower, crosses of *H. annuus* and *H. argophyllus* to breed for rust resistance, in the Bulletin of Applied Botany, Petrograd, which were reported in *The Journal of Heredity* (Cockerell 1929). *H. tuberosus*, introduced in Europe in the early 1600s, was observed to be disease resistant, and in the 1930s, breeders in Russia were reporting results from interspecific crossing with *H. tuberosus* to improve cultivated *H. annuus* (as described by Skoric and Pacureanu 2010). V. Pustovoit at VNIIMK continued interspecific breeding efforts and by the mid-1950s developed additional disease resistant varieties. G. Pustovoit continued breeding with CWR using ten additional wild *Helianthus* species; derived varieties were resistant to *Orobanche cumana*, downy mildew, rust, *Verticillium*, and other diseases (summarized in Pustovoit and Gubin 1974). Sunflower breeders in other European countries also developed interspecific breeding programs to improve cultivated *H. annuus* (Atlagic and Terzic 2015; Christov 2013). Early work with interspecific hybrids in the USA focused on the academic interests of clarifying the taxonomy of the genus and on species identification, primarily efforts by Heiser and his students beginning in the late 1940s and continuing into the 1970s (summarized in Jan 1997). In the 1960s, USDA researchers began collecting wild sunflower germplasm as a resource for crop genetic diversity (Seiler 1988), first for rust resistance, Kinman and Luciano in 1963 and Zimmer and Fick in 1972. Throughout the 1970s, Beard and others collected wild species in the southwest. In 1976 the USDA expanded the US national sunflower collection to formally include samples of wild *Helianthus* species and in 1985 the wild collections from Bushland, TX, and Davis, CA, were transferred to the National Plant Germplasm System's (NPGS) North Central Regional Plant Introduction Station in Ames, IA, which had housed a cultivated sunflower collection since 1948. The USDA-ARS Plant Exchange Office (PEO) sponsored explorations to collect seeds of *Helianthus* CWR separately as well as in joint explorations with the Food and Agriculture Organization of the United Nations (FAO) and other funders (Seiler 1992) from 1976 through 1994 which included breeders from Russia, Serbia, and India in addition to USDA sunflower scientists (Seiler 1988; Seiler and Gulya 2004). Explorations supported by the PEO for sunflower CWR commenced again in 2000 and continue through the present time, with a goal of ensuring that each taxon in the NPGS *Helianthus* collection has complete geographic representation.

For cultivated sunflower, a significant amount of useful variation existed within the landrace material that arrived in Russia, and selections by farmers resulted in improved resistance to *Orobanche cumana* and to the European sunflower moth (Skoric 2012a). Additionally, after formal breeding began in the early 1900s, significant improvement in oil content was made by selecting within the available cultivated germplasm: seed oil was increased from 30% to over 50% (Putt 1997). Because sunflower breeding initially took place in Russia and Europe, where expansive wild populations of the crop progenitor *H. annuus* (primary gene pool) did not exist, the most extensively used wild species in the early days of CWR breeding was *H. tuberosus* (tertiary gene pool) which by then had been in Europe for several centuries. Once breeders in North America developed a focus on CWR, wild *H. annuus* and other species were determined to be excellent resources for resistance to a number of diseases, and all but one of the wild species (*H. agrestis*) have been successfully crossed with cultivated breeding stock (Jan 1997).

14.2.3.1.1 Cytoplasmic Male Sterility

Because of its critical role in the establishment of sunflower as a hybrid seed crop, the CWR trait of highest commercial value in sunflower is the stable cytoplasmic male sterility (CMS) that was isolated from a cross between cultivated sunflower and a wild *H. petiolaris* collected in the St. Louis, MO area (Leclercq 1969). Kinman and others (Kinman 1970; Enns et al. 1970) discovered fertility restoration genes in several wild species which, in combination with the CMS trait, enabled the development and economical production of commercial sunflower hybrids. Cultivation of hybrids has allowed global sunflower production to increase without an accompanying increase in land use. The original *H. petiolaris* CMS cytoplasm continues to be the principal cytoplasm used in hybrid production around the world, although many additional sources of stable CMS and fertility restoration have been discovered in a range of sunflower CWR (Jan 1997; Skoric 2012b).

14.2.3.1.2 Disease Resistance

Disease resistance introgressed into cultivated germplasm from CWR has provided ongoing value to the sunflower crop (Seiler and Fredrick Marek 2011; Christov 2008; Seiler 2012). Because most pathogens continue to evolve and develop new virulent races in response to deployed resistance, some very quickly, the maintenance of resistance is an ongoing effort. Genes providing resistance to downy mildew have been incorporated into cultivated sunflower from several sunflower CWR including wild *H. annuus*, *H. tuberosus*, *H. argophyllus*, and *H. praecox* (Ma et al. 2017; Seiler et al. 2017). Comprehensive screening of the majority of the wild sunflower species for response to Sclerotinia basal stalk rot (BSR) has identified resistance in accessions of *H. argophyllus* and *H. petiolaris* ssp. *petiolaris* Nutt. which has been incorporated into cultivated sunflower (Qi et al. 2016). Unlike downy mildew, resistance to Sclerotinia BSR is not conferred by a single gene making, tracking, and evaluating successful introgressions more complex than for downy mildew. Rust resistance was observed in the 1950s in wild *H. annuus* from TX and the resistance incorporated into cultivated sunflower (Putt and Sackston 1957). The search for rust resistance is ongoing as new virulent strains develop; additional resistant germplasm has been developed and released incorporating genes primarily from *H. annuus* but also from *H. argophyllus*, *H. petiolaris*, and *H. tuberosus* (Qi et al. 2011). To date, all rust resistance genes in cultivated sunflower can be traced to wild species. The sunflower crop has been protected at some level from most pathogens by the incorporation of resistance genes from CWR (Seiler et al. 2017; Seiler 2012).

14.2.3.1.3 Resistance to *Orobanche cumana* (a Holoparasitic Weed)

Resistance to *O. cumana* incorporated from a range of sunflower CWR has been critical to the survival of the cultivated sunflower industry in ecoregions where *O. cumana* is present. Infestations of the parasite were first observed in Russia in the 1860s (Antonova 2014); selection within cultivated sunflower initially provided resistance. Beginning in the 1920s, resistance was incorporated from *H. tuberosus* which controlled *O. cumana* infestations for several decades (Molinero-Ruiz et al. 2015). However, *Orobanche* has continued to spread to new sunflower production regions, in part due to its extremely small seed size which makes it very difficult to detect (0.2 × 0.4 mm; a single plant can produce up to 100,000 seeds), and *O. cumana* has been more frequently developing new virulent races capable of overcoming deployed resistances (Skoric 2012a; Skoric and Pacureanu 2010). Most perennial *Helianthus* species are resistant, typically with near immunity, and some populations of several annual taxa have shown resistance as well (Jan et al. 2014; Seiler and Jan 2014). *O. cumana* germination is dependent on a root exudate of the host plant which apparently cultivated sunflower and most wild annual taxa produce but which most perennial and some annual taxa do not although this is just the first step of a multistep parasitism process, as discussed by

Molinero-Ruiz et al. 2015 and Louarn et al. 2016. To date, resistance to each new virulent race has been detected in a sunflower crop wild relative(s) and incorporated into cultivated breeding stock; however, the recent rapid changes in *O. cumana* populations and increased virulence make managing this biotic stress an ongoing concern (Velasco et al. 2016; Molinero-Ruiz et al. 2015). Investigating herbicides as a possible control, Garcia-Torres et al. (1989, 1994) found that *O. cumana* was susceptible to imidazolinone and sulfonylurea classes of herbicides. Chemical control of the parasite was determined to be independent of its virulence category although application timing and concentrations had to be carefully determined so as to not affect the crop.

14.2.3.1.4 Herbicide Tolerance

During the late 1990s, tolerance to several imidazolinone and sulfonylurea herbicides was discovered in a population of wild *H. annuus* growing alongside a Kansas soybean field that had been sprayed with imazethapyr for 7 consecutive years (Al-Khatib et al. 1998). The tolerance trait was introgressed into breeding lines using standard techniques (Miller and Al-Khatib 2002; Miller and Al-Khatib 2004), and the germplasm has been used by breeding programs and chemical companies throughout the world to improve weed control in sunflower.

Because of the susceptibility of *O. cumana* to these herbicides, a very valuable feature of the herbicide tolerance trait has been its incorporation into adapted sunflower germplasm also carrying genetic resistance to *O. cumana* providing integrated control of the parasitic plant (Alonso et al. 1998, 2014; Sala et al. 2012; Velasco et al. 2016). Careful management strategies are still necessary so that *O. cumana* does not become resistant to the herbicides.

14.2.3.1.5 Drought Tolerance

Southwestern sunflower CWR commonly grow in dry, sandy habitats: *H. anomalus*, *H. niveus* ssp. *tephrodes*, and *H. niveus* ssp. *niveus* grow in active dune areas; *H. neglectus* grows in deep sandy regions; *H. deserticola*, *H. petiolaris* ssp. *canescens*, and *H. petiolaris* ssp. *fallax* grow in desert floor environments, and one dune-adapted ecotype is known for *H. petiolaris* ssp. *fallax* (Andrew et al. 2013). In addition, *H. argophylus* grows in deep sand in southwestern coastal TX. Several of these species have been used to develop drought-tolerant cultivated germplasm (Seiler et al. 2017; Skoric 2016; Fick and Miller 1997). Drought represents a complex abiotic trait, and it is difficult to define appropriate traits and measuring parameters (Skoric 2012a) in part because different wild sunflower species use different survival strategies (e.g., Rosenthal et al. 2010). Understanding and improving drought tolerance in cultivated sunflower is an active research focus.

14.2.3.1.6 Ornamental Improvements

A key component in the improvement of ornamental sunflower was the discovery in 1910 of a single wild *H. annuus* plant with wine-red ray flowers by Wilmatte Cockerell in a field near her home in Boulder, CO (Cockerell 1912). Recognizing the potential value of this discovery to the ornamental industry, she and her husband transplanted the plant to their garden shortly before the field was mowed. Mrs. Cockrell crossed the red sunflower with typical *H. annuus* pollen and intercrossed the resulting progeny to conserve and recover the color trait since a single wild sunflower plant would not produce viable seed. This naturally occurring mutation in ray flower color has not been reported from the wild since. The CMS trait has also been important to the ornamental sunflower market providing cut flowers without copious pollen production from the thousands of disk flowers in the center of each head which would drop onto any surface upon which flower containers were placed. In addition, sterile disk flowers appear to extend the life span of the cut head (Kaya et al. 2012). Breeding with wild sunflower species to improve ornamental sunflowers is ongoing (Kaya et al. 2012, Atlagic et al. 2005).

14.2.3.2 Desirable Characters: From the Perspective of Use

As in any crop, desirable characteristics are those which protect the crop, such as disease and other biotic stress resistances/tolerances, and those which either allow it to fit into valuable niche markets or which maintain or expand existing markets. Desirable characteristics depend on the specific end use, but disease resistance and abiotic trait resistance continue to be a high priority for sunflower in addition to oil quality characteristics. Interest in plant architecture and structure to improve the agronomics of harvesting as well as self fertility and flowering time are all considered valuable traits.

14.2.3.3 Challenges to Increased Use of CWR

One challenge to increased use of sunflower CWR is determining if a specific taxa or plant(s) within a specific population contain a trait that would be useful for cultivated sunflower production. Sunflower CWR are self-incompatible and as a result are always segregating populations; therefore, evaluating the wild population(s) in some meaningful way requires screening (many) more than one plant and also requires some understanding of the biology underlying the trait of interest. Disease resistance is often under single gene control so evaluating wild populations for resistance is straightforward and making selection of breeding material based on the desired trait very feasible. Many other useful traits are complex, dependent on physiological and/or metabolic complexes and/or morphological structures which involve many genes and DNA regulatory elements. For example, if a wild sunflower taxon is tolerant of an abiotic stress, can the process responsible for tolerance be defined and transferred in a meaningful way to cultivated sunflower?

A second challenge is the process of interspecific breeding itself. Although incorporation of useful traits from sunflower CWR into the cultivated crop has been very successful since the early 1900s and all but one of the sunflower CWR have been successfully crossed to cultivated material, it is not a simple process to obtain an end product of fertile, agronomically useful plants especially when working with more distantly related wild relatives. The breeding process in cultivated sunflower has been well described by a number of authors including Fick and Miller (1997), Kaya et al. (2012), and Skoric (2012a). Wild annual *H. annuus* and *H. argophyllus* cross easily with cultivated *H. annuus* and the F_1 plants are fertile. Other annual species usually cross readily but the offspring generally have lower fertility. Currently, the annual *H. agrestis* is the only species for which introgressive hybridization has not been successful with cultivated sunflower (Jan 1997 and personal communication 2016). *H. agrestis* has the largest chromosomes of the *Helianthus* taxa, more than three times larger than *H. annuus* (Kantar et al. 2014), which is likely a primary factor in the lack of success in interspecific crossing. Most perennial species require embryo rescue to recover plants, and the success rate can vary greatly (Jan 1997; Sukno et al. 1999). Phenotypic evaluations are required to determine if a trait of interest has been incorporated; molecular genomic analyses have begun to facilitate the selection and evaluation process. Key to this process has been the sequencing of two cultivated sunflower genomes HA 412-HO and XRQ (Kane et al. 2011, primary text and supplemental notes Badouin et al. 2017). Sequencing of both annual and perennial CWR is underway as well by many research groups (e.g., Baute et al. 2015, 2016; Bock et al. 2014; Kawakami et al. 2014). Baute et al. (2015) have used genome scans to reveal the locations of wild species introgressions on cultivated sunflower linkage groups. Based on these kinds of information and other available genetic and genomic analyses, interspecific lines can be selected and targeted for further breeding and evaluation.

The scientific world is in the midst of a revolution in genomic technologies with the development of the CRISPR/cas9 gene editing system which is likely to have some effect on sunflower breeding, and certainly there have been significant efforts in molecular or “artificial” breeding technologies with sunflower (reviewed by Cantamutto and Poverene 2010). To date, however, the majority of sunflower market users remain adamantly opposed to any artificial breeding technologies which at the time of this writing is perceived to include the CRISPR/cas9 system. Sunflower breeders continue to use standard breeding techniques with the use of molecular markers for mapping and identification to help target efforts.

14.3 Wild Utilized Species (WUS)

There is limited direct use of sunflower CWR. In surveying online seed catalogs, the author found at least ten wild species (annuals and perennials) offered by various nurseries for gardens, and *H. debilis* and *H. tuberosus* both have semidomesticated cultivars that are readily available in the trade. *H. tuberosus* has vegetable and medicinal uses which are discussed in this book (Kantar, Chap. 19). A number of wild species are used in revegetation mixes for habitat restoration often after road construction. Some nurseries collect seeds from wild populations and manage their own increases, thereby having the ability to track the ecotype of the seed which can be critical for some habitat restoration applications (personal communication). Other retailers sell seed purchased from producers elsewhere in North America and Europe and without knowledge of the origin of the seed sources (personal communication). There are additional niche uses for wild sunflowers. For example, a farmer in the Rockport, TX, area has described growing *H. argophyllus*, the fully branched and very tall growing native of southwestern coastal TX, as a hedgerow to protect his garden from wind. As discussed earlier in this chapter, many of the wild species grow in very specific ecogeographical regions, and they are not adapted to survive long term in non-native habitats nor will they flower at non-native latitudes. In addition, the wild species, especially perennials, have some level of seed dormancy with the result that germination can be difficult.

14.4 Conservation Status of CWR and WUS

The majority of wild sunflower taxa are present in abundance across North America, although many species are found within specific ecogeographical regions. Two wild sunflower species are considered noxious weeds by seven states in the USA and one province in Canada (*H. annuus* in IA and *H. ciliaris* [Texas blueweed] in AZ, AR, CA, OR, SC, WA, and AB) although no *Helianthus* species are on the US Federal Noxious Weeds list (USDA Plants Database accessed June 2017) nor on the Canadian list of pests (plant) (Canadian Food Inspection Agency accessed June 2017). Two *Helianthus* species are considered weeds in Mexico (*H. annuus* and *H. laciniatus* A. Gray; non-federal list) although neither appear to have a noxious weed designation.

The author is aware of only one example of a preserve dedicated specifically to the conservation of a sunflower species. *Helianthus paradoxus*, listed by the US Fish and Wildlife Service (USFWS) as a threatened species, is endemic to cienega habitats in southwestern TX and NM. The State of NM established the Blue Hole Cienega Nature Preserve to protect habitat and thereby preserve an expansive population of *H. paradoxus* on the outskirts of Santa Rosa, NM. More commonly, sunflowers are protected by growing on public lands and in preserves established for other purposes with the result that populations are not actively monitored or managed except in the case of listed taxa on public lands. For example, two nature preserves established by the Texas Nature Conservancy to conserve cienega habitats in western TX which provide the last remaining natural habitat for two different pupfish also provide habitat for several other vulnerable species including *H. paradoxus*.

14.4.1 *In Situ*

Three sunflower species are currently listed as threatened or endangered by the USFWS: *H. schweinitzii* T. & G. (listed in 1991) and *H. verticillatus* Small (listed in 2014) are both considered endangered; *H. paradoxus* (listed in 1999) is considered threatened. The recovery plan for each species defines the conditions required to be met for that species to be considered recovered [USFWS webpage/endangered species/endangered plants/ information found in Environmental Conservation Online System (ECOS)]. A fourth *Helianthus* species represents a success story within the USFWS's endangered species program. *H. eggertii* Small, listed as threatened in 1997, was delisted in 2005 after reviews of all available data indicated that *H. eggertii* was more widespread and abundant than was documented at the time of listing and was more resilient and less vulnerable to certain activities than previously thought, and at least 20 geographically distinct, self-sustaining populations were protected on Federal, State, and county lands (Federal Register/vol 72, No 47/Monday, March 12, 2007 notices post-monitoring plan; 48,482–48,490 Federal Register/Vol. 70, No 159/Thursday, August 18, 2005/Rules and Regulations; Endangered Species: Many Factors Affect the Length of Time to Recover Select Species GAO-06-730 Endangered Species Recovery Sept 2006 Report to Congressional Requesters; accessed through ECOS, USFWS). No *Helianthus* species are currently listed at the federal level in Canada or Mexico.

The states in the USA and provinces and territories in Canada maintain lists of species considered at risk in their jurisdictions. Twenty-three states and 11 provinces and territories do not have any *Helianthus* species on their endangered/species of concern plants lists. Two states list only species which are federally listed, and 25 states and 2 provinces list non-US federally listed *Helianthus* species as vulnerable or imperiled, all of which are secure in another state or states except *H. carnosus*, endemic to and listed by FL and *H. niveus ssp. tephrodes* Grey (Heiser), listed by CA with US populations only in CA; the majority of populations are in Mexico.

14.4.2 *Ex Situ*

The USDA NPGS in the USA maintains the most comprehensive wild sunflower collection in the world at the North Central Regional Plant Introduction Station (NCRPIS) in Ames, IA, including samples of the three species listed by the USFWS as threatened or endangered.

The NCRPIS collection has samples of all extant taxa in the genus *Helianthus* (Table 14.3) except *H. niveus* ssp. *niveus* (Fig. 14.4) which is endemic to the Pacific Coast sand dunes of Baja California, Mexico. The accessions provide reasonable geographic representation from US populations for most taxa and collecting is ongoing for underrepresented taxa, primarily funded by the PEO. A map-based ecogeographic analysis based on verified occurrences from genebanks and herbaria of

Table 14.3 Number of active accessions of *Helianthus* taxa in the NCRPIS genebank

Number of active accessions	*Helianthus* taxa[a]
0–9	*H. niveus* ssp. *niveus*[b], *H. schweinitzii*[b], *H. arizonensis*[b], *H. verticillatus*[b], *H. longifolius*[b], *H. carnosus*[b], *H. winteri*[b], *H. occidentalis* ssp. *occidentalis*, *H. laciniatus*, *H. laevigatus*[b], *H. praecox* ssp. *hirtus*[b], *H. smithii*[b], *H. praecox* ssp. *praecox*[b], *H. simulans*
10–19	*H. agrestis*[b], *H. floridanus*, *H. x laetiflorus*, *H. debilis* ssp. *vestitus*[b], *H. glaucophyllus*[b], *H. pauciflorus*[c], *H. atrorubens*, *H. eggertii*[b], *H. microcephalus*, *H. niveus* ssp. *tephrodes*, *H. nuttallii* ssp. *rydbergi*, *H. occidentalis* ssp. *plantagineus*[b], *H. porteri*, *H. debilis* ssp. *debilis*[b], *H. debilis* ssp. *tardiflorus*[b], *H. paradoxus*, *H. debilis* ssp. *cucumerifolius*, *H. hirsutus*, *H. gracilentus*, *H. silphioides*, *H. anomalus*, *H. pauciflorus* ssp. *subrhomboidus*, *H. bolanderi*, *H. divaricatus*, *H. heterophyllus*, *H. salicifolius*
20–29	*H. petiolaris* ssp. *canescens*, *H. californicus*, *H. pauciflorus ssp. pauciflorus*, *H. debilis* ssp. *sylvestris*, *H. deserticola*, *H. resinosus*, *H. cusickii*, *H. nuttallii* ssp. *nuttallii*, *H. giganteus*, *H. petiolaris*[c], *H. mollis*, *H. decapetalus*, *H. praecox* ssp. *runyonii*[b], *H. strumosus*
30–49	*H. exilis*[b], *H. angustifolius*, *H. ciliaris*, *H. neglectus*[b], *H. radula*, *H. grosseserratus*
50–99	*H. petiolaris* ssp. *fallax*, *H. pumilus*, *H. maximiliani*, *H. argophyllus*, *H. tuberosus*
100–139	*H. petiolaris* ssp. *petiolaris*
>1000	*H. annuus*

[a] See Tables 14.1 and 14.2 for taxa authorities
[b] Taxa with limited ranges, see Tables 14.1 and 14.2; Rogers et al. (1982)
[c] Species accessions without subspecies identification

36 *Helianthus* taxa selected as "of interest" by a group of experts in sunflower research and conservation (roughly 55% of the genus, Kantar et al. 2015) were identified as taxa in need of collecting to ensure geographic representation. Several of the taxa have been targets of directed collection since the data were gathered. Original ranges have become urbanized in some regions, many herbaria voucher records on which gap analyses are based are decades old, and full geographic representation of the original extent of some taxa may not be possible. Information about the NCRPIS collection can be accessed and seeds can be requested using the online GRIN-Global public database. The Canadian national genebank (Plant Gene Resources of Canada, PGRC) at the Agriculture and Agri-Food Canada facility in Saskatoon, Saskatchewan, maintains a small seed-based wild sunflower collection as well as a tuber-based *H. tuberosus* collection, whereas the NCRPIS only distributes seeds of *H. tuberosus*. Information about the Canadian collection can be accessed and seeds requested using the online GRIN-CA database. Mexico recently built a new genebank in Tepatitlan, Jalisco, which currently houses a small collection of wild sunflower species repatriated from the NPGS collection. Other genebanks around the world maintain wild sunflower collections, the largest of which are curated by VIR (St Petersburg, Russia), INRA (Toulouse, France), NS SEME (Novi Sad, Serbia), and ICAR (Hyderabad, India). There are smaller collections in

several additional European countries and INTA (Cordoba, Argentina) also maintains a wild sunflower collection. All of the non-USDA wild collections are largely based on the USDA collection and/or FAO and/or other international and USDA sponsored collection trips made with USDA co-collectors. Some genebanks include samples of naturalized wild sunflower species from within that country.

14.4.3 Ways to Improve Conservation

Publicity surrounding the Svalbard Global Seed Vault has increased general awareness of the existence and value of crop wild relatives and ongoing presentation and publicity about this topic is needed. There are a number of CWR informational web sites; two with international sponsorship that include North American native species are the Global Crop Diversity Trust CWR web page and the Bioversity International web page. Within the USA, the Forest Service maintains a Crop Wild Relatives web page. Much of the value of crop wild relatives is as a resource for future needs in response to changing conditions, many of which are driven by climate changes; all specific future needs are unknown. Protection in the wild allows natural selection in response to changing conditions to continue although the time frame is too short for evolution per se in our lifetimes; ex situ protection of population samples from specific locations at specific time points provides a conservation framework and breeding resources and ensures long-term survival of the sampled taxa.

14.4.3.1 In Situ

Improving conservation of wild sunflowers in situ is complex and involves many issues including better and/or more complete protection and conservation of wild spaces (Dempewolf et al. 2017) and establishing equal survival value for wild plants and animals especially considering competing water use by humans. In some states, Florida, for example, destruction of listed plant species can be specifically allowed on private property which is not true for listed animals including fish. Permits to access populations of listed plants may only be required if commercial uses are intended for the collected material not as a means to ensure long-term conservation of in situ populations. Continued public outreach to expand awareness that all wild plants are not weeds but that most are endemic, well-adapted native germplasm whose preservation also provides pollinator habitat could help wild sunflower populations in two ways. First, pollinator health is essential for seed production in wild sunflowers because all but one species are self-incompatible. Second, most wild sunflower taxa flower late in the year and successful seed production and long-term population survival depend on limiting roadside and public and private property mowing until as late as early December for some taxa in more southern regions.

14.4.3.2 Ex Situ Conservation

Successful maintenance of genebank collections requires continued funding for established infrastructure, for construction of additional infrastructure as needed, and for support to ensure that seed health is monitored and that protocols exist to replace or regenerate low viability materials. A more comprehensive system for obtaining and curating evaluation data of ex situ collections could facilitate germplasm utilization.

The USDA sunflower collection contains reasonable geographic representation for many taxa with populations within the USA and the central prairie regions in Canada; however, sunflower CWR populations in eastern and western Canada are not represented and sampling and preservation of strategic populations of *Helianthus* CWR in Mexico are critically needed to ensure conservation of the full range of genetic diversity for this genus. Roughly 20% of the taxa (at least 13) in *Helianthus* have populations in Mexico (Gómez-Sánchez and González 1991; Villaseñor 2016; author observations; D Burge, personal communications 2015–2017; SEINet specimen database accessed June 2017; Sivinski 2016). Of these 13, it is likely that the majority of the populations of *Helianthus laciniatus* and *Helianthus niveus* ssp. *tephrodes* occur in Mexico and a second *H. niveus* taxa, ssp. *niveus*, grows only in Mexico. In addition, at least one population of the US federally listed *H. paradoxus*, described recently as a new subspecies (Sivinski 2016), is growing in Mexico. It is expected that the majority of the populations of each *Helianthus* taxa in Mexico would represent unique diversity. It should be a high priority to have wild sunflower populations representing the full geographic distribution of these taxa in Mexico sampled and stored in a genebank collection where they could be available to support research and crop improvement.

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Chapter 15
Wild Genetic Resources of Minor Oil and Rubber Crops

**Maria M. Jenderek, Von Mark Cruz, Andrew Salywon,
Diana Jasso de Rodriguez, Raúl Rodríguez García,
José Ángel Villarreal Quintanilla, and David A. Dierig**

Abstract Jojoba (*Simmondsia chinensis* (Link) C. K. Schneid), lesquerella (*Physaria fendleri* (A. Gray) O'Kane & Al-Shehbaz), and guayule (*Parthenium argentatum* A. Gray) originate from semiarid climate zones of North America; meadowfoam (*Limnanthes alba* Hartw. ex Benth., *Limnanthes bakeri* J. T. Howell, *Limnanthes douglasii* R. Br.) is endemic to the western part of California, Oregon, and Southern Canada and grows around vernal pools and seasonally wet areas. This chapter discusses historic and current uses, domestication efforts, breeding, and cultivation challenges and describes the conservation status of the crops' genetic resources. Meadowfoam and guayule are already cultivated on a limited industrial scale. Jojoba and lesquerella are not grown commercially in North America but are economically important in countries beyond the Americas and are of particular interest to nations with extensive areas of arid lands. North America is an important source of wild genetic resources for these crops, and further efforts are needed to ensure their conservation.

Keywords Oil crops · *Limnanthes* · *Lesquerella* · *Simmondsia* · Rubber crop · *Parthenium*

M. M. Jenderek (✉)
USDA, Agricultural Research Service, Center for Agricultural Resources Research,
National Laboratory for Genetic Resources Preservation, Fort Collins, CO, USA
e-mail: maria.jenderek@ars.usda.gov

V. M. Cruz · D. A. Dierig
Bridgestone Americas, Inc., Eloy, AZ, USA
e-mail: CruzVonmark@bfusa.com; DierigDavid@bfusa.com

A. Salywon
Desert Botanical Garden, Phoenix, AZ, USA
e-mail: asalywon@dbg.org

D. J. de Rodriguez · R. R. García · J. Á. V. Quintanilla
Universidad Autónoma Agraria Antonio Narro, Saltillo, Coahuila, Mexico

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15.1 Introduction

Jojoba (*Simmondsia chinensis* (Link) C. K. Schneid), meadowfoam (*Limnanthes alba* Hartw. ex Benth., *Limnanthes bakeri* J. T. Howell, *Limnanthes douglasii* R. Br.), lesquerella (*Physaria fendleri* (A. Gray) O'Kane & Al-Shehbaz), and guayule (*Parthenium argentatum* A. Gray) are defined as "new crops" despite the discovery of their potential economic value in the early 1900s for guayule and 1950s for jojoba, meadowfoam, and lesquerella. While their seeds (oil crops) or plants (guayule) contain a high quality and quantity of oil or rubber, cultivation is currently highly limited. The type of oil and rubber that can be produced with these plant materials has many applications as biodegradable lubricants, biofuels, cosmetics, pharmaceuticals, dietetic products (oil crops), and industrial products such as rubber, resin, and bagasse (guayule). The meal can also be used in animal feed and for soil augmentation. All described species have antimicrobial characteristics and might be useful biocides. Wild forms of all of these crops occur in North America.

This chapter describes the historic uses of the wild populations by people living nearby the natural plant populations, as well as contemporary utilization of the wild plants in initial research in cultivar development. Discussed are cultivation efforts and challenges of these crops, the wild habitats and geographic ranges that the wild species occupy, germplasm, improvement status, and characteristics to be improved to make the crops profitable to growers. The current state of the species' taxonomy and past struggles of scientific determination is also reported. Due to vanishing habitat, some meadowfoam and lesquerella species are on US federal or state plant protection listings. Unfortunately, jojoba and guayule wild populations are not currently protected.

15.2 Jojoba: A Species with Uncommon Liquid Wax

Jojoba (*Simmondsia chinensis* (Link) C. K. Schneid) is reported as "one of the most unusual and unique plants of the North American deserts" and "the only known plant in the world to produce liquid wax" (Green et al. 1936; Princen 1979; Sherbrooke and Haase 1974). The scientific name for jojoba is *Simmondsia chinensis* (Link) C. K. Schneid, and *S. californica* Nutt. is a synonym (Carlquist 1982; USDA ARS 2017b). In some countries, jojoba is domesticated and cultivated as a crop due to its tolerance to drought. It is an evergreen desert shrub with thick, leathery bluish-green leaves different in size, shape, color, and pubescence; the shrub may reach a height of 0.2–5 m and live over 200 years (Benzioni and Dunstone 1986; Gentry 1958; Hamerlynck and Huxman 2009; Khan et al. 2017; Wisniak 1994; Yermanos 1979). The species is dioecious (hermaphroditic individuals may rarely occur) and wind-pollinated (Buchmann 1987; Gentry 1958). The fruit is a dehiscent capsule containing one to three seeds. Jojoba tolerates temperatures ranging from −1.1 °C (mature shrubs may endure −9.4 °C) to 46.1 °C (Gentry 1958; Yermanos 1974). Due to its botanical and physiological nature and high adaptability, jojoba is a suitable crop for marginal lands in desert conditions (McKell 1983), and it does not compete for land with food crops. Because of its oil characteristics and potential economic value, jojoba is of interest to countries with vast desert areas (Sidibé et al. 2010; Sukkasi et al. 2010).

15.2.1 Crop Origin and History of Use Worldwide

The name jojoba was adapted by Spaniards from the Tohono O'odham Indian name "hohowi"; the species is also known as hohwi, hohovai, bucknut, bushnut, jobe, jojove, pignut, goatberry, goat nut, deer nut, wild hazel, quine nut, coffeeberry, coffeebush, gray box nut, quinine nut, sheepnut, and wild hazelnut (Castetter and Underhill 1935; Daugherty et al. 1958; Felger and Rutman 2016; Sherbrooke and Haase 1974). The species might be a remnant from a prehistoric era of an ecosystem that does not exist today (Gentry 1972); however, the origin of jojoba is not known (Stebbins and Major 1965). Jojoba nuts and their oil were used by native populations of Baja California for medicinal purposes, as cooking oil and were consumed as roasted seed (Sherbrooke and Haase 1974). The first report on using jojoba was described by Francesco Saverio Clavigero, a Mexican Jesuit in 1789 (Clavigero 1789). In 1925, the Boyce Thompson Southwestern Arboretum in Superior, Arizona, planted experimental plots of jojoba (Nagavi and Ting 1990). In the 1950s and 1960s, jojoba oil was thought as a substitute for sperm whale oil due to their chemical similarities and was hoped to be a source of income for Native Americans residing in semiarid regions of the United States (Benzioni 1995; Miller et al. 1979). However, cultivation of unimproved wild material without any agronomic knowledge resulted in low seed yield (300–400 kg/ha) and did not prove to be economical (Shani 1995; Wisniak 1977; Yermanos 1974). In the 1970s, there was a renewed interest in jojoba due to an oil embargo, subsequent price increases, and oil shortages. Additionally, sperm and other whale species were identified as endangered species, and their harvest restricted. In 1976, jojoba fields were established in Arizona and California (Palzkill and Hogan 1983); however, other authors reported 1978 as the beginning of jojoba cultivation in the United States, reaching its largest acreage of 16,000 ha in 1985 and declining after (Harington 1987). The majority of plantings were abandoned due to yield fluctuations, lack of knowledge of agronomic procedures, and unavailability of high seed-yielding cultivars (Harington 1987; McKay 1987).

More recently, jojoba cultivation, material improvement, and research are of interest in countries with semiarid environments: in Africa, Kenya (Inoti et al. 2015, Inoti 2016), Morocco (Berrichi et al. 2010), Sudan (Nimir and Ali-Dinar 1989) and South Africa (Nimir and Ali-Dinar 1989); in the Americas, Argentina (Tobares et al. 2004), Chile (Botti et al. 1998; Cappillino et al. 2003), Mexico (Foster et al. 1983; Franco-Viziano and Khattack 1990; Godoy 2011), Peru (Kolodziejczyk et al. 2000), and the United States (Palzkill and Hogan 1983; Purcell and Purcell 1988;

Purcell et al. 2000; Yermanos 1978); and in Asia, China (Li et al. 2007), India (Bhatnagar et al. 1991), Iran (Jahromi and Fard 2013), Israel (Dunstone et al. 1984), Jordan (Al-Hamamre 2013), Saudi Arabia (Al-Soqeer 2010; Osman and Hassan 2000; Osman and Abohassan 2013), and Yemen (Eed and Burgoyne 2015). Also it is of interest in Australia (Dunstone and Begg 1983) and Turkey (Ayanoğlu 2000; Ülger et al. 2002).

15.2.2 Challenges in Cultivation: Pests, Diseases, and Edaphic and Climatic Stress

The glassy-winged sharpshooter (*Homalodisca vitripennis* Germar) was observed on jojoba plants in California (Wistorm et al. 2010) and scale (*Aspidiotus nerii* Bouché) in Israel (Berlinger et al. 1999), and several sucking insects were reported in Chile (Quiroga et al. 1991). Several fungal diseases were reported on jojoba. *Verticillium dahliae* Kleb. was noticed in California (Orum et al. 1981; Orum et al. 1983). Seed fungi taxa (*Aspergillus flavus*, Link, *A. niger* Teigh., *Fusarium pallidoroseum* (Cookie) Sacc.) (Sharma and Champawat 2000), *Rhizoctonia solani* J.G. Kühn, and various species of *Fusarium* were reported in the Indian desert (Saroj and Kumar 1983; Champawat et al. 2003). A bacterial disease on leaves was observed in Australia (Cother et al. 2004). The shrub is generally considered to be salt tolerant (Hussain et al. 2011; Tal et al. 1979); however, Hassan and Ali (2014) reported membrane damage, decreased plant height, and lower number of leaves and branches under salinity stress. Its adaptation to arid and warm environments is well known, and genetic diversity in adaptation for saline conditions undoubtedly exists, considering the species' broad range in the Sonoran desert.

15.2.3 Functional Use

Seeds of jojoba contain liquid wax that is not found in any other plant species (Gentry 1958; Princen 1979). Commonly, jojoba waxes are referred to as jojoba oil. The oil content in seeds is between 48% and 65% (Busson-Breysse et al. 1994; Green et al. 1936; Jenderek and Dierig 2008; Salgin et al. 2004). The oil is odorless and light yellow, has a high normal boiling point and low chemical reactivity, and is very stable at temperatures <120 °C (Tobares et al. 2004; Torres et al. 2006). The properties of the oil and its content in seeds stay unchanged during storage over several years (Daugherty et al. 1958). The oil characteristics were summarized by McKell (1983) as being molecularly simple, unsaturated, stable under high temperature and pressure, and not prone to rancidity in storage. Mirov (1952) described the liquid wax as a composition of one long-chain alcohol molecule coupled with one molecule of fatty acid, whereas fats are comprised of a glycerine molecule with three fatty acid molecules attached. The wax composition was reported by Miwa (1971) and later by

Benzioni (1978). Analysis of the liquid jojoba wax showed that the wax is a mixture of esters (docosenyl eicosenoate 41.4%, eicosenyl eicosenoate 28.0%, eicosenyl docosanoate 10.3%, tetracosenyl eicosenoate 6.8%, and eicosenyl oleate 5.7%), triacylglycerols (eicos-11-enoic 76.7%, docos-13-enoic 12.1%, oleic 9.3%), free fatty alcohols (eicos-11-enol 52.3%, docos-13-enol 38.4%, octadec-9-enol 5.3%, and tetracos-15-enol 4.0%), and sterols (sitosterol 69.9, campesterol 16.9%, and stigmasterol 6.7%) (Busson-Breysse et al. 1994; Van Boven et al. 1997).

Jojoba oil is used as unmodified and modified derivatives to produce cosmetics (hair and skin products), pharmaceuticals, dietetic foods, lubricants, polishing products, surfactants, antifoam, resins, and coatings and as a material for production of biodiesel. The plants themselves are used in landscapes and soil conservation around desert cities and as dust protection along roadsides (Ahmed et al. 2015; Al-Hamamre and Al-Salaymeh 2014; Canoira et al. 2006; Harry-O'kuru et al. 2005; Karmakar et al. 2010; Le Dréau et al. 2009; McKell 1983; Mirov 1952; Miwa 1984; Nassar et al. 2015; Khan et al. 2017; Patel et al. 2015; Salgin 2007; Sanchez et al. 2016; Sivasankaran et al. 1988). Several oil extraction methods, oil modifications, and oil uses have been patented (Brieva et al. 1999; Brown et al. 2004; Dresdner et al. 1994; Goedde et al. 1998; Lambert and Johnson 1999; Taygi and Granica 2015). In animal models, jojoba wax showed anti-inflammatory effects (Habashy et al. 2005). Jojoba meal contains up to 15% protein. Aspartic and glutamic acids are the most abundant, which makes the meal suitable for animal feed after the toxic effects of simmondsin and simmondsin 2′-ferulate are neutralized (Verbiscar and Banigan 1978; Yermanos 1974). Stephens (1994) reported 20–30% protein content in oilless meal and suggested using it as feed supplements. Jojoba meal had an inhibitory effect on food intake in rats. The meal has antifungal, insecticidal, and feeding inhibitor properties (Abbassy et al. 2007; Ismail et al. 2009).

15.2.4 Crop Wild Relatives

Simmondsia chinensis belongs to the Simmondsiaceae family and is the only species in the family (Felger and Rutman 2016); Van Tieghem (1898), a Belgian botanist, was the first to postulate placing jojoba in its own family. Shrubs of this species are still abundant in nature and proliferate easily by seeds; as such they are not subject to plant genetic resources conservation.

15.2.5 Distribution, Habitat, and Abundance

Simmondsia chinensis is endemic to the Sonoran Desert and grows in Southwestern Arizona and California and Northwestern Mexico (Al-Ani et al. 1972; Benzioni 1995; Brooks 1978; Princen 1979) (Fig. 15.1). It grows at sea level up to 1500 m altitude. It is found on light- and medium-textured, coarse, and drained soils and

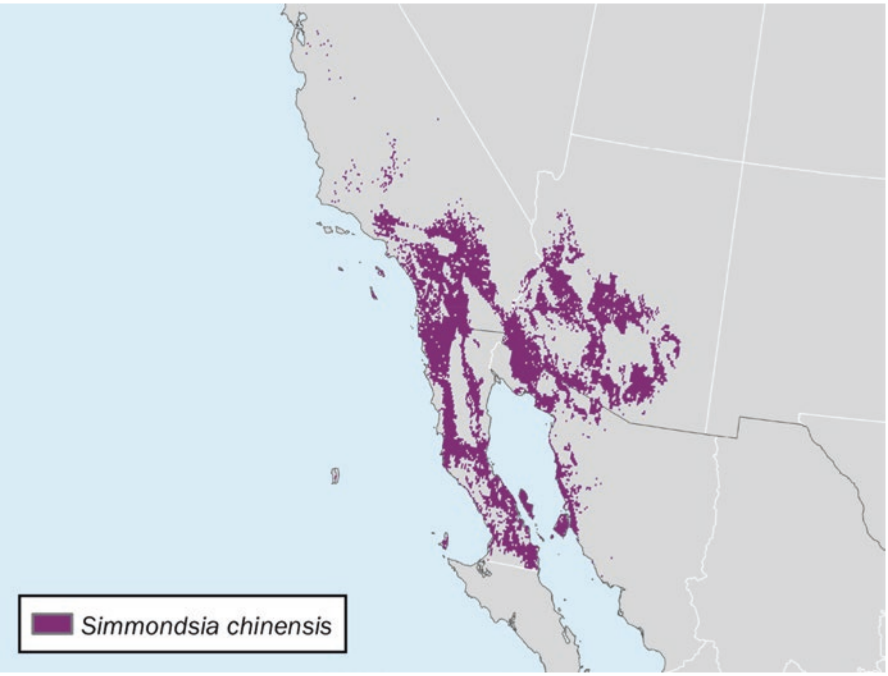

Fig. 15.1 Geographic distribution of jojoba (*Simmondsia chinensis* (Link) C. K. Schneid) based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

frequently on barren slopes. The shrub habit and height depend on environmental conditions; rainfall level of ca. 76–450 mm was reported optimal for the shrub's growth and fruiting. In cultivation, established jojoba stands require 500–600 mm of water (Benzioni and Nerd 1985; Gentry 1958; Yermanos 1974; Undersander et al. 1990; Yermanos 1978). NatureServe (2017) describes the species as secure globally, since it can be commonly local in its distribution range. Beauchamp (1986) reported the species being common in San Diego County.

15.2.6 Breeding Efforts on Wild Utilized Germplasm

All cultivated and promising selections were made from wild-growing shrubs (Fig. 15.2); but very few seed-derived plants produce an economic yield (Purcell and Purcell 1988). Seeds from endemic jojoba populations were the main source of material for research and processing (Yermanos 1974, 1977; Purcell et al. 2000). Wild populations are highly variable in seed weight and size, oil and protein content, and botanical characteristics (Clarke and Yermanos 1980; Amarger and Mercier 1996; Bhardwaj et al. 2010; Benzioni et al. 1999; Heikrujam et al. 2015; Naqavi et al. 1990; Nagavi and Ting 1990; Reddy and Chikara 2010; Tobares et al. 2004). Hence, breeding and selection of improved material are highly feasible (Ray et al. 2005; Tobares et al. 2004; Yermanos and Duncan 1976). Important characteristics for developing high-performing cultivars are high oil content, large seeds, flowers at each node, early flowering, flower frost tolerance, and erect shrub habit. Also desired is seed production beginning earlier than five years after stand establishment (Yermanos 1979). Selection in Israel was focused on characteristics promoting yield potential and reproductive traits (rapid growth, branching ability, node density, survival rate, flower density, fruit set, seed wax content, earliness that was indicated by flowering in early years of cultivation, and flower density) (Benzioni et al. 1999). Coates et al. (2006) suggested jojoba seed yield might be increased by artificial pollen distribution. For breeding and propagation purposes, early distinction between female and male plants has a practical importance. Several molecular markers, such as male-specific touchdown PCR marker JM900 (Ince et al. 2010), CAPS assay marker (Ince and Karaca 2011), and STS (Heikrujam et al. 2014), ISSR, and RAPD markers (Sharma et al. 2008, 2009), were reported to be applicable in determining plant sex.

The first selected cultivar was ‘Vista’ (Sherbrooke and Haase 1974); other reported cultivars are ‘Keiko’ averaging 1176 g/tree (Purcell and Purcell 1988) and ‘Mirov’ (Yermanos et al. 1968).

The most well-known progress on jojoba cultivation improvement was made in Israel; during a 25-year-long research effort, seed yield improved to 3000–3500 kg/ha, harvest mechanization and agronomic practices were developed, and several clones were selected (Shani 1995; Benzioni 1995). Evaluation of 30 jojoba clones in Israel showed differences in yield, chilling requirements, and morphology (Benzioni et al. 1999).

Jojoba does not transplant well (Gentry 1958). Originally it was cultivated from field-planted seeds. Later, selected clones were propagated through semi-hardwood cuttings (Eed and Burgoyne 2015; Palzkill and Feldman 1993; Prat et al. 1998), grafting (Yoffe 1980), and in vitro shoots (Agrawal et al. 2002; Andressen et al. 2009; Chaturvedi and Sharma 1989; Hegazi et al. 2014; Mohasseb et al. 2009; Singh et al. 2008).

15.2.7 Conservation Status

15.2.7.1 In Situ

Shrubs of this species are still abundant in nature and proliferate easily by seeds. It seems establishing protection on state or federal levels is not needed since wild jojoba stands are not excessively exploited or damaged, and the species has a high resilience to survive in natural conditions. Reports on in situ conservation efforts of *Simmondsia chinensis* in Arizona, California, or Mexico were not found.

15.2.7.2 Ex Situ

In the United States, the USDA-ARS National Arid Land Plant Genetic Resources Unit maintains and distributes 324 accessions as seeds or cuttings for research and cultivar improvement purposes (USDA ARS 2017a). The species is a priority industrial species in Mexico's National Plan of Action for the Conservation of Plant Genetic Resources for Food and Agriculture and 237 accessions, which include 122 wild accessions, are held in the Mexico Conservation Centers Network ex situ collection (see de la Torres et al., Chap. 3, this volume). Botanical gardens in Santa Barbara, CA; San Diego, CA; and the Boyce Thompson Arboretum, AZ, list *S. chinensis* in their planting catalogs (BTA 2017; SBBG 2017; SDBG 2017), and the Botanical Gardens Conservation International database lists 85 accessions (BGCI 2017). Midterm preservation efforts of jojoba using tissue culture were reported (Bekheet et al. 2016; Tyagi and Prakash 2004), but reports of in vitro maintained jojoba collections are not known. In vitro methods have been reported for germplasm distribution (Kumar et al. 2010, 2012). The ex situ germplasm collection of the United States is currently the only source where improved germplasm in the public domain and wild-collected accessions can be obtained. Because of the current interest in using and improving jojoba by many countries having arid land areas, maintaining a diverse collection of jojoba genetic resources is warranted.

15.3 Meadowfoam: A Genus with Unique Oil

15.3.1 Crop Origin and History of Use Worldwide

Meadowfoam (*Limnanthes* sp.) plants got the name from their spectacular appearance during full bloom resembling white-light cream foam. In the 1820s, David Douglas, a Scottish explorer and botanist, collected meadowfoam (*L. douglasii*) during his expedition to Northwestern Pacific regions of America and introduced it as an ornamental to England (Douglas 1836; Gentry and Miller 1965; Purdy and Craig 1987). The species collected by Douglas is still grown in European gardens as an ornamental (Gentry and Miller 1965).

In the 1960s, meadowfoam emerged as a potential new industrial crop as USDA-ARS scientists searched for renewable oil sources in wild, native plant populations in the United States (Earle et al. 1959; Gentry and Miller 1965; Miller et al. 1964; Smith et al. 1960). Seeds of *Limnanthes* plants contain unsaturated long-chain fatty acids ($C_{20–22}$), holding a high level of $\Delta 5$ double bonds; those fatty acids have a high oxidative stability which makes meadowfoam oil applicable in industrial products including lubricants, rubber additives, plasticizers, and cosmetics and in production of biodiesel (Cermak et al. 2013; Isbell et al. 1999; Lardans and Trémoliérs 1991; Miller et al. 1964; Moreau et al. 1981; Moser et al. 2010; Phillips et al. 1971; Purdy and Craig 1987; Smith et al. 1960). Meadowfoam has no known nutritional value for humans.

The total oil content in dry seeds varies from 27 to 35 wt. %, and the oil has more long-chain fatty acids than that of rapeseed (*Brassica napus*) and crambe (*Crambe* sp.) (Pollard and Stumpf 1980). Four long-chain fatty acids *cis*-5-eicosenoic (20:1), *cis*-5-docosenoic (22:1), *cis*-13-docosenoic (erucic acid, 22:1), and *cis*-5-*cis*-13-docosadienoic (22:2) make up almost 95% of the total meadowfoam oil (Smith et al. 1960; Bagby et al. 1961). *Limnanthes* oil may be converted to solid waxes with a high melting point similar to carnauba (*Copernicia prunifera*) and candelilla (*Euphorbia* sp.) and to a liquid wax similar to jojoba (*Simmondsia chinensis*) (Gentry and Miller 1965; Miwa and Wolf 1962). Beyond the United States, meadowfoam industrial oil and its oil-derived products are of interest in New Zealand, Europe (Metzger 2009), Japan (Cheng and Gordon 2000; Knapp and Crane 1999; McKenzie et al. 2011; Van Soest 1993; Wynn-Williams and Logan 1985), and Canada (Small 1995). Meadowfoam oil is currently used only in personal care products (Gunestone 2009; Isbell and Cermak 2001). Processing of several meadowfoam oil derivatives is patented (e.g., Erickson et al. 1990; O'Lenick 1997, 1998, 2001; O'Lenick and Wohlman 2001). Meadowfoam seed meal might be suitable for animal feed (Throckmorton et al. 1981). The seed meal also has phytotoxic characteristics making it applicable as bioherbicide (Intanon et al. 2014; Vaughn et al. 1996; Zasada et al. 2012) and potentially as bioinsecticide due to the presence of ecdysteroid glycosides (Bartlet and Mikolajczak 1989; Stevens et al. 2008; Velasco et al. 2011). Added to soil, it contributes to the soil nutrient profile and influences the microbial biome (Intanon et al. 2015). Meadowfoam flower petals and leaves *(L. douglasii)* contain flavonoids (Parker and Bohm 1975) that might be used as natural additives to nutraceutical and pharmaceutical products. Some species are used as ornamentals. Despite the oil's outstanding characteristics and many research reports on successful production of its useful derivatives, *Limnanthes* still belongs to the "promising new species" oil plant group (Zanetti et al. 2013).

Meadowfoams are winter-spring annual plants that are most productive when sown in fall as a winter crop; temperatures ≥16 °C inhibit seed germination, and temperatures ≤5 °C are detrimental to the plants which shorten the available sowing window (Cole 1974; Ehrensing et al. 1997; Nyunt and Grabe 1987; Toy and Willingham 1966). During hot weather, seed matures almost immediately (Higgins et al. 1971) which might prevent full seed development. The best growing areas are in valleys with abundant rain precipitation. The main meadowfoam cultivation area is in Willamette Valley, Oregon; however, agronomic trials have been performed in California, Maryland, and Alaska (Higgins et al. 1971). In Oregon, cultivation of meadowfoam is rotated with grass seed production (Jolliff and Hoffman 2002), but *Limnanthes* may also be double cropped with rice (Jain et al. 1977). The cultivation acreage varied with years; in 2012, 2200 acres of meadowfoam were grown in the Willamette Valley (Knapp and Crane 1999; Sparling 2015). According to the Agricultural Marketing Resource Center (2012), the largest acreage was planted in 2006–5000 acres; however, Isbell and Cermak (2001) reported a cultivation area of 8000 acres for 1997.

Limnanthes domestication and cultivar development have almost a 50-year history. All cultivars known in the United States have been developed from *L. alba* and released by Oregon State University; these are 'Foamore', 'Knowles', 'Mermaid', 'OMF64', ‘Ross’, ‘Floral’, and ‘Wheeler’ (Calhoun and Crane 1975; Calhoun and Crane 1984; Crane and Knapp 2002; Jolliff et al. 1984; Knapp et al. 2005). ‘Moginie’ is an open-pollinated meadowfoam selection reportedly being used in New Zealand seed trials (Cheng and Gordon 2000). Overproduction of seeds in 1997 that were not purchased by the industry set back meadowfoam cultivation for a few years; also the price of meadowfoam oil is too high to be used in the manufacturing of other cosmetic products (Isbell and Cermak 2001). One of the main factors contributing to the high oil price is the necessity to use bees for pollination. Reported seed yields for experimental settings varied depending on location. Yields up to 1700 kg/ha were reported for California, Maryland, and Oregon when cultivated as a winter-sown annual crop, much less for Alaska where meadowfoam was grown as a spring-sown crop (Higgins et al. 1971; Krebs and Jain 1985). In New Zealand, seed yield varied from 0.6 to 1.6 t/ha depending on the cultivation sites (McKenzie et al. 2011). In production fields, the seed yields are lower. Increasing meadowfoam oil supply will require development of new, improved cultivars with high seed yield, good seed retention, high oil content, self-pollination, and resistance to logging and fruit fly (*Scaptomyza apicalis* Hardy) (Jain and Abuelgasim 1981; Jolliff and Hoffman 2002; Knapp and Crane 1999; Meyers et al. 2010). Cultivars already developed are cross-pollinated and require the use of bees for pollination; in an experimental setting, cross-pollinated cultivars produced higher seed yields than self-pollinated cultivars (Jolliff and Hoffman 2002; Meyers et al. 2010). High-performing cultivars might lower the production costs and make the oil price competitive with fossil materials currently used by the industry.

Limnanthes plants do not have a lot of adversaries. The most serious is a fruit fly (*S. apicalis*) (Knapp and Crane 1999; Panasahatham 2000), also called a meadowfoam fly (*S. apicalis*) (Whaley 2016) that affects buds and crowns causing seed yield reduction. Some tolerance to the insect has been found in breeding material at Oregon State University, but the genetics of the tolerance is not known. A powdery mildew (*Oidium limnanthis*) was observed on potted plants of *L. alba* but was not found in production fields (Putnam and Glawe 2007). Meadowfoam grows well on many types of soil including soils deficiently drained. Temperatures above 16 °C induces secondary seed dormancy (Cole 1974; Ehrensing et al. 1997; Toy and Willingham 1966); hence, warming temperatures will force meadowfoam cultivation to cooler areas. Such changes may also lead to the need for irrigation, as warming is projected to alter precipitation patterns and deplete surface and soil water availability for vernal pools and seepages that are the natural habitats for *Limnanthes* vegetation (Bliss and Zedler 1998; Brooks 2009; Erwin 2009; Pyke 2004).

15.3.2 Crop Wild Relatives, Genepool Classification, Distribution and Habitat, Breeding, and Relative Importance

In natural habitats, meadowfoam plants are low-growing annual herbs, with glabrous to hairy leaves and stems; white, light pinkish, yellow, or a combination of these colors flower petals; and rose or brown anthers and veins, often growing in masses forming dense colorful rings around vernal pools or patches in wet meadows. *Limnanthe*s plants were described by numerous botanists and explorers (Brown 1833; Bayer and Appel 2003; Mason 1952; Ornduff 1969; Ornduff and Crovello 1968). Flowers of all species are hermaphroditic and self-compatible (Kesseli and Jain 1985), and their sexual breeding pattern includes cleistogamy and chasmogamy (Kesseli and Jain 1984; Mason 1952; McNeill and Jain 1983; Ornduff and Crovello 1968).

The family Limnanthaceae, containing two genera, *Limnanthes* R. Br. and *Floerkea* Willd., belongs to the order Brassicales (Rodman et al. 1998). Both genera are endemic to North America (Fig. 15.3) and are closely related; *Floerkea* has three-petaled flowers, whereas *Limnanthes* has five-petaled flowers, with one four-petaled species (*L. macounii* Trel.) (Meyers et al. 2010). Taxonomy of the meadowfoams has been debated over years starting with Brown (1833), including a discussion on separating or combining of the two Limnanthaceae genera. Based on molecular phylogenetic studies, Plotkin (1998) proposed to keep the two genera separate. Mason (1952) identified eight *Limnanthes* species and grouped them into two sections based on petal appearance following fertilization: Inflexae (petals surround a developing seed) and Reflexae (petals reflex from a developing seed). Following nomenclatural rules proposed by the International Code of Botanical Nomenclature, the section name Reflexae should be changed to *Limnanthes* (Meyers et al. 2010; McNeill et al. 2006). In 1969, Ornduff identified a new species *L. vinculans* and placed it into the Reflexae section. Meyers et al. (2010) suggested distinguishing only four *Limnanthes* species in the

Fig. 15.2 Ornamental 2-year-old jojoba (*Simmondsia chinensis* (Link) C. K. Schneid)

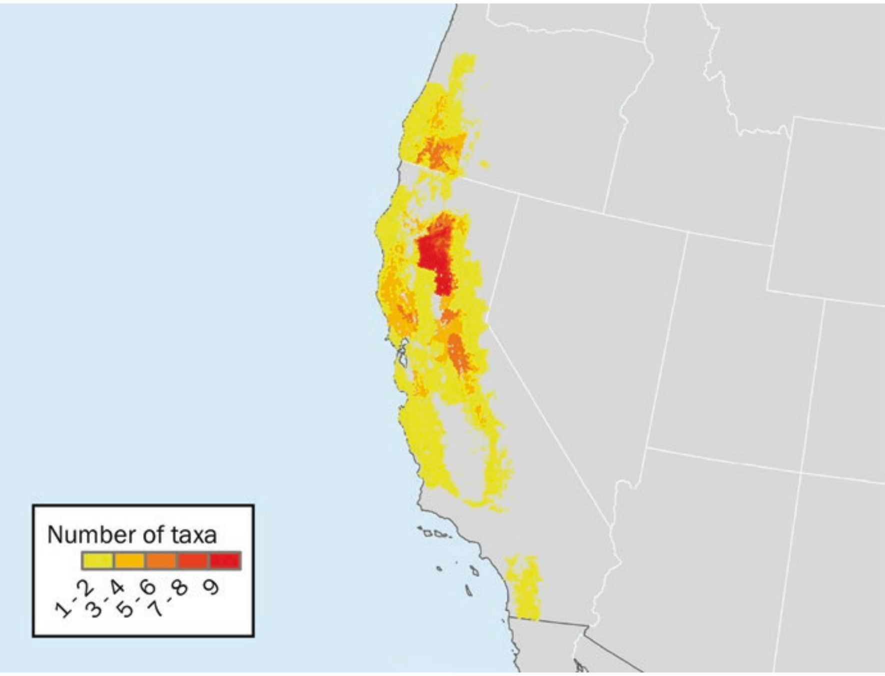

Fig. 15.3 Richness of meadowfoam (Limnanthes R. Br.)

Limnanthaceae genus. Buxton (2013) proposed separating a tetramerous population of *L. douglasii* R. Br. found in San Mateo County, California as a new subspecies *L. d.* subsp. *ornduffii* E. G. (Ornduff's meadowfoam); it is a single population endemic to Moss Beach in San Mateo, California. Buxton claimed that this is an independently occurring relic taxon; the taxon is not yet recognized.

The US National Plant Germplasm System lists ten species including *L.* hybr. which do not have a common name (Table 15.1). Common names of the *Limnanthes* species refer to names of their discoverers, appearance, or location they were found.

Meadowfoam's natural habitats are around vernal pools, seepages, and seasonally wet meadows (Fig. 15.3). In California, they are also found along road edges and occasionally in abandoned agricultural fields (Arroyo 1975). Specific natural *Limnanthes* populations were reported in six locations (Table 15.2). *L. macounii* is the most north-occurring meadowfoam species (Karron 1991).

Wild *Limnanthes* populations have high intra- and interpopulation variability (Kesseli and Jain 1987; Pierce and Jains 1977). Kishore et al. (2004) developed conserved SSR markers that might be useful in genetic conservation, phylogenetics, and ecological studies. Using SSR fingerprints for 61 *Limnanthes* accessions collected in natural habitats in California and Oregon, Donnelley et al. (2008) suggested all

Table 15.1 Scientific and common names of *Limnanthes* species in the National Plant Germplasm System

Scientific name[a]	Common name[b]
The Inflexae section includes	
L. alba Hartw. ex Benth.	White meadowfoam
L. alba subsp. *alba* Hartw. ex Benth.	White meadowfoam
L. alba subsp. *versicolor* (Greene) C.T. Mason	White meadowfoam
L. floccosa Howell	Woolly meadowfoam
L. floccosa subsp. *bellingeriana* (M. Peck) Arroyo	Woolly meadowfoam
L. floccosa subsp. *californica* Arroyo	California meadowfoam
L. floccosa subsp. *floccosa* Howell	Woolly meadowfoam
L. floccosa subsp. *grandiflora* Arroyo[c]	Woolly meadowfoam
L. floccosa subsp. *pumila* (Howell) Arroyo	Woolly meadowfoam
L. gracilis Howell	Slender meadowfoam
L. gracilis subsp. *gracilis*[d] Howell.	Slender meadowfoam
L. gracilis subsp. *parishii* (Jeps.) R. M. Beauch.[e]	Parish's slender meadowfoam
L. montana Jeps.	Mountain meadowfoam
L. vinculans Ornduff	Sebastopol meadowfoam
The Reflexae[f] section comprised of	
L. douglasii R. Br.	Douglas' meadowfoam
L. douglasii subsp. *douglasii* R. Br.	Douglas' meadowfoam
L. douglasii subsp. *nivea* (C.T. Mason) C. T. Mason	Douglas' meadowfoam
L. douglasii subsp. *rosea* (Hartw. ex Benth.) C.T. Mason	Douglas' meadowfoam
L. douglasii subsp. *sulphurea* (C.T. Mason) C. T. Mason	Douglas' meadowfoam
L. striata Jeps.	Foothill meadowfoam
L. bakeri J. T. Howell	Baker's meadowfoam
L. macounii Trel.	Macoun's meadowfoam

[a] US National Plant Germplasm System (USDA ARS 2017b)

[b] Classification of *Limnanthes*; Common Names (USDA Plants 2016)

[c] Also listed as *L. pumila* subsp. *grandiflora* (Arroyo) S.C. Meyers & Chambers (ECOS 2017b, USFW 2017)

[d] Synonymous to *L. alba* Hartweg ex. Bentham subsp. *gracilis* (Howell) Morin; (ITIS report 2017)

[e] Active name: *L. alba* (Jeps.) Morin subsp. *parishii* (Jeps.) Morin (Calflora, Taxon report 4834)

[f] "Reflexae" name should be referred to as *Limnanthes* (McNeill et al. 2006)

Table 15.2 Location of specific natural *Limnanthes* populations

Taxon	Location	Reference
L. alba Hartw. ex Benth.	West of Cascade Mountain ranges, California and Oregon	Arroyo (1975)
L. floccosa Howell	Tehama Co., California and northern part of Jackson Co. Oregon	Arroyo (1975)
L. douglasii R. Br.	Central Valley, California	Runquist (2012)
L. vinculans Ornduff	Laguna de Santa Rosa near Sebastopol, Sonoma Co., California	Ornduff (1969)
L. macounii Trel.	Southeast of Vancouver Island, Canada	Arroyo (1975), Catling and Porebski (1998), Jain (1994), and Ornduff (1969)
L. montana Jeps.	Southwestern USA, California	USDA ARS (2017b)

evaluated accessions contained unique alleles. The highest level of genetic diversity was observed in *L. alba*, *L. floccosa*, and *L. douglasii*. According to Jolliff et al. (1981), those species have the greatest potential for novel cultivar development. Evaluation of seed and selected plant characteristics of 21 *L. alba* accessions collected in California also demonstrated a large diversity within the species (Jenderek and Hannan 2009). Both sets of genetic resources evaluated by Donnelley et al. (2008) and Jenderek and Hannan (2009) are maintained at the National Arid Land Plant Genetic Resources site, USDA-ARS, Parlier, CA (2016).

Wild meadowfoam genotypes are essential for development of cultivars with characteristics desired by growers and the meadowfoam oil industry. They are the potential gene source for increasing seed yield and developing self-pollinating breeding material. Genotypes with upright, short stems and uniform seed maturing time might support the development of cultivars for mechanical seed harvest of the crop. The ability of wild meadowfoam plants to grow on poorly drained soils might give rise to a crop that can be cultivated on marginal semi-marsh lands.

15.3.3 Conservation Status

15.3.3.1 In Situ

L. floccosa subsp. *californica*, *L. floccosa* subsp. *grandiflora* (*L. pumila* subsp. *grandiflora*), and *L. vinculans* are listed as endangered by the US Fish and Wildlife Service (CDFW 2017a, c; USFW 2017). In California, *L. douglasii* subsp. *sulphurea* and *L. alba* subsp. *parishii* are listed as endangered and *L. bakeri* as rare (Calflora 2017; Dole and Sun 1992; Meyers et al. 2010; CDFW 2017a, c); *L. floccosa* subsp. *pumila* is on the Oregon's threatened list (Oregon Department of Agriculture, Dwarf meadowfoam 2017).

Limnanthes taxa listed as "endangered," "threatened," or "rare" on federal or state levels are legally protected in their endemic habitats, and germplasm collection from such populations requires obtaining a collection permit from the CDFW Scientific Collecting Permits (2017b). Conservation of the diversity in these species is dependent on adequate protection of their habitats. In the last 50–100 years, California lost an estimated 88% of vernal pool habitat due to urban sprawl, grazing, and land conversion to cultivation (Barry 1998; Holland 1978; Jensen 2011). Disappearing vernal pools is also reported for Agate Desert, Oregon, the habitat for *L. floccosa* subsp. *grandiflora* (Wille and Petersen 2006). A permanent protection of remaining vernal pools is imperative for conservation of natural *Limnanthes* vegetation environments.

Fragmentation and geographical isolation of populations of many species contribute to low genetic diversity, low heterozygosity, and high fixation indices (Sloop et al. 2011). Increased knowledge of population size, breeding patterns, behavior of pollination vectors, seed dispersal mechanisms, and molecular markers will provide guidelines for conservation and reintroduction of known genotypes into the vanishing plant communities in their habitats. Such recommendations have been reported for the endangered *L. floccosa* subsp. *californica* (Sloop et al. 2011, 2012; Warne and

Sloop 2009) and *L. vinculans* (Ayres et al. 2008; Sloop et al. 2012; Sloop and Ayres 2009). Significant current conservation efforts are also being made by the US and California Fish and Wildlife Departments as well as the US Department of the Interior and the Oregon Fish and Wildlife Office (US Department of the Interior 2017). Scientific information on the natural habitats, plant communities, and conservation needs is published by scientists from the University of California, San Francisco Joint Venture, and others (CDFW 2017a, b; Griggs and Jain 1983; Sloop et al. 2012). Conservation of in situ *Limnanthes* diversity is not easy due to limited resources; open, physically unprotected growing areas; and conflicting interests of urban/demographic/agricultural developments, but maintaining the diversity is necessary for current and future purposes; the beauty and the economic potential of natural meadowfoam populations are irreplaceable. Further, climatic temperature increase may impact wild *Limnanthes* populations by inducing seed dormancy and preventing their germination. Urban development and grazing represent additional real threats to the natural habitats of meadowfoam (Pyke and Marty 2005).

15.3.3.2 Ex Situ

A collection of 78 meadowfoam accessions is preserved in Parlier, CA, at the USDA ARS National Arid Land Plant Genetic Resources Unit (NALPGRU), a genebank of the NPGS (Table 15.3).

Table 15.3 *Limnanthes* taxa and number of accessions preserved in the NPGS collection

Taxon	No. of accessions preserved at NALPGRU, CA
L. alba Hartw. ex Benth	21
L. alba subsp. *alba* Hartw. ex Benth	10
L. alba subsp. *versicolor* (Greene) C.T. Mason	3
L. bakeri J. T. Howell	2
L. douglasii R. Br.	3
L. douglasii subsp. *douglasii* R. Br.	2
L. douglasii subsp. *nivea* (C.T. Mason) C.T. Mason	7
L. douglasii subsp. *rosea* (Hartw. ex Benth.) C.T. Mason	6
L. floccosa Howell	9
L. floccosa subsp. *bellingeriana* (M. Peck) Arroyo	2
L. floccosa subsp. *grandiflora* Arroyo	1
L. floccosa subsp. *pumila* (Howell) Arroyo	2
L. gracilis Howell	2
L. gracilis subsp. *gracilis* Howell	2
L. gracilis subsp. *parishii* (Jeps.) R. M. Beauch	1
L. hybr.	1
L. montana Jeps.	1
L. spp.	1
L. striata Jeps.	2

Regeneration of these accessions is done in isolation cages with and without pollination vectors. The origin of the genetic resources is documented; plants are evaluated and characterized and upon request freely distributed to breeders and researchers. Evaluation data are available through research publications and germplasm characterization documented on the Germplasm Resources Information System (USDA ARS 2017a). Evaluation and characterization of the collection are the bases for informed meadowfoam germplasm utilization. Regenerated seed is backed up at the USDA-ARS, National Laboratory for Genetic Resources Preservation in Fort Collins, CO. Although the USDA collection is considered to be relatively diverse, inclusion of populations from habitats not yet collected would add diversity to the already existing meadowfoam collection and provide a broader gene pool to future users and possible future restoration (Figs. 15.4, 15.5, 15.6, 15.7, 15.8, and 15.9).

Oregon State University, Corvallis, OR, also holds a large breeding and crop wild relative collection of *Limnanthes* (Kling 2017, personal communication). Conservation efforts at Rancho Santa Ana Botanic Gardens, CA include establishment

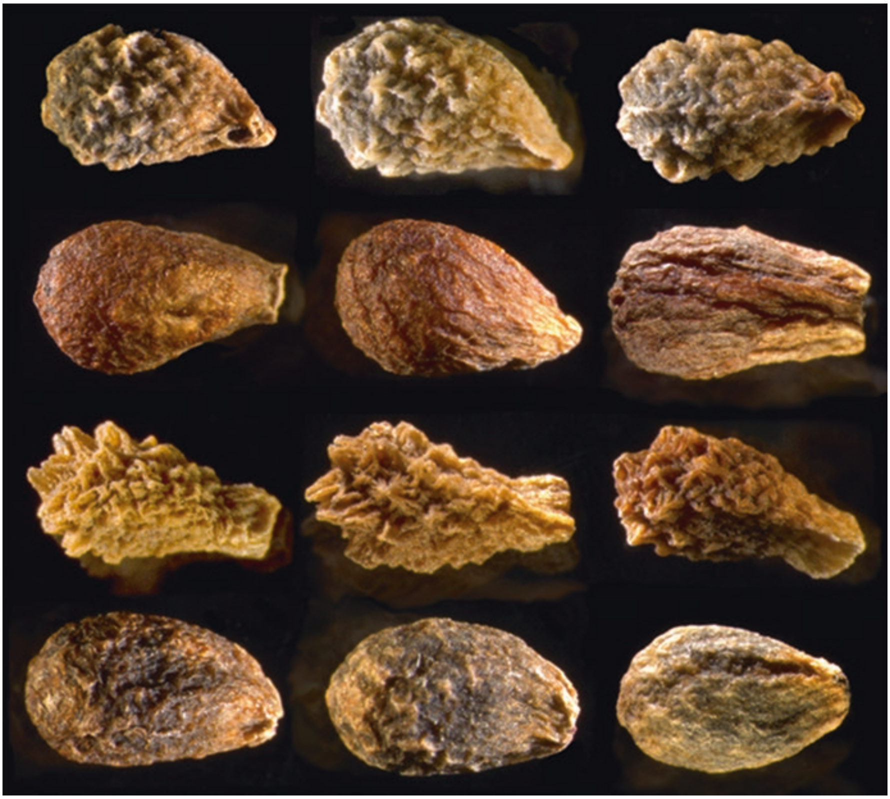

Fig. 15.4 Meadowfoam (*Limnanthes* R. Br.) seed. Top to bottom: *L. alba* Hartw. ex Benth., *L. douglasii* R. Br., *L. floccosa* Howell, and *L. gracilis* Howell (*L. a.* subsp. *gracilis*). (Photo: J. Donald, NALPGRU, USDA-ARS, Parlier, CA)

Fig. 15.5 Nuttles *of L. alba* Hartw. ex Benth., PI 374793. (Photo: NALPGRU, USDA-ARS, Parlier, CA)

Fig. 15.6 Flower of *L. alba* Hartw. ex Benth., PI 374791. (Photo NALPGRU, USDA-ARS, Parlier, CA)

Fig. 15.7 Flowers of *L. striata* Jeps., PI 283728. (Photo, NALPGRU, USDA-ARS, Parlier, CA)

Fig. 15.8 Flowers of *L. gracilis* subsp. *gracilis* Howell., PI 283723. (Photo NALPGRU, USDA-ARS, Parlier, CA)

of new vernal pools and inoculation with seeds of tested meadowfoam genotypes similar to the natural ones. Botanical gardens play an important role in meadowfoam conservation by displaying the *Limnanthes* flower beauty to the broad public, maintaining diversity, seed banking, research, and educational activities.

Fig. 15.9 Flower of *L. douglasii* subsp. *rosea*, PI 283716. (Photo NALPGRU, USDA-ARS, Parlier, CA)

15.4 Lesquerella

15.4.1 Origin of the Crop and Brief History of Use Worldwide

Lesquerella [*Physaria fendleri* (A. Gray) O'Kane & Al-Shehbaz, synonym *Lesquerella fendleri* (A. Gray) S. Watson], is an oilseed species in the mustard family (Brassicaceae). It is native to the Southwestern United States and Northern Mexico where it is best suited to be integrated into existing crop production systems as a winter annual. The species produces about 30% seed oil with lesquerolic fatty acid predominating and oleic and linolenic acids contributing minor components to its seed oil (Barclay et al. 1962; Dierig et al. 1996a, b; Salywon et al. 2005; Wang et al. 2010). As a source of hydroxy fatty acids, it can provide important raw materials for manufacturing industrial lubricants, plastics, cosmetics, and pharmaceuticals (Roetheli et al. 1991; Isbell et al. 2006). The distinguishing characteristic of this species compared to other taxa in the genus is the more favorable agronomic characteristics and high seed productivity.

Lesquerella is considered a new crop since there is currently no commercial production and as domestication and formal breeding research and development activities started in the 1980s (Van Dyne 1997). The initial utility of lesquerella species was identified in the 1950s during a large national oilseed screening program of over 200 plant families growing in native habitats initiated by the New Crops Research Branch of the US Department of Agriculture (USDA)-Agricultural Research Service (ARS) (Barclay et al. 1962; Dierig et al. 1993). The US Government was interested in finding unusual kinds of oils that would not compete with vegetable oils and finding a domestic species that could be grown locally instead of importing petroleum-based commodities (Jones and Wolff 1960; Princen 1983). Of the many plant species analyzed, species of *Physaria* (Nutt. ex Torr. & A. Gray) A. Gray and *Paysonia* O'Kane & Al-Shehbaz (then all included in *Lesquerella*) received attention due to fatty acid composition that is similar to ricinoleic acid from castor oil but without the highly toxic seed meal. Castor oil is mostly imported to the United States (Brigham 1993). The hydroxy fatty acid present in *Physaria* is lesquerolic acid (14-hydroxy-eicosa-11-enoic, 14-OH-20:1) with densipolic acid (12-hydroxy-octadec-cis-9,15-enoic, 14-OH-18:2) in *Paysonia* and auricolic acid in *Paysonia auriculata* (Engelm. & A. Gray) O'Kane & Al-Shehbaz (14-hydroxy-eicos-cis-11,17-enoic, 14-OH-20:2). The hydroxy fatty acid content in the seed oil of lesquerella and related species is between 45 and 55% (Barclay et al. 1962; Salywon et al. 2005; Dierig and Ray 2009). Lesquerolic acid is two carbons longer than the ricinoleic acid (12-hydroxy-octadeca-9-enoate, 12-OH-18:1) in castor oil, while densipolic and auricolic acids have an additional unit of unsaturation (double bond), and auricolic acid also is two carbons longer (Engeseth and Stymne 1996). The chemical similarity of these fatty acids to ricinoleic acid allows it to be used as replacements for castor oil, while their chemical differences may lead to novel products. To date castor oil has been the major commercial source of hydroxy fatty acids (Smith et al. 1998).

Lesquerella seed oil is suitable for producing triglyceride estolides that have numerous applications in industry and can be used in biodegradable lubricants for superior low-temperature properties (Cermak et al. 2006; Cermak and Evangelista 2013). For example, lesquerella oil additives in ultralow sulfur diesel (ULSD) have been demonstrated to increase lubricity (Moser et al. 2008). Other value-added products from lesquerella seed have also shown potential. The seed gum has applications in the food industry as a thickener (Holser et al. 2000). In addition to having industrial application, the high protein content of lesquerella was found to be a good additive to animal and poultry feed (Carlson et al. 1990). Feeding dehulled lesquerella seed to chickens resulted in a slightly better feed conversion, and the additive had no negative effect (Beier et al. 2014).

There were previously two public crop germplasm improvement programs on *lesquerella* that focused on improving the agronomy and yield of the crop. The first was a program of the University of Arizona under D.D. Rubis which operated from 1966 to 1978 and the second at the USDA-ARS US Water Conservation Laboratory (now USDA-ARS Arid Land Research Center) by A.E. Thompson and D.A. Dierig, from 1984 to 2010 (Thompson and Dierig 1994). Germplasm from Dr. Rubis's program was transferred to the USDA. Currently, there are several advanced germplasm lines developed by the USDA, with improved seed and oil yield as well as abiotic stress tolerance. Plants with 45% oil content have been obtained from breeding activities (Dierig et al. 2006a, b). Small yield trials as well as observations from farmer fields showed that the improved germplasm yields in excess of 2000 kg/ha (Wang et al. 2010). In terms of suitable production areas, the US southwestern region was reported to be where the highest yields of current germplasm were obtained. Agronomic trials have also been conducted in other areas such as Oregon, Northern

Mexico, Canada, Argentina, and parts of Europe (Roseberg 1993; Rodríguez Garcia et al. 2007; Windauer et al. 2004; EuroBioRef 2015). However, the yield and performance of the existing germplasm grown in these environments were poorer. Continued research activities and the development of germplasm lines that are more adapted to these regions will help overcome these problems and establish lesquerella along with other industrial crops that are adapted to broader areas.

As a new crop, lesquerella does not have major issues with diseases and insect pests. One important insect pest in arid land crops, *Lygus hesperus* Knight, which feeds on cotton, alfalfa, and many vegetable species, has been studied for its effect on lesquerella. Naranjo and Stefanek (2012) found that *Lygus* insects did not significantly impact lesquerella agronomic performance. The insects feed mostly on flowers, leaves, and petioles, but the damage is not as much as compared to other new industrial crops (Hagler et al. 2016). Studies to determine potential insect and pest problems on large acreage still need to be conducted. Due to the early-spring flowering season of lesquerella, Naranjo et al. (2011) previously noted it may harbor significant populations of *Lygus* as well as their natural enemies and these may affect the pest dynamics across multiple crops. There were also important fungal pathogens found in lesquerella including *Helminthosporium namum* Nees, *Phoma punctiformis* Desmazières, *Phymatotrichum omnivorum* Duggar, and *Puccinia aristidae* Tracy (Duke 1983).

The influence of warmer temperatures expected with climate change has not been researched within lesquerella. Higher temperatures during the growth period were observed to positively influence root traits (Cruz et al. 2012a), as well as to increase biomass and seed yield (Dierig et al. 2006a). There have been no studies reporting neither the response of lesquerella to other environmental factors such as increased carbon dioxide levels nor the effects of extreme temperature on pollination. Since lesquerella is an outcrossing species with self-incompatibility mechanisms, the abundance of pollinators and pollen viability are critical for successful seed production (Mitchell 1997; Hatfield and Prueger 2015).

15.4.2 *Crop Wild Relatives, Genepool Classification, Distribution and Habitat, Breeding, and Relative Importance*

Lesquerella is an herbaceous short-lived perennial plant also known as Fendler's bladderpod, yellowtop, desert mustard, and cloth of gold. The wild populations of *P. fendleri* are usually found on limestone outcrops, gravels, sandy washes, rocky slopes, shallow drainage areas, and roadcuts in the plains and desert regions in the US Southwest (Arizona, New Mexico, and Texas) as well as Coahuila, Chihuahua, and Nuevo Leon, Mexico (Rollins 1993) (Fig. 15.10). These populations often depend on soil moisture and are usually found among mixed, sparse vegetation with predominance among creosote habitats (Cabin and Marshall 2000). Plants in native populations were found in areas that range 315–1643 m^2 with plant density of

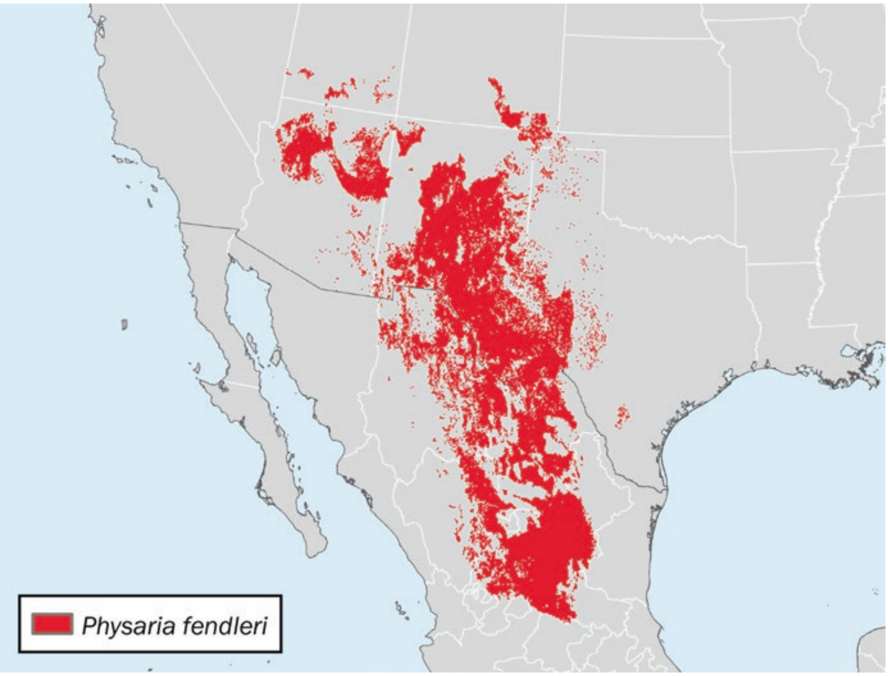

Fig. 15.10 Geographic distribution of lesquerella [*Physaria fendleri* (A. Gray) O'Kane & Al-Shehbaz] based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

1–12 plant/m^2 (Cruz et al. 2013b). The number of plants in native populations varies according to changes in short-term climatic and edaphic factors that may influence seed production and germination. There have been collections of *P. fendleri* germplasm from Arizona, Colorado, New Mexico, Texas, and southern Utah as well as from provinces in Mexico (Rollins and Shaw 1973; Dierig et al. 1996b; Salywon et al. 2005). Currently, there are ~106 *Physaria* species. Among the recently discovered species include the Navajo bladderpod (*P. navajoensis*) (O'Kane) O'Kane & Al-Shehbaz found in New Mexico and *P. scrotiformis* O'Kane which is a high-elevation species in Colorado (O'Kane and Al-Shehbaz 2002; O'Kane 1999, 2007). Since lesquerella is a new crop, the utilization of the other wild relatives has not been fully researched.

Lesquerella flowers between March and May depending on the elevation and also after suitable rain events in the summer and fall. The seed dormancy in wild populations of lesquerella may persist for up to 3 years, allowing individuals from different generations to be represented in the soil seed bank (Cabin et al. 1998). The population genetic structure resulting from this event may change every season, as various seed genotypes are believed to have accumulated in soil seed banks ensuring genetic diversity (Cabin 1996). This seed dormancy in advanced germplasm lines is not as pronounced as in wild populations; however seed pretreatment with gibberellic acid was found desirable to increase germination, eliminate the light requirement, and allow for synchronous germination during plant propagation and field plantings (Cruz et al. 2012b; Puppala and Fowler 2002).

Lesquerella is easily recognized by their glabrous siliques and fused trichomes which set the species apart from other *Physaria*. Plants have an indeterminate growth habit with densely pubescent silvery leaves that grow to about 40 cm high. The yellow flowers of lesquerella have petals that are 8–12 mm long and sometimes observed with orange guidelines (Rollins 1993). The flowers are hermaphroditic and self-incompatible. In natural populations, pollinations are accomplished by a wide array of pollinator generalists that are foraging for nectar and pollen. Successful seed set was found to be related to plant density, with higher densities positively correlated to the number of seeds found per fruit (Roll et al. 1997).

Several wild *Physaria* species are on the federal and state list of imperiled and vulnerable species, as well as some with habitats protected under the Endangered Species Act (Table 15.4). Only four of these critical species have representative accessions in the NPGS to date. There is limited information on the genepool clas-

Table 15.4 *Physaria* species in decline that may be in danger of extinction. Figure 15.11 shows a map of US NPGS and Mexico lesquerella [*Physaria* (Nutt. ex Torr. & A. Gray) A. Gray] collection sites

Scientific name	Common name	Global rank	State rank	State	NPGS accessions
P. alpina Rollins	Avery Peak twinpod	G2	S2	CO	0
P. aurea (Wooton) O'Kane & Al-Shehbaz	Golden bladderpod	G2	S2	NM	0
P. bellii G. A. Mulligan	Bell's twinpod	G2, G3	S2, S3	CO	0
P. calcicola (Rollins) O'Kane & Al-Shehbaz	Rocky Mountain bladderpod	G3	S3	CO	0
P. congesta (Rollins) O'Kane & Al-Shehbaz	Dudley Bluffs bladderpod	G1	S1	CO	0
P. didymocarpa subsp. *didymocarpa* (Hook.) A. Gray	Common twinpod	G5	S1	WA	0
P. dornii Lichvar	Dorn's twinpod	G1	S1	WY	
P. douglasii subsp. *tuplashensis** (Rollins et al.) O'Kane & Al-Shehbaz	White Bluffs bladderpod	G4	S2	WA	1
*P. filiformis** (Rollins) O'Kane & Al-Shehbaz	Missouri bladderpod	G3	–	AR, MO	0
*P. globosa** (Desv.) O'Kane & Al-Shehbaz	Short's bladderpod	G2	S1	IN, KY, TN	0
P. grahamii C. V. Morton	Graham's twinpod	G1	S1	UT	0
P. iveyana O'Kane, K.N. Sm. & K.A. Arp		G1	S1	NM	0

(continued)

Table 15.4 (continued)

Scientific name	Common name	Global rank	State rank	State	NPGS accessions
P. navajoensis (O'Kane) O'Kane & Al-Shehbaz	Navajo bladderpod	G2	S1	NM	0
*P. obcordata** Rollins	Piceance twinpod	G1, G2	S1, S2	CO	0
P. pallida (Torr. & A. Gray) O'Kane & Al-Shehbaz	White Bladderpod	G1	S1	TX	5
P. parviflora (Rollins) O'Kane & Al-Shehbaz	Piceance bladderpod	G2	S2	CO	0
P. parvula (Greene) O'Kane & Al-Shehbaz	Pygmy bladderpod	G3?	S2	CO	0
P. pruinosa (Greene) O'Kane & Al-Shehbaz	Pagosa bladderpod	G2	S1, S2	CO, NM	0
P. pulvinata O'Kane & Reveal	Cushion bladderpod	G1	S1	CO	0
P. rollinsii G. A. Mulligan	Rollins' twinpod	G1	S1	CO	0
P. scrotiformis O'Kane	West silver bladderpod	G1	S1	CO	0
P. subumbellata (Rollins) O'Kane & Al-Shehbaz	Parasol bladderpod	G3	S2	CO	0
P. thamnophila (Rollins & E. A. Shaw) O'Kane & Al-Shehbaz	Zapata Bladderpod	G1	S1	TX	1
P. vicina J.L. Anderson, Reveal & Rollins	Good- neighbor bladderpod	G2	S2	CO	0
P. stylosa Rollins	Duchesne River twinpod	G1	S1	UT	0
P. tumulosa (Barneby) O'Kane & Al-Shehbaz	Kodachrome bladderpod	G1	S1	UT	0
P. vitulifera Rydb.	Rydberg twinpod	G3	S3	CO	1

Notes: G1/S1, critically imperiled; G2/S2, imperiled; G3/S3, vulnerable; G4/S4, apparently secure; G5/S5, secure Information compiled from CNHP (2017), ECOS (2017a, b), IDNR (2017), NatureServe (2017), TPW (2017), US Fish and Wildlife Service (2015a, b), USDA-ARS (2017a), and WNHP (2015). Asterisks denote species protected under the Endangered Species Act of 1973

sification of *Physaria*. The outcrossing rate in lesquerella is 86–89% (Dierig et al. 1996a). In Colorado, naturally occurring hybrids between the rare *P. bellii* G. A. Mulligan and more common congener *P. vitulifera* Rydb. have been found, which initiated a study to look into the threat of gene swamping (Kothera et al. 2007). Though some groups of *Physaria* can easily cross-pollinate, Dierig and Ray (2009) noted that hybridization among some species found in the Western United States was challenging and necessitated ovule culture and colchicine treatments to overcome the sporophytic incompatibility system. Bud pollination is used in *P. fendleri* to overcome self-incompatibility. It can be speculated that these species comprise those in the secondary genepool. The species of *Paysonia* found in the Eastern United States do not have the same issue, and interspecific hybridization is common. The genus *Paysonia* is sister to *Physaria*, yet DArT (Diversity Arrays Technology) markers only shared about 70% similarity between the genera (Cruz et al. 2013a). Several *Paysonia* species have desirable characters that maybe of interest due to the densipolic type of HFA in their seed oil. Rollins (1988) and Rollins and Solbrig (1973) reported that there was successful interspecies hybrid swarm among *P. stonensis* (Rollins) O'Kane & Al-Shehbaz, *P. densipila* (Rollins) O'Kane & Al-Shehbaz, *P. lescurii* (A. Gray) O'Kane & Al-Shehbaz, *P. lyrata* (Rollins) O'Kane & Al-Shehbaz, and *P. perforata* (Rollins) O'Kane & Al-Shehbaz also called *Lesquerella* 'Kathryn'. The hybrids obtained showed a range of flower color, silique, and trichome characteristics relative to the parents (Rollins and Solbrig 1973). Outcrossing in these auriculate-leaved *Paysonia* species found in Tennessee and Alabama is obligated with the hybrids also exhibiting self-incompatibility (Rollins 1988).

Intergeneric hybridization of lesquerella to *Brassica napus* L. has been investigated by conducting protoplast fusion. Hybrid plants were obtained which were fertile and able to cross-pollinate to *B. napus* (Skarzhinskaya et al. 1996, 1998). In addition, cross-fertilization between *B. napus* and *Physaria fendleri* using the latter as a pollen source resulted in F1s with higher levels of linoleic, linolenic, eicosanoic, and erucic acids than the *B. napus* parents. The wide crosses resulted to chromosome elimination and doubling as well as genomic reorganization in *B. napus* (Du et al. 2008). These results indicate the possible utility of lesquerella to enhance traits in other Brassica oilseeds.

15.4.3 Wild Utilized Species

Introgression of desirable traits from *Physaria* and *Paysonia* species to lesquerella was a focus of the USDA breeding program (Dierig and Ray 2009). Among the important *Physaria* sister species already utilized include *P. lindheimeri* (A. Gray) O'Kane & Al-Shehbaz and *P. gracilis* (Hook.) O'Kane & Al-Shehbaz which were found to have higher lesquerolic acid content with 89% and 60–70%, respectively (Buchanan and Duke 1981; Dierig et al. 1996b; Salywon et al. 2005). These species have the same chromosome number as lesquerella ($2x = 2n = 12$) (Dierig and Ray 2009). Successful production of hybrids from these species as well as *P. pallida* has been reported (Dierig et al. 1996a, b, 2004) with some hybrids, showing elevated levels of lesquerolic acid that were 20% greater than *P. fendleri*. However, most hybrids were sterile or had low seed production and had low seedling vigor.

Two species, *P. pallida* (Torr. & A. Gray) O'Kane & Al-Shehbaz and *P. mcvaughiana* (Rollins) O'Kane & Al-Shehbaz, have been identified to exhibit self-fertility which could increase seed yield under commercial production. Lesquerella seed yield depends on pollinator activity (Roll et al. 1997; Mitchell 1997). With self-fertile germplasm, the requirement for insect pollinators may be circumvented reducing production cost and attaining consistent yield (Dierig and Ray 2009). As pollinators are very important in lesquerella, a detailed study of its floral structure was made to understand floral nectary structure and distribution of gynoecial stomata. Results indicated that the flower morphology ensures insect-assisted cross-pollination and that monitoring these structures for changes during the breeding selection activities was recommended (Kehl and Erickson 1995).

Another important trait that needs study is yield and productivity at colder regions. The importance to derive adaptation when growing the crop at these regions at higher elevations was investigated in Arizona and in Argentina. It was determined that *P. pallida* and *P. angustifolia* (Nutt.) O'Kane & Al-Shehbaz are more productive when planted at higher elevations (Dierig et al. 2006a, b; Ploschuk et al. 2003). *P. angustifolia* was recommended as an alternative crop in the Chubut River Valley, Patagonia, Argentina, where the field testing was conducted. Another species, *P. mendocina*, native to the Patagonia and Monte regions of Argentina was also evaluated for suitability in cold arid growing regions (Ravetta and Soriano 1998; Windauer et al. 2004).

During phenotypic characterization of the *Physaria* and *Paysonia* germplasm collection, several species were identified to have potential to be directly utilized as ornamentals. This germplasm represents *Physaria* species (*P. mcvaughiana*, *P. mexicana* (Rollins) O'Kane & Al-Shehbaz, *P. ovalifolia* (Rydb. ex Britton) O'Kane & Al-Shehbaz, *P. pallida*) and *Paysonia* (*P. perforata*, *P. stonensis*) reported to have plants that show white flowers, as well as plants that show full bloom for a longer period (*Physaria*, *P. argyraea* (A. Gray) O'Kane & Al-Shehbaz; *Paysonia*, *P. grandiflora* (Hook.) O'Kane & Al-Shehbaz, *P. lasiocarpa* (Hook. ex A. Gray) O'Kane & Al-Shehbaz) (Jenderek 2006). As more genetic and genomic information are obtained in *Physaria*, the significance of native genes and genomic sequences should become evident. To date, a *P. fendleri* promoter *LfKCS3* has been identified useful for modifying the levels of saturated fatty acids in cells of biotech canola plants (Gachotte et al. 2014).

15.4.4 Conservation Status

15.4.4.1 In Situ

The federal and state conservation programs include several *Physaria* species as indicated in Table 15.4. Critical habitat areas have been designated by the US Department of the Interior for *P. globosa* (Desv.) O'Kane & Al-Shehbaz and *P. douglasii* subsp. *tuplashensis* (Rollins et al.) O'Kane & Al-Shehbaz in 2014 and 2013, respectively (ECOS 2017a, b). For the other imperiled and endangered species, respective state agencies monitor and track the status of wild populations. Among the major threats to populations in *Physaria* natural habitat include grazing, impact of nonnative species, soil erosion, wildfires, and damage from off-road vehicles (O'Kane 2006). Small fragmented populations are also more susceptible to genetic erosion due to genetic drift. The relative diversity among the species listed in Table 15.4 is not known, but in lesquerella there is substantial genetic diversity being maintained within the soil seed bank. Seed dormancy influences the number of plants that will germinate along with other edaphic factors (Cabin et al. 1998).

In Colorado, best management practices to populations of *P. obcordata* Rollins, *P. congesta* (Rollins) O'Kane & Al-Shehbaz, and *P. bellii* G. A. Mulligan (endemic in the state) have been formulated to reduce the impact of road maintenance and revegetation activities. Special management areas have been created, as well as plans to control noxious weed species that occupy habitat areas of *P. bellii* (Panjabi and Smith 2014). The suggested actions for *P. obcordata* and *P. congesta* conservation included more intensive coordination with private landowners and energy companies, who conduct activities in areas near natural habitats (Panjabi and Neely 2010). In *P. parvula* (Greene) O'Kane & Al-Shehbaz, although no protected federal area has been designated, a technical conservation assessment has been conducted. *P. parvula* has a very limited distribution occupying windswept and barren mountain slopes at elevations of 6000–8900 ft. in Colorado, Wyoming, and Utah (O'Kane 2006). Climate change is hypothesized to impact *Physaria* species in their natural habitat, especially those adapted to colder habitats such as *P. parvula* as not only the temperature and rainfall patterns may change but the timing availability of pollinators may not coincide with plant flowering (Grossman 2004; Scaven and Rafferty 2013).

In Texas, monitoring of habitats of *P. thamnophila* (Rollins & E. A. Shaw) O'Kane & Al-Shehbaz at the Tamaulipan thornscrub near the Rio Grande has been conducted routinely for 6 years to develop a management plan. It was determined that there were more plants on areas that were brush-cut, suggesting that the plant litter helps prevent soil erosion allowing the seedlings of this species to get established (Fowler et al. 2009). A recent review (US Fish and Wildlife Service 2015b) listed ten elements of occurrence of *P. thamnophila* in two counties in Texas. Among the future plans to assist recovery is to conduct public outreach activities to increase awareness on this species, as well as seed collection and subsequent reintroduction to suitable protected habitats creating designated refugia (Fig. 15.11).

15.4.4.2 Ex Situ

Lesquerella germplasm is being conserved in the United States by the NPGS and in the United Kingdom by the Millennium Seed Bank Partnership. A total of 238 accessions of 34 *Physaria* species are under ex situ conservation (Table 15.4) (Genesys 2017). The NPGS has 214 of these accessions available for distribution (USDA ARS 2017b) (Fig. 15.12).

The *Physaria* germplasm and related *Paysonia* species at the NPGS have been fully characterized for oil and fatty acid content (Jenderek et al. 2009) as well as morphological and phenological traits (Salywon et al. 2005; Dierig et al. 1995). These characterization and evaluation data are publically available online at the USDA germplasm database (USDA ARS 2017a). There are a total of 36 descriptors encompassing oil composition, growth, and morphological, phenological, and production traits.

In addition to morphological characterization, the *Physaria* collection along with a limited number of *Paysonia* germplasm at USDA has been analyzed using molecular markers. Analysis of genetic diversity has been conducted on the collection using 2833 DArT and 27,748 DArT-seq markers (Cruz et al. 2013b). Two distinct genetic

Fig. 15.11 A native population of lesquerella [*Physaria* (Nutt. ex Torr. & A. Gray) A. Gray] found on a roadside to Ft. Davis, Texas

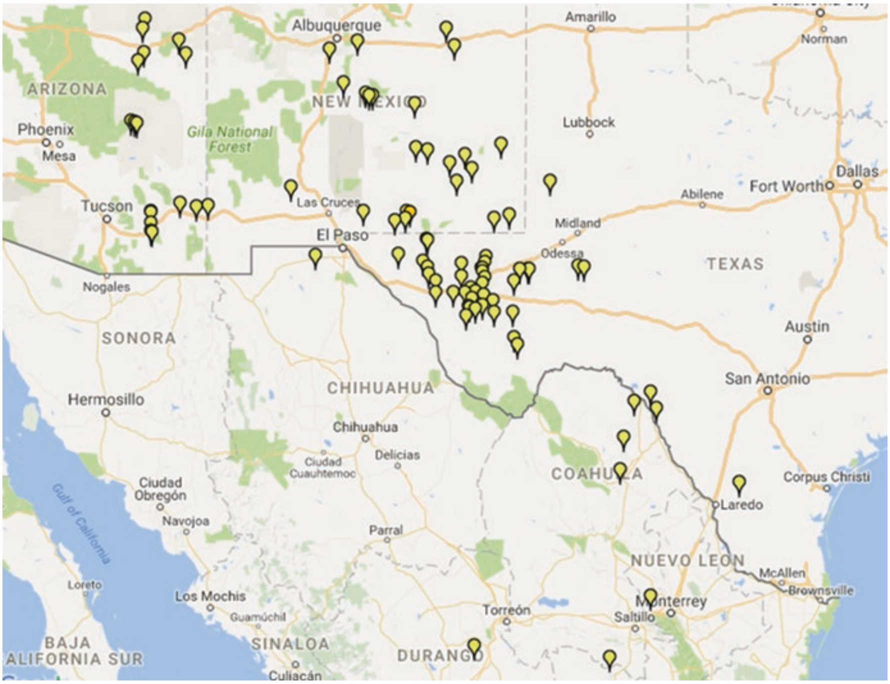

Fig. 15.12 US NPGS collection sites of lesquerella [*Physaria* (Nutt. ex Torr. & A. Gray) A. Gray] across three US states and four provinces in Mexico

clusters in the *P. fendleri* collection were identified separating germplasm from Texas and Mexico. The study also found that there was high genetic similarity among the two *P. pallida* accessions included in the study, suggesting that a follow-up analysis focusing on underrepresented species in the collection might be necessary.

In 2010, several native sites in the US Southwest were revisited to collect seeds (Cruz et al., 2013a) (Fig 15.13). During the collecting trips, several sites in New Mexico and Texas were found to be nonexistent. However, because of highly variable environmental factors, the dynamics of population establishment is expected to change depending on whether the year was favorable for growth or not. In addition to genebank-stored seeds, there are a few *Physaria* species that are being maintained as living collections in botanical gardens. The Denver Botanic Gardens have plants of *P. alpina*, *P. bellii*, *P. eburniflora* Rollins, and *P. subumbellata* (Denver Botanic Garden 2017). The Desert Botanical Garden in Phoenix, AZ, also has accessions of *P. fendleri*, *P. gordonii* (A. Gray) O'Kane & Al-Shehbaz, and *P. tenella* (A. Nelson) O'Kane & Al-Shehbaz stored as seeds with some plants grown in the gardens in the past (Desert Botanical Garden 2017). Continued utilization of germplasm as well as sustained efforts to commercialize *P. fendleri* and the other promising *Physaria* species will help ensure a sustainable source of domestic raw material (Table 15.5).

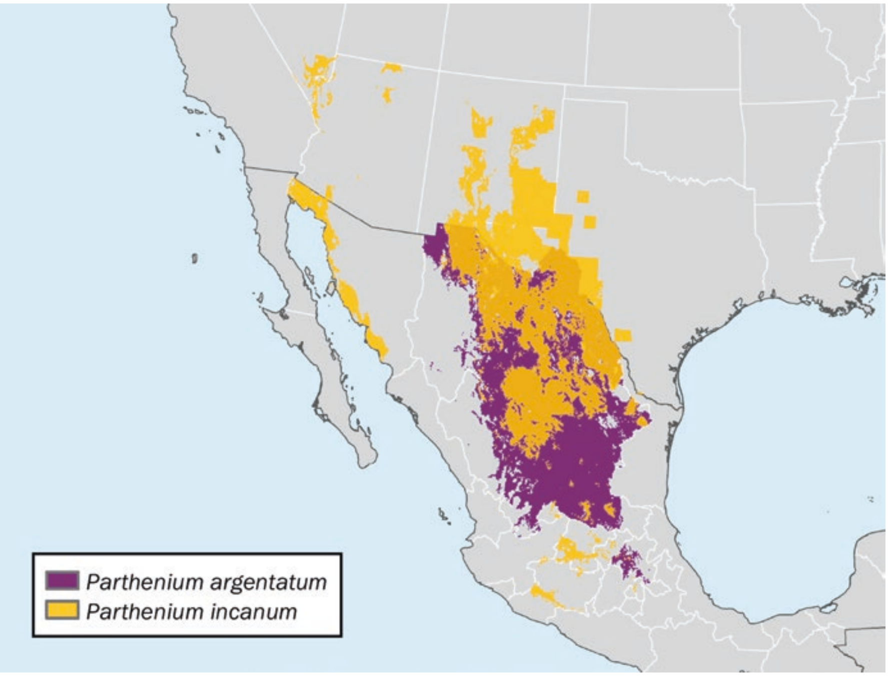

Fig. 15.13 Geographic distribution of guayule (*Parthenium argentatum* A. Gray) and mariola (*Parthenium incanum* Kunth) based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

Table 15.5 Number of germplasm accessions of *Physaria* (Nutt. ex Torr. & A. Gray) A. Gray and holding institutes

Millennium Seed Bank Partnership, Royal Botanic Gardens, Kew		**USDA-ARS Western Regional Plant Introduction Station, Pullman, WA**	
P. acutifolia Rydb.	1	*P. acutifolia* Rydb.	2
P. chambersii Rollins	1	*P. chambersii* Rollins	1
P. rollinsii G. A. Mulligan	1	*P. gordonii* (A. Gray) O'Kane & Al-Shehbaz	1
P. vitulifera Rydb.	1	*P. macrocarpa* (A. Nelson) O'Kane & Al-Shehbaz	1
		P. rollinsii G. A. Mulligan	1
		P. tenella (A. Nelson) O'Kane & Al-Shehbaz	2
		P. vitulifera Rydb.	2
USDA-ARS National Arid Land Plant Genetic Resources Unit, Parlier, CA			
P. acutifolia Rydb.	1	*P. mcvaughiana* (Rollins) O'Kane & Al-Shehbaz	1
P. angustifolia (Nutt.) O'Kane & Al-Shehbaz	4	*P. mexicana* (Rollins) O'Kane & Al-Shehbaz	2
P. argyraea (A. Gray) O'Kane & Al-Shehbaz	11	*P. montana* (A. Gray) Greene	2
P. arizonica (S. Watson) O'Kane & Al-Shehbaz	1	*P. multiceps* (Maguire) O'Kane & Al-Shehbaz	1
P. bellii G. A. Mulligan	1	*P. ovalifolia* (Rydb. ex Britton) O'Kane & Al-Shehbaz	5
P. chambersii Rollins	2	*P. pallida* (Torr. & A. Gray) O'Kane & Al-Shehbaz	6
P. cinerea (S. Watson) O'Kane & Al-Shehbaz	1	*P. palmeri* (S. Watson) O'Kane & Al-Shehbaz	3
P. densiflora (A. Gray) O'Kane & Al-Shehbaz	1	*P. pinetorum* (Wooton & Standl.) O'Kane & Al-Shehbaz	2
P. douglasii (S. Watson) O'Kane & Al-Shehbaz	3	*P. rectipes* (Wooton & Standl.) O'Kane & Al-Shehbaz	4
P. fendleri (A. Gray) O'Kane & Al-Shehbaz	119	*P. recurvata* (Engelm. ex A. Gray) O'Kane & Al-Shehbaz	2
P. gordonii (A. Gray) O'Kane & Al-Shehbaz	30	*P. reediana* O'Kane & Al-Shehbaz	1
P. gracilis (Hook.) O'Kane & Al-Shehbaz	2	*P. rollinsii* G. A. Mulligan	1
P. intermedia (S. Watson) O'Kane & Al-Shehbaz	4	*P. schaffneri* (S. Watson) O'Kane & Al-Shehbaz	1
P. kingii (S. Watson) O'Kane & Al-Shehbaz	3	*P. sessilis* (S. Watson) O'Kane & Al-Shehbaz	1
P. lindheimeri (A. Gray) O'Kane & Al-Shehbaz	1	*P. tenella* (A. Nelson) O'Kane & Al-Shehbaz	2
P. ludoviciana (Nutt.) O'Kane & Al-Shehbaz	2	*P. thamnophila* (Rollins & E. A. Shaw) O'Kane & Al-Shehbaz	1
USDA-ARS National Laboratory for Genetic Resources Preservation, Fort Collins, CO			
P. fendleri (A. Gray) O'Kane & Al-Shehbaz	3		

15.5 Guayule

15.5.1 Origin of the Crop and Brief History of Use Worldwide

Guayule, *Parthenium argentatum* A. Gray, is a source of natural rubber suitable for production in arid and semiarid regions of the world. This xerophytic, perennial shrub species is the only member of the *Parthenium* L. genus producing significant quantities of natural rubber to be economically useful. Guayule is a member of the family Compositae (Asteraceae) and is native to the desert regions of the Southwestern United States and Northern Mexico (Chihuahuan desert region) (Fig. 15.13). The wild relatives of guayule are native to a more expansive region covering North and South America.

Aztec Indians in Mesoamerica knew of the rubber-containing plant and made balls for sporting events long before this. Rubber was extracted by communal mastication of the bark for recreational use (Wilcox 1991; Haury 1937). Rubber balls from prehistoric times have been discovered in the Southwestern United States and verified by archeologists at the US National Park Service as guayule rubber.

Guayule was first discovered for scientific purposes in Texas by Dr. J. M. Bigelow as part of the Mexican boundary survey in 1852. The collected shrub specimen was from near Escondido Creek, Texas (on the border of the United States and Mexico), and sent to Professor Asa Gray of Harvard University who named *Parthenium argentatum* with A. Gray as the naming authority (McGinnies and Haase 1975). The first commercial use of guayule natural rubber was made by the New York Belting and Packing Company which imported 22,000 kg of guayule shrub in 1880 and extracted the rubber by immersing it in hot water (McGinnies and Haase 1975). In 1904, 22 kg of rubber was shipped from Mexico by the Continental Mexican Rubber Company who adopted the most successful extraction method using pebble mill and water floatation (McGinnies and Haase 1975). The rubber was sent to the Manhattan Rubber Company in New York where it was found to be equivalent to the rubber from the *Hevea* Aubl. rubber tree grown in the tropics. In 1910, it made up 24% of the rubber imported to the United States. The shrub was also an excellent smelter fuel and burned in large mining smelters. The bagasse (what is left of the ground shrub after rubber and resin are extracted) was used as a fuel in extraction factories in Mexico (McGinnies and Haase 1975). An extraction plant was also built in the United States in Marathon, Texas, where surveys showed there was an estimated 2500 tons of shrub in this general area (McGinnies and Haase 1975). Native stands were apparently harvested for rubber extraction without concern for replenishment of the genetic resources during this period and perhaps a reason for the scarcity of stands present in Texas today. It was reported that only tetraploid stands were found in Texas when surveyed during the Emergency Rubber Project (ERP) (Hammond and Polhamus 1965). At this time it was estimated that there were 254,000 metric tons of shrub available in Mexico in the states of Chihuahua, Coahuila, Durango, Nuevo Leon, San Luis Potosi, and Zacatecas. In 1942, four guayule mills were consuming180 metric tons of shrub for a 24-h day (McGinnies and Haase 1975).

There is a documentation of guayule being cultivated on private farms especially when Continental Rubber Co. moved to the United States and became the Intercontinental Rubber Co. around 1910. They planted 3240 ha of guayule selections/strains, indicating that some breeding and selection were occurring. However, it was not known at that time that reproduction of most guayule germplasm occurred by facultative apomixis and was a reason for the lack of improvement. This was not discovered until later (Esau 1944, 1946). Research fields to explore cultivation practices increased, and production fields developed during this time (McGinnies and Haase 1975).

Many of the native guayule stands in Texas and Mexico were used to feed extraction facilities during the beginning of the rubber industry. The shrub was pulled by hand and thrown into large carts, then towed by small crawler tractors to collecting locations, and there baled by the contractor (Bonner 1975). The current practice of cutting plants at ground level and allowing regrowth was not practiced until the ERP era. Seed sources from known localities from that time no longer exist.

Guayule has a history of association with wartime needs in both Mexico and the United States. In 1930 the War Department (precursor to the US Department of Defense) studied guayule production to lessen dependence on Southeast Asia and as a source of domestic jobs. Legislation provided for a takeover of the Intercontinental Rubber Company by the US Government and for the EPA to be the sole guayule grower in the United States, with company land holdings including a 26 ha nursery and 567 ha plantation. The physical inventory included the Spence Mill for extraction of rubber, about 10,432 kg of seed, 14,000 nursery seedlings, and 273 ha of shrub plantations. The legislation signed by President Roosevelt in 1942 was supported by the General Tire and Rubber Company, the Goodrich Company, the Goodyear Tire and Rubber Company, and the Firestone Tire and Rubber Company (now Bridgestone Corporation) (McGinnies and Haase 1975).

A reconnaissance survey of some 13 million ha of land was made and the classification of over 2 million ha for guayule culture. Land acquisition work was intensified and some 25,000 ha were leased. Because of later curtailment of the project, the planting goal was never reached, with only 13,000 ha being planted during the life of the ERP.

Research and development came to a halt at the end of the ERP in the early 1950s although informally continued until 1959 (Hammond and Polhamus 1965). One explanation for the end of the project besides the end of the war was the promise of synthetic rubber replacing natural rubber which has never been achieved. Today synthetic rubber comprises much of requirements for passenger car tires; however, larger tires for trucks, agriculture equipment, and aircraft require natural rubber. In the late 1970s with the US Congressional Action, research was revived. This time it was a petroleum crisis that made many countries aware of their dependence on uncertain geopolitical rubber sources (Nakayama 2005). The National Academy of Science recommended in 1977 the need to increase research on guayule. The Native Latex Act of 1978 followed, and as petroleum prices continued to rise, the US Congress enacted the Critical Agricultural Materials Act in 1984 to replace the Native Latex Act. This project was terminated with the stabilization of the source and price of petroleum and the subsequent decrease in the price of *Hevea* rubber. During that time, a solvent extraction processing plant was built in Sacaton, Arizona, and commercial fields nearby planted and managed by the Gila River Indian Community. The variety of guayule that was planted was Gila 1, a naturally occurring interspecific hybrid between guayule and *P. tomentosum* var. *stramonium* (Greene) Rollins. Later this was confirmed to be the same as line AZ 101 from the University of Arizona (D.T. Ray, personal comm.). Although the shrub grew quickly, it had very little rubber yield. Both Goodyear Tire Company and Firestone Tire and Rubber Company (now Bridgestone Corp.) had roles in that project producing various types of tires.

15.5.2 Modern Day Use

Unlike past government driven efforts, the current era is being driven by a consortium of industry that will profit from utilization of all plant products (rubber, resin, bagasse). Crop improvement utilizing modern breeding tools is being applied as well as better agronomic management including seed establishment and rate, irrigation efficiency, pesticide registrations, and harvesting equipment led by industry with government support.

Guayule is either solvent extracted for solid rubber (tire) use or water extraction for latex products. There are a growing number of industrial companies in the early stages of development occurring in the Southwestern United States, Mexico, and parts of Europe. Guayule has a resin coproduct composed of fatty acid triglycerides and complex mixtures of terpene and sesquiterpenoid compounds (Schloman et al. 1983). Resins make up around 8–10% of the shrub's biomass. The chemical composition of the resin and rubber has been used as a tool toward developing taxonomic relationships and evolution of *Parthenium* species (Nakayama 2005; Hashemi et al. 1986) since it's the only species of the taxon with any substantial quantities of rubber and resin. The resin has recently been demonstrated to have utility as a recycling agent in hot asphalt mixes (Lusher and Richardson 2015).

In addition to the rubber and resin, the guayule bagasse is a critical component of the economics of the crop. This could be used as a high-energy-value fuel pellet or as a biofuel (Nakayama 2005). When unprocessed wood or flake boards were impregnated with guayule resin or the bagasse with residual resin, they were made resistant to termite and wood-rot attack (Nakayama 2005).

15.5.3 Challenges in Cultivation

Commercial guayule cultivation is very limited. However, industry is pursuing a sustainable effort to supplement the supply of natural rubber from *Hevea*. Most planted fields are less than 40 ha in size and are for research or scale-up purposes. Guayule is still in the research and development stage and not commercially available for most markets. Commercial production areas will likely include the Southwestern United States and Mexico. We do not know the extent of pests and diseases affecting guayule until more acreage and more geographic areas are planted. Areas suitable for production may be discounted due to disease and insect pressure (Tysdal and Rands 1952).

Guayule is a perennial crop that needs to be grown for at least 2 years to optimize rubber yield. It can be harvested by cutting at ground level and allowed to regenerate from the roots which adds another growing cycle and ties up land for an additional 2 or more years. Most farmers grow annual crops, so a crop like guayule may pose some challenges. Direct seeding has now replaced transplanting at a significant savings in production costs. An insect encountered is the flea beetle (*Systena blanda*) that feeds on the newly emerged seedling; however, transplants are not affected. Seedlings from direct seeding are also more sensitive to herbicides.

There are a number of literature reports identifying pathogenicity and other pests in guayule. For the purposes of this chapter, we will not review this literature but only note that sources of resistance are present within *P. argentatum*. Other wild relatives used to cross with *P. argentatum* to confer resistance or increased biomass are found in the NPGS. Cal 1 and Cal 2 are interspecific hybrids between *P. argentatum* x *P. tomentosum* DC. and *P. argentatum* x *P. fruticosum* Less., respectively. Both are identified in GRIN as resistant to *Verticillium albo-atrum* Reinke & Berthe. to have higher biomass but diluted in rubber content, as a result of *P. tomentosum*. The University of Arizona tested lines of *P. argentatum* with the same disease resistance. Those lines have not been released but indicate that resistance is available within species.

15.5.4 Anticipating Climate Change

Other species of *Parthenium* have a wider range of geographic distribution than *P. argentatum* and found at high elevations and colder climates. These species may be valuable for adaptation of guayule. The challenge is that other *Parthenium* species do not contain rubber. Collections of *P. incanum* Kunth are limited compared to historical sites at higher elevations, so new collection efforts would be needed if this were the choice for introgression. It is likely that variation for cold tolerance can be found within *P. argentatum* (Mitchell 1944). In the past, 11,591 plants (accession PI 478640) were planted in Texas, and some plants survived extreme cold conditions during those experiments (Foster et al. 2011). Reports from the ERP indicated that some plants survived in Texas at −15 °C, so some plants appear to have tolerance, at least for a short exposure time. Mitchell (1944) reported that outdoor plants adapted much better to low temperatures compared to plants grown first in the greenhouse and allowed to develop more lush, succulent growth. It was also shown that seedlings that were unhardened could withstand long exposures of −4° C, while unhardened potted plants 15–18 months withstood exposure to −7 °C. Roots were sensitive in these experiments, and when exposed to soil temperatures of −3° C plants for 8–10 h, plants were subject to injury. When plants were hardened, the stems of transplants withstood repeated and prolonged exposures to −15 °C. An accession named A5058 (no longer available from USDA) showed more tolerance than others indicating there is room for selection within the germplasm pool.

15.5.5 Crop Wild Relatives

15.5.5.1 Crop Wild Relatives and Their Genepool Classifications

Table 15.6 lists accepted named species of *Parthenium*. These all occur in the Western Hemisphere; however, Mexico is the primary center of diversity. Species are both annuals and perennials that include herbaceous plants, woody shrubs, and small trees.

Table 15.6 List of 14 accepted names of *Parthenium* species from The Plant List (www.theplantlist.org)

Species	2*n* count if available	Miscellaneous notes on origin
P. alpinum (Nutt.) Torr. & A. Gray	72	NM, CO, WY
P. argentatum A. Gray	36 + polyploids	TX and Mexico
P. bipinnatifidum (Ortega) Rollins	24	
P. cinereum Rollins		Bolivia, Paraguay
P. confertum A. Gray	34 / 68	AZ, NM, TX, N. Mexico
P. fruticosum Less. ex Schltdl. & Cham.	36	Tamaulipas to Chiapas, Mexico
P. hysterophorus L.	34	Aggressive weed N. and S. America
P. incanum Kunth	36 + polyploidy	Nearest relative of *P. argentatum*; NV, UT, AZ, NM, TX, N. Mexico
P. integrifolium L.	72	Perennial herb, Eastern United States; TX to MA + MN
P. ligulatum (M.E. Jones) Barneby	36	CO, UT
P. parviceps S.F.Blake		
P. rollinsianum Rzed.		San Luis Potosi, Mexico
P. schottii Greenm. ex Millsp. & Chase	36	Yucatan, Mexico
P. tomentosum DC.	36	Oaxaca and Puebla, Mexico

Rollins (1950) reports that the genus *Parthenium* does not appear to be closely related to any other genus in the Compositae family. In his publication he describes the morphological characteristics distinguishing species and subspecies. The taxonomic key to the species of *Parthenium* by Rollins lists 16 species. A more updated list is found on the Plant List website with 14 accepted species (Table 15.6). There are 42 accessions of guayule in the NPGS collection based on the recent genotyping study by Ilut et al. (2017). Two accessions (AZ-2 and AZ-3) released by Ray et al. (2005) that were thought to be guayule were found to be interspecific hybrids of guayule and another species (possibly *P. tomentosum*) (Ilut et al. 2017). AZ-2 is the primary germplasm line used by private companies trying to commercialize guayule due to many desirable traits such as more vigorous seedlings and plant growth and high biomass. The biomass production of this germplasm line accounts for the high rubber yield/ha compared to other lines in the USDA collection. This shows promise for utilization of other species in a breeding program. *P. incanum* (mariola) is the only species beside guayule to have a slight amount of rubber/latex. This species is also apomictic with a polyploid series somewhat similar to *P. argentatum*. The two species are known to naturally hybridize in the wild. *P. incanum* compared to other species may have some utility in a breeding program because it has a wider geographic distribution and adaptability to colder areas than *P. argentatum* (Fig. 15.13). There is always the possibility when more is known about the metabolic components involved in rubber production in a shrub; other species with faster growth, such as *P. schottii* Greenm. ex Millsp. & Chase, *P. tomentosum*, or *P. fruticosum*, could be candidates for genetic modification and contribute to increased biomass.

15.5.5.2 Distribution, Habitat, and Abundance of *P. argentatum* and *P. incanum*

15.5.5.2.1 *P. argentatum*

The guayule in Mexico is localized in six states, three of them bordered by the United States and the rest in neighboring states (Fig. 15.13). In the United States, it is only found in the state of Texas in the Big Bend area. The Mexican state of Coahuila has the largest concentration of wild sites (total of 27), which are distributed from the north to the southeast of the state, followed by the state of Durango with 19 sites in the northeast and central east region, and Zacatecas with 16 sites located in the northern region. Twelve sites were identified in the Southwestern Nuevo Leon, nine sites in the north region of San Luis Potosi, and six sites in the east and south portion of Chihuahua. In addition, two sites were identified in the Northwestern Hidalgo. The map of the guayule region (Fig. 15.13) was drawn with revised information from the databases of herbarium specimen collections of Universidad Autónoma Agraria Antonio Narro (ANSM) from collections carried out during the period of 1964–2015, as well as of the University of Texas (TEX) and Arizona State University (ASU) database. Guayule is native to North-Central Mexico, in the states of Coahuila, Chihuahua, Durango, Zacatecas, San Luis Potosi, Nuevo Leon, and Southwestern United States in the Big Bend area of Texas (Rollins 1950). It is largely restricted to outwash slopes of calcareous soils in regions having an annual rainfall of 10–15 inches (McGinnies and Haase 1975). Some of these native sites have plants sparsely scattered in small areas, while others are many acres in size. Plants are often found growing sympatrically with lesquerella (*Physaria fendleri*) throughout North-Central Mexico. The distribution shown from Fig. 15.13 and Table 15.7 reveals that climatic (temperature, precipitation) conditions of the Mexican desert, as well as the different soil types and pH, favor the natural development of the guayule (Angulo-Sánchez et al. 2002).

Table 15.7 Herbarium information of Mexican collections of *P. argentatum* A. Gray (guayule)

State	City	Region	Site description and associated plants
Coahuila	Saltillo	Southeast	Microphyllous desert scrubland associated with *Viguiera brevifolia* Greene.; *Parthenium incanum* Kunth; *Larrea tridentata* (DC.) Coville; *Flourensia cernua* DC.
Coahuila	Parras de la Fuente	Southeast	Microphyllous scrubland of *Agave lecheguilla* Torr.; rosetophile scrubland of *Dasylirion cedrosanum* Trel; *Mortonia palmeri* Hemsl.; *Quercus intricata* Trel.; *Q. saltillensis* Trel.; *Yucca carnerosana* (Trel.) McKelvey
Coahuila	Torreón	Laguna	Scrubland of *Acacia* Mill.; *Yucca* L.; *Opuntia* Mill; *Mortonia* A. Gray; *Rhus* L.; *Fouquieria* Kunth; *Agave* L.; *Cercocarpus* Kunth; *Senegalia crassifolia* (A. Gray) Britton & Rose (syn. *Acacia crassifolia* A. Gray); *Senegalia berlandieri* (Benth.) Britton & Rose (syn. *Acacia berlandieri* Benth.); *Lindleya mespiloides* Kunth; *Cercocarpus mojadensis* C.K. Schneid.; *Vauquelinia californica* (Torr.) Sarg.
Coahuila	Ocampo	Center-Desert	Scrubland of *Vachellia constricta* (Benth.) Seigler & Ebinger (syn. *Acacia constricta* Benth.); *Flourensia cernua* DC. and *Prosopis glandulosa* Torr.; microphyllous scrubland with *Parthenium argentatum* A. Gray and *Agave lecheguilla* Torr.; *Yucca* L. sp.; *Vachellia constricta* (Benth.) Seigler & Ebinger (syn. *Acacia constricta* Benth.); *Aristida* L.; *Stipa* L.; *Acourtia* D. Don; *Koeberlinia* Zucc.; scrubland of *Larrea tridentata* (DC.) Coville, *Senegalia berlandieri* (Benth.) Britton & Rose, *Fouquieria splendens* Engelm., *Dasylirion* Zucc. sp. *Lycium berlandieri* Dunal.
Coahuila	Sierra Mojada	Center-Desert	Scrubland of *Larrea tridentata* (DC.) Coville, *Agave* L., *Opuntia imbricata* (Haw.) DC., *Prosopis glandulosa* Torr., and *Vachellia farnesiana* (L.) Wight & Arn. (syn. *Acacia farnesiana* (L.) Wild. Saline soil
Nuevo León	Doctor Arroyo Municipality	South	Desert scrubland Limestone hillside (abundance-excess)

(continued)

Table 15.7 (continued)

State	City	Region	Site description and associated plants
Zacatecas	Mazapil Municipality	North	Rosetophile scrubland of *Agave lechuguilla* Torr., *Larrea tridentata* (DC.) Coville, *Parthenium incanum* Kunth, *Pinus pinceana* Gordon & Glend., *Yucca carnerosana* (Trel.) McKelvey, *Rhus virens* Lindh. ex A. Gray, *Sophora secundiflora* (Ortega) Lag. ex DC.
Zacatecas	Norias de Guadalupe	North	Scrubland of *Flourensia cernua* DC. and *Chenopodium* L.
Durango	Mapimi West	Northeast	*Agave lechuguilla* Torr.; *Yucca carnerosana* (Trel.) McKelvey; *Parthenium incanum* Kunth
Durango	Cuencame	Central east	*Larrea tridentata* (DC.) Coville; *Vachellia vernicosa* (Britton & Rose) Seigler & Ebinger (syn. *Acacia neovernicosa* Isley); *Cordia parvifolia* A.DC.
San Luis Potosí	Charcas	North	*P. argentatum* A. Gray, 15–40-cm-high microphyllous scrubland, rosetophile scrubland with *Yucca decipiens* Trel., *Berberis trifoliolata* Moric., *Rhus microphylla* Engelm., and *Agave salmiana* Otto ex Salm-Dyck
Hidalgo	Highway Mexico-Pachuca	Southwest	Sharp slopes. Stony limestone soil. Hills with desert scrubland

15.5.5.2.2 *P. incanum*

Mariola (*Parthenium incanum*) is native to Mexico and the Southwestern United States (Rollins 1950) (Fig. 15.13). It is a perennial, small (10 cm high), aromatic, spreading, and very branched shrub with grayish bark below and tender and small leaves (Rollins 1950). It is a facultative apomictic plant with a natural ploidy series ranging from triploid to pentaploid (Sanchez et al. 2014). Mariola is considered the closest related taxon of guayule as it coexists with guayule in the wild (Rollins 1945). Interspecific hybrids between guayule and Mariola have been detected in the wild and have been produced by controlled crosses in order to extend the genetic base of guayule (Rollins 1945). Several accessions in the NPGS collection identified as guayule were found to be guayule and mariola hybrids based on SNP markers. There are 15 mariola collections from Arizona and Texas in the NPGS collection.

Mariola is one of the most abundant forages in the Northeast Coahuila, Mexico. It is used as part of goat diets throughout the year in rural communities (Mellado et al. 2007). The low-molecular-weight latex from mariola, named “tsacurra” by the Huicholes (indigenous people living in the state of Nayarit, Mexico), has been empirically used to cure stomach and throat ailments (Casillas Romo 1990). It has been reported that the Kickapoo Indians, who live in Northern Coahuila, use the tea of the mariola leaves to heal wounds (Latorre 1977).

Mariola has a wide distribution in Mexico and is reported in 14 states and in Texas, New Mexico, and Arizona in the United States. The largest number of wild sites occurs in the state of Coahuila (total of 23), from the US border to the southern tip of the state. In Chihuahua 13 sites are reported: San Luis Potosí with 11 sites and Nuevo León, Guanajuato, and Zacatecas eight, six and four sites reported, respectively. Durango and Querétaro were reported with four sites for each state. Also, Sonora and Hidalgo had two sites identified in each state. Finally, in Jalisco, Michoacán, Tamaulipas, and Guerrero had one site reported for each state. The map of mariola region (Fig. 15.13) was drawn with revised information from the databases of herbarium specimen collections of Universidad Autónoma Agraria Antonio Narro (ANSM) from collections carried out during the period of 1972–2015 as well as from the University of Texas (TEX) and Arizona State University (ASU) database (Native Plants 1981).

The wide geographic distribution of mariola in Mexico (Fig. 15.13) shows that this plant is able to adapt to a diversity of climates that arises from the North to Central and Western Mexico (Angulo-Sánchez et al. 2002). Information on associated vegetation with guayule and mariola in some documented native sites in Mexico is shown in Tables 15.7 and 15.8.

15.5.6 Conservation Status

None of the *Parthenium* species are listed as threatened or endangered. Guayule germplasm has been on the decline in the United States. Many historical sites in Texas listed in herbarium records are no longer present based on the collection attempt in Texas in 2005 and 2008 by Drs. M. Foster and T. Coffelt. Only three accessions of guayule were obtained in 2005 and two accessions in 2008. Figure 15.13 is a model-generated richness map that offers potential areas of distribution based on historical collection sites for both species. Although guayule has never been documented in the warmer climates about the western coast in Sonora (see yellow area), it's an area similar to Arizona where guayule is not native but grows very well for production.

One barrier is that some native collections occur on National Park Service lands which make it very difficult for the USDA to collect seed from another agency's jurisdiction due to differing objectives. The legal process to collect in Mexico is prohibitive due to International treaties. Few new collections have gone into the NPGS since the 1980s from Mexico. Some previous collections made by J. Tipton or R. Rollins are no longer viable. The NPGS curates guayule and its relatives at NALPGRU in Parlier, CA. Germplasm from this area appears to offer distinct diversity from the remainder of the public collection (Ilut et al. 2017).

The largest research effort on guayule occurred in the 1940s during the US Government's ERP. The breeding effort that took place included many collections and characterization of germplasm. The documentation of their work was a lasting contribution. Unfortunately, many of the fields were destroyed, and a relatively small amount of the germplasm was conserved in long-term seed storage. When there was a resurgence in guayule research in the late 1970s, there were a number of public projects working on plant improvement. Again, when some of these projects

Table 15.8 Herbarium information on Mexican collections of *P. incanum* Kunth (mariola)

State	City	Region	Site description and associated plants
Coahuila	Saltillo	Southeast	Rosetophile scrubland of *Agave lecheguilla* Torr. with *Opuntia microdasys* (Lehm.) Pfeiff. and *Dasylirion cedrosanum* Trel; abundant herbaceous stratum with *Heteropogon contortus* (L.) P. Beauv. ex Roem. & Schult.; *Bouteloua gracilis* (Kunth) Lag. ex Griffiths; *Rhus virens* Lindh. ex A. Gray; *Yucca carnerosana* (Trel.) McKelvey; *Ephedra aspera* Engelm. ex S. Watson; *Flourensia cernua* DC.; and *Prosopis glandulosa* Torr. Stony soil. Microphyllous desert scrubland of *Viguiera greggii* (A. Gray) S.F. Blake isolated shrubs of *Larrea tridentata* (DC.) Coville; isolated trees of *Pinus pinceana* Gordon & Glend.; temperate zone. Scrubland of *Ziziphus obtusifolia* (Hook. ex Torr. & A. Gray) A. Gray; *Aristida* L. sp.; *Erionerum* Nash; and *Stipa* L. Submontane scrubland of *Purshia plicata* (D. Don) Henrickson; *Lindleya mespiloides* Kunth; *Mimosa biuncifera* Benth. with *Zinnia acerosa* (DC.) A. Gray; *Cyphomeris crassifolia* (Standl.) Standl. Scrubland of *Condalia warnockii* M.C. Johnst.; *C. spathulata* A. Gray
	Parras de la Fuente	Southeast	Microphyllous scrubland of *Agave lecheguilla* Torr; *Brickellia laciniata* A. Gray; *Larrea tridentata* (DC.) Coville; *Sericodes greggii* A. Gray; *Yucca carnerosana* (Trel.) McKelvey; *Berberis trifoliolata* Moric.; *Purshia plicata* (D. Don) Henrickson; *Agave falcata* Engelm.; *Pinus pinceana* Gordon & Glend.; *Juniperus saltillensis* M.T. Hall; *Quercus pringlei* Seemen General Cepeda: *Pinus pinceana* Gordon & Glend; *Zexmenia brevifolia* A. Gray; *Bouteloua curtipendula* (Michx.) Torr.; stony hillsides with vegetation of desert material; *Parthenium incanum* Kunth very abundant
	Ramos Arizpe	Southeast	Microphyllous desert scrubland of *Larrea tridentata* (DC.) Coville; *Parthenium argentatum* A. Gray; *P. incanum* Kunth. Plants of *Vachellia rigidula* (Benth.) Seigler & Ebinger (syn. *Acacia rigidula* Benth.), *Rhus virens* Lindh. ex A. Gray., *Pistacia mexicana* Kunth, and *Fraxinus greggii* A. Gray. Limestone hillside very stony; scrubland of *Senegalia berlandieri* (Benth.) Britton & Rose (syn. *Acacia berlandieri* Benth.); *P. glandulosa* Torr.
	Torreón	Laguna	Scrubland of *Agave* L.; *Yucca* L.; *Rhus* L.; *Mortonia* A. Gray; *Cercocarpus* Kunth; *Senegalia crassifolia* (A. Gray) Britton & Rose (syn. *Acacia crassifolia* A. Gray); *Senegalia berlandieri* (Benth.) Britton & Rose (syn. *Acacia berlandieri* Benth.); *Lindleya mespiloides* Kunth; *Cercocarpus mojadensis* C.K. Schneid.
	San Buenaventura	Center-Desert	Grazing land with *Hymenoxys odorata* DC.; *Physaria fendleri* (A. Gray) O'Kane & Al-Shehbaz; *Acoutia parryi* (A. Gray) Reveal & R.M. King

	Cuatro Ciénegas	Center-Desert	*Agave lechuguilla* Torr.; *Senegalia greggii* (A. Gray) Britton & Rose (syn. *Acacia greggii* A. Gray); *Larrea tridentata* (DC.) Coville; *Viguiera stenoloba* S.F. Blake; regosol and lithosol soils. Microphyllous scrubland of *Larrea tridentata* (DC.) Coville, *Flourensia cernua* DC., *Vachellia vernicosa* (Britton & Rose) Seigler & Ebinger (syn. *Acacia neovernicosa* Isley), *Prosopis glandulosa* Torr.
	Candela	Center	Chaparral of *Vachellia rigidula* (Benth.) Seigler & Ebinger (syn. *Acacia rigidula* Benth.), *Leucophyllum frutescens* (Berland.) I.M. Johnst., *Mortonia greggii* A. Gray, *Cercocarpus* Kunth, *Senegalia crassifolia* (A. Gray) Britton & Rose (syn. *Acacia crassifolia* A. Gray), *Senegalia berlandieri* (Benth.) Britton & Rose (syn. *A. berlandieri* Benth.), *Prosopis* L., *Lippia* L., *Mimosa* L., *Opuntia* Mill., *Bouteloua* Lag., *Heteropogon* Pers., *Agave lecheguilla* Torr., *Chamaecrista greggii* (A. Gray) Pollard ex A. Heller, *Neopringlea integrifolia* (Hemsl.) S. Watson.
	Ocampo	Center-Desert	*Agave lecheguilla* Torr.; *Larrea tridentata* (Cav.) Coville; *Flourensia cernua* DC.; *Opuntia* Mill.s; *Bouteloua* Lag.; *Prosopis glandulosa* Torr.; *Dasylirion* Zucc.; *Acourtia* D. Don.; *Koeberlinia* Zucc; *Andropogon spadiceus* Swallen; *Celtis pallida* Torr.; *Flourensia cernua* DC.; *Bouteloua hirsuta* Lag.; *Lippia graveolens* Kunth; *Jatropha dioica* Sessé; *Vachellia vernicosa* (Britton & Rose) Seigler & Ebinger (syn. *Acacia neovernicosa* Isley); *Opuntia leptocaulis* DC. Halophyte grazing land of *Sporobolus airoides* (Torr.) Torr., *Yucca* L., *Bouteloua curtipendula* (Michx.) Torr., *Aristida* L.
	Sierra Mojada	Center-Desert	Xerophilic scrubland of *Larrea* Cav., *Flourensia* DC., *Senegalia berlandieri* (Benth.) Britton & Rose (syn. *Acacia berlandieri* Benth.), *Vachellia vernicosa* (Britton & Rose) Seigler & Ebinger (syn. *A. neovernicosa* Isley), and *Agave lecheguilla* Torr.
	Progreso	North	Mezquital of *Prosopis glandulosa* Torr.; shrub stratum composed of *Celis pallida* Torr., *Aloysia gratissima* (Gillies & Hook.) Tronc., and *Baccharis glutinosa* Pers.
Nuevo León	Doctor Arroyo	South	Chaparral with *Larrea* Cav. and *Yucca* L.
	Galeana	South	*Larrea* Cav. and *Yucca* L.
	Aramberri	South	Limestone hillside with *Agave lecheguilla* Torr.
	Monterrey	Center	Arborescent plants, disturbance zones
Durango	San Juan de Guadalupe		Xerophilic scrubland with dominant *Larrea* Cav., *Prosopis* L., *Flourensia* DC. desert, rocky hillside
	Cuencame	Central east	Scrubland of *Larrea* Cav., *Acacia* Mill., *Prosopis* L., and *Flourensia* DC. Microphyllous scrubland of *Larrea tridentata* (DC.) Coville, *Vachellia vernicosa* (Britton & Rose) Seigler & Ebinger (syn. *Acacia neovernicosa* Isley), *Prosopis laevigata* (Humb. & Bonpl. ex Willd) M.C. Johnst., and *Cordia parvifolia* A.DC.
	Ceballos	Northeast	Xerophilic scrubland
	Mapimi	Northeast	Xerophilic scrubland; secondary vegetation; scarce shrub

(continued)

Table 15.8 Continued

State	City	Region	Site description and associated plants
Zacatecas	La Pardita	North	Shallow soil
San Luis Potosí	Guadalcazar	North	Scrubland of *Agave striata* Zucc., *Rhus virens* Lindh. ex A. Gray, *Pinus pinceana* Gordon & Glend., and *Quercus* L.
	Villa de Santo Domingo	Northeast	Association zacaton-gobernadora (*Larrea tridentata* (DC.) Coville)
	Matehuala	North	Deep soil-sand-clay
	Charcas	North	Microphyllous scrubland with *Larrea tridentata* (DC.) Coville, *Yucca decipiens* Trel., *Opuntia* Mill., and *Agave salmiana* Otto ex Salm-Dyck. Alluvial limestone scrubland
	Moctezuma Train Station	Center	Shrubs about 60 cm high, abundant greenish yellow inflorescence. Microphyllous desert scrubland
	Venado	Center	Crassicaule scrubland with *Prosopis* L. and *Dalea* L. Deep soil very shepherded, shrubs from 30 to 70 cm high
Tamaulipas	Tula	Southwest	Xerophilic scrubland with *Crasirroso*. Limestone low hills, shrubs of regular abundance
Guanajuato	San Luis de la Paz	Northeast	Grazing land. Plain terrain
	La Aurora Mine		Submontane scrubland on hillside, shrubs 1 m
Chihuahua	Manuel Benavides	East	Forest of pine-oak
	Rancho El 45		Microphyllous desert scrubland
Querétaro	Pinal de Amoles	North	Xerophilic scrubland, in hillside, suffruticose herbaceous plants from 40 to 50 cm high
	Vizarrón Municipality of Cadereyta	East	Microphyllous scrubland of *Larrea tridentata* (DC.) Coville
	San Pablo Tolimán	West center	Crassicaule scrubland of *Lama oreocereus*

ended, the germplasm did not always get deposited into a long-term seed storage facility such as the USDA, National Laboratory for Genetic Resources Preservation at Fort Collins, Colorado. The Crop Germplasm Committees (CGC) are trying to help this situation. Guayule is part of the New Crops Crop Germplasm Committee which started in 1991.

An obvious gap in the USDA collection is the lack of sexually reproduced diploids. Only two accessions (W6-429 and Cal 3) are available, and they are genetically highly similar. Very little breeding work has been done with diploids even though they have the most potential for improvement. It is not known if the current USDA germplasm collection adequately represents what is available in the wild. The USDA accessions have only recently been genotyped and phylogenetic relationships proposed based on SNP markers (Ilut et al. 2017). Thompson and Ray (1988) described the source of 23 of the 26 USDA cultivars and germplasm lines as originating from two collections of five bulk plants each. One resulted in the diploid accession W6-429, and the other resulted in 22 polyploid apomictic accessions. Molecular markers for genotypic analyses have been identified since (Estilai et al. 1990; Brown et al. 2008), but more recent analyses provided a comprehensive look at the phylogenetic relationships among germplasm using SSRs and SNPs (Cruz et al. 2015) and genotyping by sequencing (GBS) (Ilut et al. 2015, 2017). The results provide great insights into the relationships of accessions when combined with collection and breeding records. Ilut et al. (2015, 2017) were able to group accessions into four distinct clades and trace the heritage of collections. However, existing information still shows the need for more genotyping to determine intra-accession variation, along with phenotypic characterization of the entire collection.

To improve conservation, it is important that what is available in Texas and in the six states of Mexico be preserved both in situ and ex situ. The public USDA collection is very small in comparison to other crops. Acquisition of more germplasm may be helpful; however, the current collection needs to be better characterized to be useful to breeding programs. A descriptor list for guayule was previously proposed by Coffelt and Johnson (2011) which could be utilized and further refined. More information must be obtained through genetic analysis to determine phylogenetic relationships, increase understanding of traits through analysis of gene regulation and expression patterns, and exploit what diversity is currently available. Hopefully we are at a historical time when guayule has a good chance to become what was dreamt for the past 100 years of becoming a viable crop for arid climates. The key to this success is the available germplasm (Fig. 15.13).

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Chapter 16
Fiber Crops: Cotton and Hesperaloe

Maria M. Jenderek and James Frelichowski

Abstract Fibers derived from wild cotton (*Gossypium* L.) and hesperaloe (*Hesperaloe* Engelm.) plants have a long history of use from prehistoric times to the present. Cotton is currently the most important source of natural fibers in North America, whereas hesperaloe is considered as a potential "new" crop whose value may increase with changing weather patterns. Cotton in particular faces several pest and conservation challenges in its natural habitats. Cultivated and wild relatives of both plant genera are preserved in national germplasm collections; however, due to its economic importance, major conservation and evaluation efforts are focused on cotton. Conservation of cotton genetic resources is threatened by pest eradication programs that are a barrier to reestablishing wild *Gossypium* species in their natural habitats as well as maintaining germplasm nurseries in genebanks, while hesperaloe native populations are subjected to uncontrolled animal foraging and human outdoor activities. Wild populations of *Gossypium* were the foundation to the development of today's cultivated crops. Conservation of genetic resources of both genera in in situ and ex situ environments is crucial for future crop development.

Keywords Boll weevil · Bollworm · Bt · CAM · Collection · Conservation · Genebank · Genome · Germplasm · *Gossypium* · Wild relatives · Cotton · Hersperaloe

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M. M. Jenderek (✉)
USDA, Agricultural Research Service, Center for Agricultural Resources Research,
National Laboratory for Genetic Resources Preservation, Fort Collins, CO, USA
e-mail: maria.jenderek@ars.usda.gov

J. Frelichowski
USDA, Agricultural Research Service, Crop Germplasm Research,
College Station, TX, USA
e-mail: james.frelichowski@ars.usda.gov

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16.1 Introduction

Cotton (*Gossypium* L.) plants are the main source of natural fibers in North America, whereas hesperaloe (*Hesperaloe* Engelm.) might be considered as a “new” fiber crop. For centuries, fibers from both genera have been gathered from wild plant populations; however, cotton has a many millennia domestication and cultivation history. This chapter has two separate parts for each plant group. The first one describes the history of utilizing these plants for fiber production or products containing the fibers using their crop wild relatives (CWR). Characteristics that are useful or desired in breeding and the potential for selection of new cultivars from wild relatives are also covered. The second part contains information on challenges facing the utilization of these resources, as well as conservation efforts to preserve wild populations in their native habitats, as well as the history of establishing national plant collections. The chapter concludes with some speculations on the cultivation and utilization of these crops and their wild relatives in changing weather patterns.

16.2 Cotton

16.2.1 Origin of the Crop and Brief Use History

The word cotton originates from the Arabic word *quotn* and is the most significant renewable source of fiber. It originates from trichomes on the surfaces of the seeds and is nearly pure cellulose in composition (Kim 2015). Cotton is harvested from four species in the genus *Gossypium* L. (family Malvaceae), *G. hirsutum* L.*, G. barbadense* L., *G. arboreum* L., and *G. herbaceum* L. (Lee and Fang 2015). At least 48 species are described by Fryxell (1992), and several recent proposals were made for two additional species with one from the Dominican Republic, *G. ekmanianum* Wittm. (Krapovickas and Seijo 2008; Grover et al. 2015; Schwendiman et al. 1986). *Gossypium* is distinguished by the key feature of gossypol in glands throughout the plant and gives the appearance of small black dots on the entire plant. It acts as a feeding deterrent, and only a few herbivores (e.g., boll weevil, ruminant animals) can digest or tolerate these compounds (Stipanovic et al. 2010). The evolution of the genus *Gossypium* and radiation of species throughout the continents have been covered by Wendel and Grover (2015) and Percival et al. (1999). Separation of species is generally straightforward by means of taxonomic treatment, cytogenetic observations, interfertility with interspecific hybrids among most related species, and finally their geographical origins (Endrizzi et al. 1985; Beasley 1942). The National Cotton Germplasm Collection (NCGC) uses this information to code species with an alphanumeric ID with the letter as the genome type and the number for species. Thus species sharing the same letter show some degree of interfertility. Stewart (2010) roughly divided the genus *Gossypium* into primary, secondary, and tertiary sources of genetic diversity in terms of the potential to improve elite germplasm of cotton. Primary germplasm is the five tetraploid species because of their genetic compatibility with commercial cotton. Secondary germplasm represents A, B, and D diploid species because of compatibility with the A or D subgenome of tetraploid cotton. The remaining genome type species (C, E, F, and K) are the tertiary source because significant efforts are needed to bridge their genomes into cotton germplasm. The intriguing aspect of *Gossypium* evolution is the formation of the polyploid ancestor of the New World cotton from a native New World diploid most likely *G. raimondii* Ulbr. and an Old World cotton species (*G. arboreum* L. or *G. herbaceum* L.) Wendel and Cronn (2003). Transoceanic dispersal was a driving force behind this and other species and is most evident in the sole occurrence of *G. tomentosum* Nutt. ex Seem. in Hawaii and *G. darwinii* G. Watt and *G. klotzschianum* Andersson in the Galapagos (Fryxell 1992).

The four species used to grow cotton underwent additional dispersal and selection from domestication, likely for improved properties of the fiber, which makes it challenging to find ancestral or truly wild populations and explains their discovery in tropical areas worldwide (Yoo and Wendel 2014; Stephens 1974a, b). The Old World is the origin of the diploid species *G. arboreum* and *G. herbaceum* (Lee and Fang 2015; Chowdhury and Burth 1971; Stephens 1967; Hutchinson et al. 1947). The New World is the origin of the tetraploid species, with *G. hirsutum* and *G. barbadense* producing the longest and strongest seed fibers used for cotton (Brubaker et al. 1999). Extensive review of these four species has resulted in the naming of landraces, and accessions were also discovered as dooryard or ornamental plants, commensal or feral populations, and wild-growing cotton (Kulkarni et al. 2009; Lubbers and Chee 2009; Percy 2009; Hutchinson 1951). The term Wild Utilized Species (WUS) will be used for 11 "D" genome diploid species of the subgenus *Houzingenia* Fryxell (Fryxell 1992). *G. thurberi* Tod., a D genome diploid, occurs in North America (Arizona) and Northern Mexico. Ten other D genome diploids are in Mexico. *G. hirsutum* occurs primarily in North America, with scarce representation as far north as the American Southwest (as "Hopi" cotton) and wild/feral in Southern Florida ("Yucatanense"). The bulk of *G. hirsutum* CWR consist of landraces and feral plants in Mexico, Central America and even the Caribbean Islands (Smith and Stephens 1971). The range of *G. barbadense* overlaps that of *G. hirsutum* but is discovered at a much lower frequency (Percy and Wendel 1990; Stephens and Moseley 1974).

Because information is scant on CWR and WUS in situ, the material discussed in the following topics rely heavily on what is known in cotton and the CWR and WUS from the literature and from conservation ex situ, primarily as accessions in the NCGC.

16.2.2 Cultivation

Cotton has been cultivated as a source of natural fiber, nutrient-rich cotton seed livestock feed, and oil for food and in some cases as an ornamental (Lee and Fang 2015; Brubaker et al. 1999). Archaeological evidence in Peru unearthed yarns with colored cotton and suggested that various naturally colored forms of cotton existed for thousands of years (Damp and Pearsall 1994). Hopi Indians selected for reduced gossypol in the seeds of *G. hirsutum*, allowing the seeds to be used as a food source or feed for animals (Fulton 1938; Lewton 1912). “Braziliense,” a variant of *G. barbadense*, produces seeds that remain clumped together, in a kidney-shaped design, and perhaps facilitated easier removal of fiber from multiple seeds at once (Turcotte and Percy 1990). Cotton CWR and even WUS will often have flowering dictated by combination of photoperiod and moisture and even temperature (Fryxell 1986; Stephens 1976; Lewis and Richmond 1960). Typically tropical winters are the dry period, and thus CWR of *G. hirsutum* and *G. barbadense* and typically the D genome WUS as well are photoperiodic and generically called “short day” flowering plants. Adaptation to higher altitudes or further north or south of tropical latitudes required selection for shorter maturation times and day neutral flowering (Cook 1906, 1905). As a result, cotton cultivars were cultivated as an annual crop because the tropical plants often matured more slowly into a small tree or bushy perennial (Lee and Fang 2015; Stephens 1976; Mauney and Phillips 1963). Adaptation to subtropical production regions still requires a minimum of degree days, often calculated as “heat units” or “degree days” to fully ripen the cotton fibers (Kerby 1986; Mauney 1986; Wang 1960). Late-season dry periods enable the harvesting of high-yield, high-quality cotton and viable seeds for secondary uses such as oils, feedstock protein source, etc. (Dowd 2015; Gregory et al. 1999; Cherry et al. 1986; Halloin 1986). Only two species, *G. hirsutum* and *G. thurberi,* grow wild in specific habitats in the mildest regions of the continental USA, Southern Florida and Southern Arizona. But cultivation of cotton in the USA required collection of short-season landraces in North America with continual plant breeding to improve yield, fiber quality, disease resistance, etc., which eventually incorporated specific traits from many CWR and WUS.

Systematic collection throughout the Americas and the Caribbean and preservation of this germplasm in the USA became a priority in response to the outbreak of the boll weevil in the 1880s (Percival et al. 1999). Other collecting trips would follow and eventually cooperators from federal, university, and state experiment stations began to assemble the cotton germplasm collections (Frelichowski and Percy 2015; Percival 1987). Also from these activities sprang collaborative efforts that were formalized into US regional projects involving scientists and members from all aspects of the US cotton industry. These efforts established a priority of acquiring and studying diverse germplasm for cotton improvement (SCSB 1981, 1968, 1956). In 1960, the cotton subcollections were deposited at the National Laboratory for Genetic Resources Preservation (formerly National Seed Storage Laboratory) with their passport data, and in the early 1980s a working collection was consolidated in College Station, TX, USA, with a USDA-ARS-employed cotton curator. A full-time technician, greenhouses, seed processing, and storage facilities were added. Germplasm continued to be added from publicly donated cultivars and germplasm lines, explorations, and exchanges with other collections. Worldwide commercialization of cotton relied on CWR to incrementally improve germplasm for yield, quality, and stress resistances but at the same time threaten to render CWR and

WUS obsolete or treat them as a threat to shelter and overwinter cotton crop pests. Long-term conservation of CWR and WUS depends on the NCGC, other genebanks, and local efforts. The NCGC relies on outside support and collaboration to bolster operations, such as the National Cotton Council, and now Cotton Incorporated, providing support for a counter season nursery in Mexico and now Costa Rica for seed increases of the NCGC, with emphasis on photoperiodic accessions of cotton and its CWR and WUS.

16.2.3 Agronomic Practices

Cotton has benefitted from many of the general advances in agronomy, but only a few practices that are mostly specific to cotton are mentioned here. In the USA, the southern states, from the east coast to the west, are termed the cotton belt, and cotton is grown in relatively fertile areas. There are specific pests and diseases that require selection for host plant resistance and/or application of pesticides. Season-long insect control is needed to prevent early loss of flower buds (squares) all the way to open bolls so that the fiber development is unimpeded and clean and reaches maximum quality (Luttrell et al. 2015; Leonard et al. 1999; Ridgway et al. 1984). The most effective control strategy was selection for earliness of crop maturity to achieve a profitable harvest before economic thresholds of insect pests were reached, most notably the migration of cotton boll weevil (*Anthonomus grandis* Boheman) and/or bollworm (various, but typically *Helicoverpa* spp. Hardwick) from the tropics. While localities may differ in the presence and severity of these and other pests, they must be monitored throughout the cotton belt to prevent their destructiveness and slow their migration (e.g., Boll Weevil Eradication Programs, Bradley 1999; Brazzel et al. 1999). A conflict would eventually arise between cotton crop plantings and native stands of CWR and WUS, where insect pests survived. These stands became a logical target of pest eradication, with natural populations of *G. hirsutum* in Florida and *G. thurberi* in Arizona being rouged. This significantly reduced native populations, but their efficacy is in doubt in some cases with insect pests being race specific to either the cotton crop or native *Gossypium* but not necessarily developing on both. Insecticides are frequently used to reduce outbreaks and/or late-season surges in pest populations, and year-round scouting of one or both of these two key pests is standard in most of the US cotton belt. A thorough plow up of the field is mandatory to prevent overwintering of key pests, notably bollworm and boll weevil. Cotton is one of the first crops to undergo genetic modification to afford season-long control of bollworm, because of its polyphagous nature on many crops and difficulty in season-long control (John and Stewart 2010; Paterson and Smith 1999; Zhang 2015). Inserted into the *G. hirsutum* genome was the genetic construct coding for *Bacillus thuringiensis* (i.e., Bt) C-endotoxins, because the crystals are highly toxic to larvae of bollworms. There are concerns of cross-pollination between commercial cotton and wild cotton. Permits are required in Florida before one can grow cotton and show the dual concern over diluting the native *Gossypium* with the modified genomes of cotton crops and preventing perceived overwintering of cotton pests on *Gossypium* plants that are not properly managed or plowed up to control insect pests.

Gossypium seed is classified as orthodox seed, meaning it can be stored at reduced humidity and cold temperatures to prolong viability (Baskin et al. 1986). After ginning, seed is conventionally cleaned by acid delinting (to remove residual fuzz), rinsed, neutralized with lime, dried, and stored in cold, dry conditions until planting (Delouche 1986). For the NCGC it is stored at 4 °C at ~20% relative humidity. Numerous other commercial uses for ginned seed exist, such as high-quality oils for cooking and protein for feeding livestock, to name a few. CWR and WUS typically have harder seed coats. Seed scarification, pretreatment with hot water (Walhood 1956), and even exposure to "smoke water" (Light et al. 2005; Dixon et al. 1995) are examples of techniques needed to improve ex situ germination success of CWR of cotton. Ex situ conservation of CWR and WUS requires a tropical counter season winter nursery and/or greenhouses to trigger flowering and to harvest sufficient seed for storage and distribution (Frelichowski and Percy 2015). Boll weevil and bollworm eradication policies prevent the establishment of an outdoor nursery in the mildest areas of the continental USA; therefore the NCGC depends on a tropical counter season nursery to generate most of the seed of CWR and greenhouses for the WUS.

16.2.4 Pests, Diseases, and Climatic Limitations

Cotton is subjected to a wide number of insects, diseases, and environmental challenges at the local level, and some span wide areas of the cotton belt. Host plant resistance is the foundation of controlling the damage from these stresses (El-Zik and Paxton 1989; Painter 1951). Earliness of plant maturity is the first means to achieve profitable harvest before economic thresholds of pests are reached. Monitoring of widespread pests such as boll weevil and bollworm is essential to apply additional insecticide or enforce other control measures to limit their spread areas across the cotton belt (Luttrell et al. 2015; Leonard et al. 1999; Brazzel et al. 1999; Bradley 1999; Ridgway et al. 1984). Genetic modification of cotton with constructs to produce Bt toxins as a protection against lepidopteran pests has been helpful (Zhang 2015; Paterson and Smith 1999). Several diseases are of worldwide concern, and their entry into the USA will harm the crop as well as its CWR and WUS. Cotton leaf curl disease (CLCuD) is present in Africa and Asia (Briddon and Markham 2000), but similar viruses exist elsewhere such as leaf crumple virus (Idris and Brown 2004) in North America and blue disease virus (Ebert and Cartwright 1997) in South America. Research into host plant resistance control for CLCuD may be applicable to these two New World viruses as well. Whitefly is the vector of CLCuD, and bacterial boll rots (Medrano et al. 2015) are spread by stink bugs means the pests may shuttle diseases between cotton and CWR and even WUS. Rules for importing cotton seed and related plants and following quarantine regulations when applicable are essential to prevent new diseases and pests from infecting cotton crops as well as CWR and WUS, particularly when they may exist as perennials and become year-round hosts of new pests and diseases. Climate change, land development, and natural succession are additional forces that may threaten populations CWR and WUS.

16.2.5 Crop Wild Relatives (CWR)/Wild Utilized Species (WUS) of the Crop

North America and select islands of the Gulf of Mexico and Caribbean support cotton CWR and WUS of *Gossypium*. The Islands covered include Antigua, Barbuda, Bahamas, Barbados, Belize, Cuba, Dominica, The Dominican Republic, Grenada, Haiti, Jamaica, Saint Kitts and Nevis, Saint Lucia, Saint Vincent and the Grenadines, and Trinidad and Tobago. The species included are *G. hirsutum* L., *G. barbadense* L., *G. aridum* (Rose & Standl.) Skovst., *G. armourianum* Kearney, *G. davidsonii* Kellogg, *G. gossypioides* (Ulbr.) Standl., *G. harknessii* Brandegee, *G. laxum* L. Ll. Phillips, *G. lobatum* Gentry, *G. schwendimanii* Fryxell & S. D. Koch, *G. thurberi* Tod., *G. trilobum* (DC.) Skovst., *G. turneri* Fryxell. *G. hirsutum*, and *G. barbadense* are grown for cotton and local landraces; unimproved, feral, or "wild" accessions of these two species are treated as CWR. The other 11 species are diploid, without cotton, and have limited value but may be sources of stress resistances for cotton breeders or have ornamental value with shrub-tree-like growth and showy flowers (Fryxell 1992).

16.2.6 Relationship to Distribution/Habitat/Abundance

Status of the CWR and WUS in North America and the selected islands is scarce, and the NCGC has recently made it a priority to update their status in the USA because of ease in travel and access. Essential to the collection trips is the incorporation of GPS and high-quality digital images, for better characterization of habitat and distribution, and to create a baseline to monitor abundance. Experience, familiarity with records of previous explorations, discovery by botanists, consultation with locals, and de novo exploration are involved to locate this cotton, because the CWR are in some way affiliated with man's activities, often called dooryard cotton. Persistent feral or truly wild populations are more consistent to habitats, but again the short-lived nature of the plants means that actual locations are fleeting. Previous trip reports, plant introduction books, and location descriptions have been the key resources to plan new collection trips. However most of the collected materials in the NCGC are lacking precise location information, making it difficult to re-collect germplasm, predict habitats, and/or update their status. Local location names are often problematic to find on modern maps and require new collection efforts to assign GPS data to plant locations, particularly those that are feral or wild. Simple abandonment appears to be a big concern for CWR of cotton, and loss of land to development threatens WUS. Recent US scientist-led exploration trips have incorporated GPS annotation of collection sites (Ulloa et al. 2013, 2006) allowing for characterization of habitat and abundance.

A cooperative expedition was conducted by M. Ulloa (USDA), J.M. Stewart (Univ. of Arkansas), and several researchers from Mexico's INIFAP for *Gossypium* in Mexico (Ulloa et al. 2013, 2006). They documented sites with GPS coordinates and collected CWR of *G. hirsutum*, *G. barbadense*, and a significant number of WUS "D" genome species of the subgenus Houzingenia (Fryxell 1992). These collecting efforts covered the Pacific west coast of Mexico, from the state of Sonora (North) to the state of Chiapas (South) and included several trips from 2002 to 2004. A significant number of *Gossypium* accessions of the subgenus Houzingenia from various parts of Mexico were placed in a nursery or botanical garden in Iguala, Guerrero, Mexico, including several accessions of each of the arborescent species for ex situ conservation. An assessment of these collection trips is that increasing human population, modernization of agriculture, and urbanization are threatening in situ Mexican *Gossypium* resources. Even the most encountered species (*G. aridum*) of the subsection Erioxylum, with the widest geographic and botanical diversity of the diploid species, should be a target of conservation because collection sites are relatively isolated across mountainous terrain and valuable ecotypes could be lost (Alvarez and Wendel 2006). The species *G. trilobum* favors habitat that is heavily cultivated for guava (*Psidium* L. spp.) suggesting they share optimum environments often of similar altitude (around 4000 ft). Fryxell (1992) reported this species as common, but these surveys (Ulloa et al. 2013, 2006) suggest that agricultural development is driving this species close to extinction. According to information obtained from local sources, eradication of cotton CWR was attempted in areas of southern Mexico in the 1980s in efforts to remove perceived insect reservoirs. No commercial fields of cotton were encountered during expeditions between 2002 and 2004 in the central and southern part of Mexico (Ulloa et al. 2013, 2006). Currently, not counting the northern cotton production regions of Mexico, the diversity of *G. hirsutum* is limited to feral plants that occur opportunistically in waste areas and as occasional home garden plants maintained by rural peoples or village residents. Wild cotton thus has poor or slow rebounding ability in the wild or is dependent on man's intervention for survival.

The NCGC staff conducted an exploration trip, for *G. thurberi*, in Arizona, in October 2015. Accessions of *G. thurberi* in the NCGC have little or no detail in their collection sites, thus planning this trip depended on GPS locations and habitat descriptions found in online herbarium databases summarized at SEINet (http://swbiodiversity.org/seinet/collections/index.php). Information was retrieved by typing in Gossypium *thurberi* in the taxon search and using the interactive map for specimens with GPS locations. A large number of sites were reported, but it spanned many decades of discoveries by botanists. In general, the reported sites of *G. thurberi* were from altitudes between 2000 and 5000 ft and in association with mountainous regions, often maintained as National Forests. Therefore the targeted areas were in the US Forest Service Prescott National Forest, Superstition Mountains, Dragoon Mountains, Chiricahua National Monument, Cochise Stronghold, Santa Rita Mountains, Santa Catalina Mountains, and Baboquivari Mountains. Most of the GPS records overlay the improved roads in Google Map in these regions, and the closest roads to hot spots were selected for travel routes. The overall trip was designed to provide an overview of the general occurrence of *G. thurberi* in the state, with the goal of creating a baseline to monitor future changes of *G. thurberi*, and to add germplasm to the NCGC with GPS coordinates. Collection of new germplasm was intended to be spread widely over the state to obtain isolated populations, likely to be genetically diverse. To quickly find *G. thurberi* in many different locations, spotting of *G. thurberi* was done from the roadsides with limited hiking. The combinations of GPS tags and digital images of the located plants and surrounding habitats are essential approaches to guide future exploration trips. A Garmin GPS (Montana 650t) was used to continuously record all routes traveled to indicate the relative frequency of *G. thurberi* in the traveled regions.

Less *G. thurberi* was collected than expected based on the large number of collection locations reported online at SEINet and raised concerns of possible loss of habitat. Extensive ranching in Arizona and prior efforts to remove *G. thurberi* in the hopes of reducing cotton insect pests of Arizona cotton fields may have severely reduced populations of *G. thurberi*. Populations of an insect pest such as boll weevil may be specialized in their preference for wild or cultivated *Gossypium* and make futile the eradication programs specifically aimed at cotton crop pest populations (Kuester et al. 2012). Generalization of the collection sites suggests that freshly disturbed or cleared areas are preferred locations of *G. thurberi*. Their frequency declines rapidly as habitats approach the tree line or actively grazed rangeland and suggests that they exist in fleeting populations often in the vicinity of recently cleared areas such as roadsides. The GPS locations and habitat clues from both trips act as a baseline to monitor the wild cotton or *Gossypium* and guide any conservation or future exploration efforts. Hopefully more *G. thurberi* grows in areas only accessible through hiking.

More exploration is needed to update the status of *G. hirsutum* in North America. Only collection trips of Ulloa et al. (2013, 2006) can give a reasonable status of this and the other species in Mexico. In addition to *G. thurberi*, at least ten other diploid species occur in Mexico, and updating the status of each is a daunting task. *G. trilobum* is already considered endangered, and other species are also in limited locations. For example, *G. armourianum* (Fig. 16.1) is only known from San Marcos Island in the Gulf of California and its current status is not known. *G. hirsutum* has protected status in Florida and in some cases is considered an endangered species. Their populations are monitored by the USDA, primarily as part of management of the Everglades. Exploration to update the status of *G. hirsutum* in Florida is needed. Cooperation with the USDA and the state of Florida will be necessary to investigate the status of conservation in situ because the status of *G. hirsutum* is only publicly known from various reports on informal outlets on the Internet. The primary role of the NCGC is ex situ conservation, and permissions will be sought to conserve seed of wild-collected *G. hirsutum* in Florida to protect

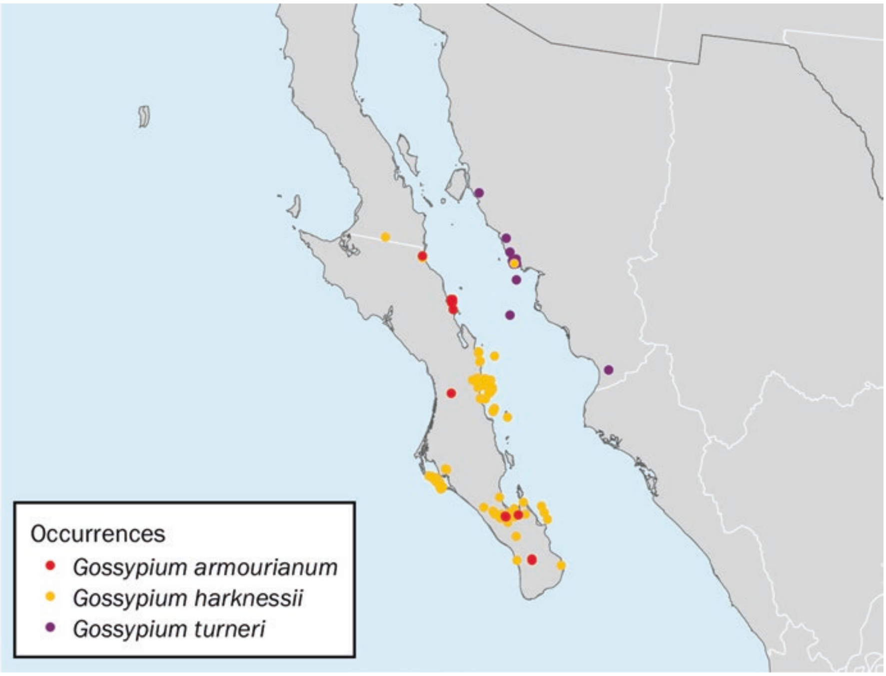

Fig. 16.1 Modeled potential distribution of *G. armourianum* Kearney, *G. harknessii* Brandegee, and *G. turneri* Fryxell, based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

this heritage from further eradication, land development, insect pressures, and even climate change. Reseeding *G. hirsutum* in the wild in Florida may eventually require the resources of the NCGC.

Based on occurrence data from herbarium samples, and NCGC accessions, including the most recent surveying and collecting trips, we used spatial modeling to predict the distribution of the following *Gossypium* species: *armourianum*, *harnessii*, and *turneri* (Fig. 16.1); *aridum*, *laxum*, *lobatum*, *schwendimanii* (Fig. 16.2), and *davidsonii* (Fig. 16.3); *hirsutum* and *tomentosum* (Fig. 16.4); and *gossypoides* (Fig. 16.5), *thurberi*, and *trilobum* (Fig. 16.6). There is a clear need to continue survey work to validate the occurrence of cotton CWR and WUS in North America.

16.2.7 Utilization

Bowman et al. (2006) and Esbroeck and Bowman (1998) demonstrated the narrowing of the germplasm base in commercial cotton, often from intense selection to improve yield and achieve higher standards of fiber quality. Improvements of these traits and others such as biotic and abiotic resistances require genetically

Fig. 16.2 Modeled potential distribution of *G. aridum* (rose & Standl.) Skovst., *G. laxum* L. Ll. Phillips, *G. lobatum* Gentry, and *G. schwendimanii* Fryxell, based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

diverse sources such as in the NCGC. Scientific research and cotton improvement with the NCGC and many accessions representing CWR are extensive, and a very cursory review is attempted here. Growth of *G. hirsutum* and *G. thurberi* as ornamentals is known from the numerous requests made of the NCGC from users living in Florida and Arizona. Their use may conflict with the state's interests in controlling alternate host plants of cotton crops grown in the state. This is unfortunate as some users appear to have a genuine interest in maintaining CWR and WUS. The diversity of CWR of *G. hirsutum* and *G. barbadense* and WUS of D genome diploids has been useful for much of cotton improvement. Fryxell (1976) summarized some early use of exotic germplasm for cotton improvement, and these are also enumerated elsewhere (Endrizzi et al. 1984; Bourland and Meyers 2015; Percy et al. 2015). A range of traits were found in the diversity of CWR and WUS, for cotton crop improvement and even to assemble early cotton genetic linkage maps. Examples are numerous, but a few are: okra (dissected) leaf shapes (Andries et al. 1969) and nectariless traits for less insect feeding (Schuster et al. 1976), thus protecting plant health and reducing mold growth on cotton; cluster character resulting in narrower plant profiles and enhanced yield and harvesting potential, glandless trait (Kohel and Lee 1984) for seeds with minimal or no toxicity from gossypol and direct use for consumption; bacterial blight (Knight 1963)

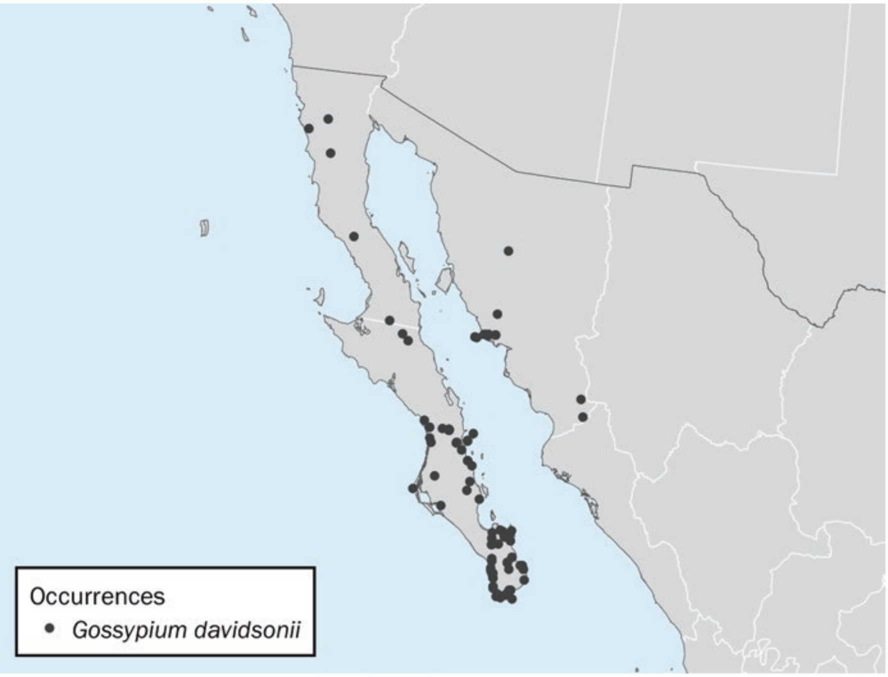

Fig. 16.3 Modeled potential distribution of *G. davidsonii* Kellogg based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

and reniform resistances (Gutierrez et al. 2011) to maintain/improve cotton productivity; trichome density (Lee 1985) which impacts feeding by insects such as Jassids or whitefly (Butler and Henneberry 1984) or absence of which can reduce leaf trash on harvested cotton, and male sterility to facilitate large-scale hybridization in cotton breeding programs (Percy and Turcotte 1991).

16.2.7.1 Breeding History and Use

Several sources summarize use of *Gossypium* genetic resources for research and cotton breeding (Percival and Kohel 1990; Endrizzi et al. 1984; Fryxell 1976; Culp and Harrell 1973). Within the US cotton community, updates on use of the NCGC are given in status reports such as Wallace et al. (2009) and still underestimate the utilization by such users as scientists in other countries, or small-scale or home growers in the USA. Evaluations and characterizations are continuing with the CWR and WUS of the NCGC and present a wealth of possibilities to improve tolerance/resistances to existing and emerging biotic and abiotic stresses. Large-scale evaluations of the NCGC have been done for resistance to boll weevil (Jenkins and Parrott 1978a), leaf spot and Verticillium wilt (Jenkins and

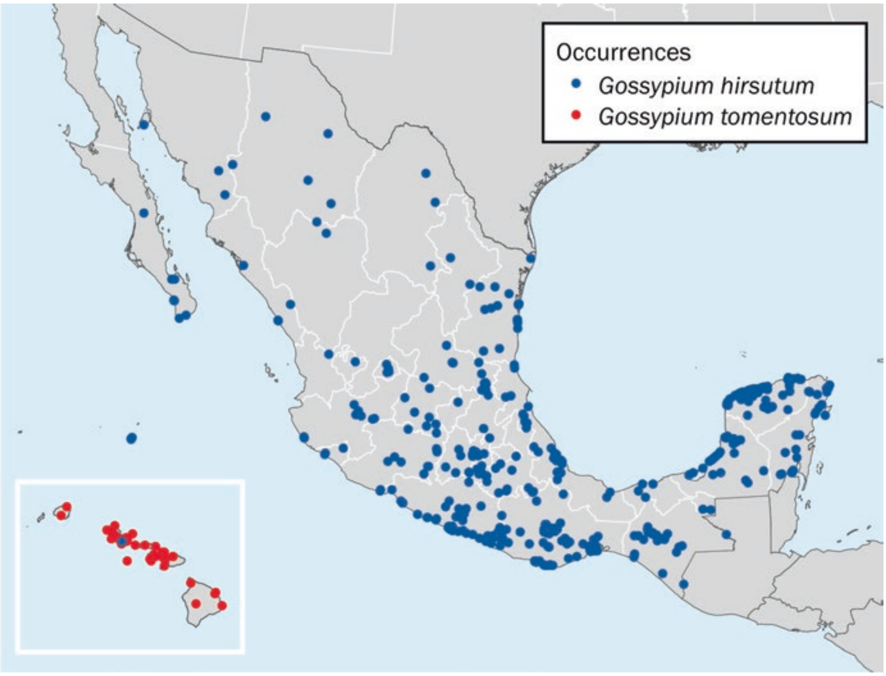

Fig. 16.4 Modeled potential distribution of *G. hirsutum* L. and *G. tomentosum* Nutt. ex Seem., based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

Parrott 1978b), seed protein content (Kohel et al. 1985), seed oil (Kohel 1978), bollworm resistance (USDA 1975), root-knot nematodes (Robinson et al. 2007; Shepherd 1983), and thrips (Bowman and McCarty 1997) to name a few. Opportunities exist to select for greatly reduced or nontoxic gossypol in the seeds so that the plants are still protected against herbivores, but the seed can be directly utilized as a versatile source of oil and protein (Stipanovic et al. 2005; Altman et al. 1987; Dilday 1986). Morphological and molecular marker characterization of the NCGC is underway (Hinze et al. 2016, 2015) to provide a baseline to better gauge the diversity of the NCGC for the users and guide further genetic and genomic research into CWR and WUS.

16.2.7.2 Challenges to Increased Use

Cotton is still grown locally as evidenced by dooryard cotton found in Mexico (Ulloa et al. 2013, 2006), exploration in Puerto Rico by the NCGC, and observations in Mexico and Costa Rica of feral and dooryard cotton near where the counter season nursery of the NCGC is located. Cultivation of cotton, in the vicinity of CWR and WUS, may place them at risk with these pests and/or diseases (Menezes

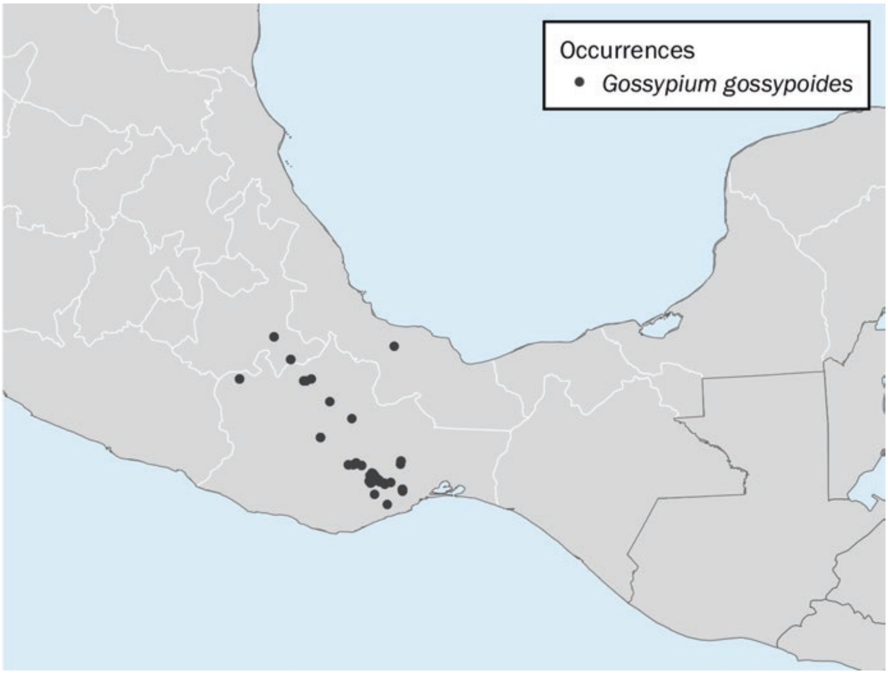

Fig. 16.5 Modeled potential distribution of *G. gossypioides* (Ulbr.) Standl., based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

et al. 2014; Messing et al. 2007). Cross-pollination between wild and commercial cotton has been demonstrated, but evidence of permanent introgression into the wild has not been conclusive (Lehman et al. 2014; Pleasants and Wendel 2010). Growers in Florida must apply for permits to grow cotton and suggest a twofold concern, crossing of commercial and genetically modified cotton with native *Gossypium* and survival of cotton pests on *Gossypium* plants if not managed according to the terms of the permit and the State of Florida regulations. This almost amounts to a barrier to reestablishing *G. hirsutum* as a wild species in Florida because of the overriding concern for the cotton crop. Elsewhere, cheap cotton products, as well as competition from polyester, have reduced much of local interests in cotton and place much of native CWR at risk of abandonment. Eradication programs for cotton pests still encourage the removal of CWR and WUS, even though the rarity of CWR and WUS and host specificity of some pests make this approach marginally effective in pest control for commercialized cotton. Stagnant prices for cotton are reducing the acreage of cotton planted. Water shortages curtail the high yields needed to realize a profit margin. Support for germplasm conservation and utilization of cotton and CWR and WUS is a long-term federal-, state-, or commodity group-sponsored investment, but funding and support remains tied to the economic success of the crop. All new germplasm of CWR must be tested for adventitious presence of the foreign constructs used in genetically modified cotton

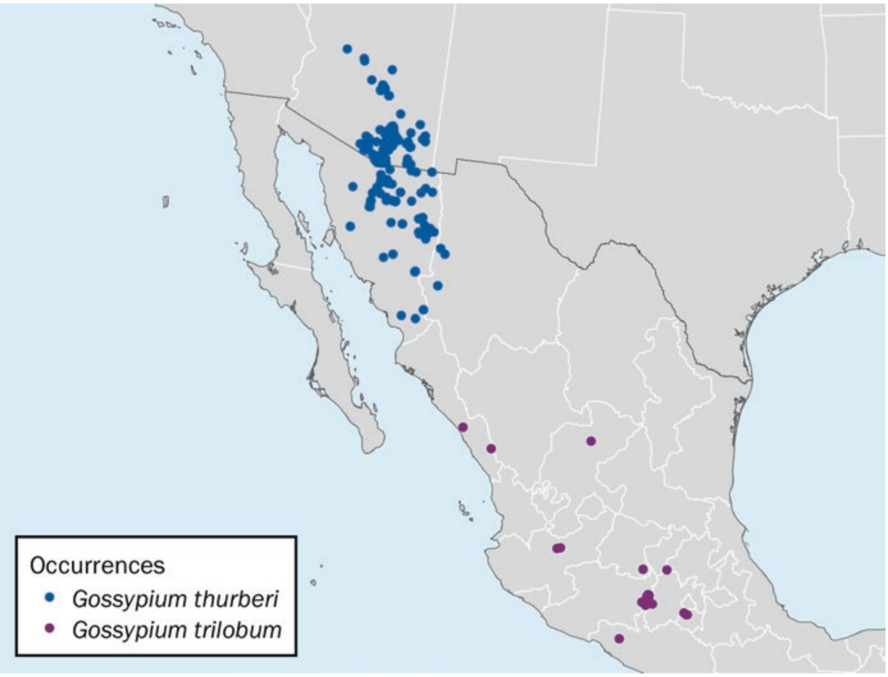

Fig. 16.6 Modeled potential distribution of *G. thurberi* Tod. and *G. trilobum* (DC) Skovst., based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

(to rule out accidental seed or pollen contamination). The time and resources associated with these procedures slow the acceptance of new germplasm, but it is essential for legal reasons and to maintain our permits to increase seed at the counter season nursery and assure the users they are receiving conventional cotton and CWR accessions (Martin 2013). Stagnant budgets in the USDA National Plant Germplasm System and a slowed cotton economy affecting all our public, state, and private cooperators limit the NCGC activities when priorities for acquisition and distribution still remain high. Continued operation of the tropical CSN nursery is threatened in the near future with stagnant operating budgets and rising costs but is essential for seed propagation of the photoperiodic landraces.

16.2.7.3 Conservation Status of CWR and WUS

16.2.7.3.1 In Situ

The in situ conservation status of CWR and WUS is not known for *G. thurberi* in Arizona and not well characterized as a whole for *G. hirsutum* in Florida. The locations of *G. thurberi* were updated by a survey by the NCGC. Status reports by the USDA and State of Florida and scant Internet sites reveal some locations of *G.*

hirsutum in Florida that are hopefully persistent local populations. The involvement of the USDA and the state of Florida in monitoring *G. hirsutum* in their reserves suggest that at least *G. hirsutum* has protected status in some locations of Florida. *G. thurberi* exists in abundance in specific locations in Arizona, and development in these areas or even climate change could threaten their in situ status because overall their frequency was low in the state of Arizona. Both species need ex situ representation in the NCGC as a backup, to ensure their permanent survival, if events should destroy their limited wild populations.

16.2.7.3.2 Status (Threatened/Endangered)

The status of each of the species remains unknown. In the USA *G. hirsutum* "Yucatanense" is treated as endangered in South Florida. Historical practices of elimination of feral and native cotton (to Florida) to reduce boll weevil and bollworm populations have doubtless contributed to this status. Wild cotton has been reduced to protected areas like the Everglades, where it is not permissible to collect seed. Planting of cotton in Florida requires specific permits as to not "pollute" the native cotton or repopulate pests of cotton. *G. trilobum* was scarcely located during explorations in Mexico, and the authors considered its status as threatened, particularly when its habitats are favored for expanded guava (*Psidium* L.) production (Ulloa et al. 2013, 2006). The unsupported belief that specific cotton pests can be controlled by elimination of native *Gossypium* continues to threaten their status. Insect pest populations can have complex host plant preferences as well as long-range migration capabilities, thus generally rendering this strategy ineffective in controlling cotton crop pests.

16.2.7.3.3 Needs and Opportunities

G. thurberi was found in abundance in relatively few locations in Arizona. Because it was also grown as an ornamental and collected frequently as evidenced in the output of SEINet online database, it is a good candidate to monitor and perhaps find willing partners to revegetate areas with *G. thurberi*. However the status of *G. thurberi* in neighboring Mexico is not known. Increase in interest by NCGC users from Mexico and significant expansion of their plant germplasm facilities may create opportunities to explore and conserve their *Gossypium* resources. Communication with other genebanks (Cambell et al. 2010) may improve cotton CWR and WUS conservation if they focus on their native *Gossypium* species as is being done by the NCGC.

16.2.7.3.4 Ex Situ

Because wild cotton is often a roadside plant, or germinates opportunistically in recently cleared or disturbed areas, their populations can be considered fleeting. To insure against permanent loss, ex situ conservation of selected or representative populations is needed and is a seed source to repopulate the species in the wild. Landraces are abandoned as residents move on, plants perish, or commercial cotton is favored or the CWR becomes diluted with cross-pollination with nearby commercial cotton. Retracing past exploration trips is the first means to plan collection, but communication with locales and their genebanks is a much more productive approach considering the large areas involved, limited resources of the NCGC, and the international treaties respecting sovereignty and mutual benefit sharing of host country plant germplasm. The NCGC believes that it plays a valuable role in ex situ conservation because when users know of a publicly available source of many *Gossypium* plants, then it removes the temptation to remove them from the wild.

16.2.7.3.5 Genebank Coverage and Gaps

Table 16.1 reviews the current ex situ status of cotton and its wild relatives at NCGC. The GPS locations of *G. thurberi* were updated by the latest exploration by the NCGC. This needs to be repeated for *G. hirsutum* in Florida. Collections were made from populations of *G. thurberi* from very specific habitats, most of which benefit from some clearing activities by man, but not destroyed by cattle grazing or shaded by forest succession. Roadsides and ditches and some steep rocky ravines were the typical habitats and not likely to be grazed by cattle or quickly overgrown by trees. Representation of *G. hirsutum* from Florida is poor in quantity and quality because of poor description of habitats and lacking GPS information.

Table 16.1 Cotton (*Gossypium* L.) CWR and WUS represented in the National Cotton Germplasm Collection, also indicating Genome ID, quantities, environment of seed increase, and flowering season. For reference are holdings of GENESYS and BGCI

Species	Genome ID	NCGC Holdings	Increase Environment	Flower Time	GENESYS Holdings	BGCI Holdings
***hirsutum* L.** Obsolete cultivars	$(AD)_1$	3532 (48)[a]	CSN, CS	Neutral	11,618	6
Landraces	$(AD)_1$	2140 (1261)	CSN, GH	1–5, 10–12		
***barbadense* L.** Obsolete cultivars	$(AD)_2$	1608 (128)	CSN, CS	Neutral	1932	43
Commensal	$(AD)_2$	n/d	CSN, GH	1–5, 10–12		
tomentosum Nutt. ex seem.	$(AD)_3$	16	GH	1–6, 8, 10–12		
mustelinum Miers ex G. Watt	$(AD)_4$	23	GH	1–5, 11, 12	23	1
darwinii G. Watt	$(AD)_5$	138	GH	1–5, 12	144	4
herbaceum L.	A_1	194	CSN	Neutral	231	60
arboretum L.	A_2	1729	CSN	Neutral	1760	50

(continued)

Table 16.1 (continued)

Species	Genome ID	NCGC Holdings	Increase Environment	Flower Time	GENESYS Holdings	BGCI Holdings
anomalum Wawra	B_1	7	GH	1–5, 9–12	20	3
triphyllum (Harv.) Hochr.	B_2	2	GH	n/a		
capitis-viridis Mauer	B_3	1	GH	1–5, 10–12	1	1
stocksii mast.	E_1	4	GH	1–6, 8–12	10	1
somalense (Gürke) J. B. Hutch.	E_2	3	GH	1–5, 8–12	8	1
areysianum Deflers	E_3	2	GH	3–12	3	1
incanum (O. Schwartz) Hillc.	E_4	4	GH	3–8, 10–12	5	1
longicalyx J. B. Hutch. & B. J. S. Lee	F_1	4	GH	1–6, 9–12	13	1
thurberi Tod.	D_1	41	GH, CS	1–12	53	14
armourianum Kearney	D_{2-1}	10	GH	4, 5, 11	17	1
harknessii Brandegee	D_{2-2}	19	GH	2, 4–12	23	8
davidsonii Kellogg	$D_{3\text{-d}}$	32	GH	1–6, 9–12	37	5
klotzschianum Andersson	$D_{3\text{-k}}$	59	GH	1–5, 10–12	66	1
aridum (Rose & Standl.) Skovst.	D_4	20	GH	1–5, 12	36	1
raimondii Ulbr.	D_5	56	GH, CSN	1–5	62	4
gossypioides (Ulbr.) Standl.	D_6	8	GH	1–5, 11, 12	12	3
lobatum Gentry	D_7	4	GH	2–5, 12	10	2
trilobum (DC.) Skovst.	D_8	11	GH	1–5, 10–12	15	1
laxum L. Ll. Phillips	D_9	5	GH	1–4, 12	9	1
turneri Fryxell	D_{10}	8	GH	1, 3–11	9	4
schwendimanii Fryxell & S. D. Koch	D_{11}	2	GH	2–4, 12	3	1
sturtianum J. H. Willis	C_1	8	GH	1–12	34	14
nandewarense Derera	C_{1N}	6	GH	1–9, 11	8	1
robinsonii F. Muell.	C_2	3	GH	n/a	12	4
bickii Prokh.	G_1	5	GH	1, 6–9, 12	11	3
australe F. Muell.	G_2 (C_3)	11	GH	1–12	41	11
nelsonii Fryxell	G_3 (C_9)	4	GH	1, 3–12	11	2
costulatum Tod.	K_1 (C_5)	2	GH	2–12	4	1
populifolium (Benth.) F. Muell. ex Tod.	K_2 (C_6)	4	GH	1, 4–12	23	2

(continued)

Table 16.1 (continued)

Species	Genome ID	NCGC Holdings	Increase Environment	Flower Time	GENESYS Holdings	BGCI Holdings
cunninghamii Tod.	K_3 (C_7)	1	GH	n/a	7	1
pulchellum (C. A. Gardner) Fryxell	K_4 (C_8)	1	GH	1–12	1	1
pilosum Fryxell	K_5 (C_{10})	1	GH	n/a	5	1
anapoides J. M. Stewart et al., nom. Inval.	K_6	n/a	n/a	n/a		
enthyle Fryxell et al.	K_7	1	GH	n/a		
exiguum Fryxell et al.	K_8	1	GH	2–5, 7–11		
londonderriense Fryxell et al.	K_9	1	GH	n/a		
marchantii Fryxell et al.	K_{10}	2	GH	1, 3–12		
nobile Fryxell et al.	K_{11}	2	GH	1–12		
rotundifolium Fryxell et al.	K_{12}	1	GH	2–7, 9–12		1

Boldface species are those represented as CWR and WUS from North America and selected nearest countries of the Atlantic Ocean

[a]Number in parentheses are the subset of the NCGC accessions that have an origin specific to North America and selected countries of the Atlantic

CSN counter season nursery, *CS* College Station Texas field, *GH* greenhouses in CS, Texas

n/d – not determined, cultivated and commensal types not separated for tallying numbers

Neutral flowering is not seasonally dependent

Month of recorded flowering represented by number, January = 1, December = 12

n/a – not currently in the NCGC or not currently grown

16.2.7.3.6 Needs and Opportunities

Resources for germplasm conservation have plateaued in the USA and have severely decreased in other nations. It is a global concern as even the Russian (VIR) and Australian (CSIRO) collections have dwindled rapidly for lack of funds and support, because support was driven by their overall economy. Work within the NCGC is important to streamline activities and avoid duplicative maintenance. Traditional morphological, agronomic, and modern molecular characterization activities of collections add to costs but are essential to improve exchanges and even guide specific explorations for priority conservation activities and closing genetic gaps in collections. Knowledge of the status of CWR and WUS facilitates discussion on in situ conservation. Ex situ conservation is the failsafe so that seed can be used to repopulate habitats that lost wild populations of WUS and save CWR that have been abandoned. The distribution trends by the NCGC shows that users will continually revisit the CWR and WUS for using naturally colored cottons, ornamental WUS, helping in the conservation efforts, and researching the wide genetic diversity offered by CWR and WUS. Identification and prevention of further duplication of material is essential to streamline activities and cut down on costs. Collection sizes are kept to a minimum to save costs, and resources and germplasm exchanges are more focused on gaps.

16.2.7.3.7 Suggestions on Ways to Improve Conservation

Historically exchange and cooperative exploration among collections was considerable (Frelichowski and Percy 2015) but has declined with a variety of international treaties. Uneven financial resources across nations worldwide make it imperative that the major collections communicate with other nations for opportunities to conserve germplasm. The major collections can coordinate efforts to identify gaps in their collections and communicate their status, as was done in Campbell et al. (2010). Cotton suffers from not having an international center like ICRISAT, CIMMYT, etc. that helps keep international focus and resources on conservation. Each nation has its own valuable genetic resources for conservation, and efforts by all nations represent a balanced and equitable approach to ensuring the safety of future agriculture by conservation of their own unique agricultural resources. Development of a core collection in the NCGC with taxonomic, passport, descriptor, and marker characterization data may streamline the exchange of smaller sets of accessions to fill in gaps and provide necessary cotton genetic diversity to safeguard each collection. For example resistances to CLCuD identified in cotton germplasm would be essential to distribute to all countries so the disease outbreak and further spread (to CWR and WUS) can be prevented as well as safeguard their agronomic resources, the true intent of all genetic resources.

The plant breeding sector accounts for the biggest users and proponents of the NCGC (Gepts and Hancock 2006). The greater access to the NPGS online and general promotion of plants and agriculture in many outlets, primarily the Internet, have helped to expand popular public interest and demand (DeSilva 2012). This is evident with greater public awareness of genetic resources, such as through GRIN-Global (Postman et al. 2010), Seed Savers Exchange (Volkening 2006), Svalbard Global Seed Vault (Fowler 2008), and others. Even with a primarily commercialized crop such as cotton, the average consumer is showing greater interest in the NPGS, evident by an increased demand for seed at the NCGC. A popular use of cotton is as a source of organic fiber for homespun products and with natural brown or green coloring to avoid the use of chemical dyes. Much of this interest demands conventionally bred cotton germplasm which is practically nonexistent commercially. Its similarity to *Hibiscus* L. (Fryxell 1979) also has some users marveling at the ornamental value of some cotton or *Gossypium* accessions. The interaction of the USDA-ARS, University and Extension Scientists, and commodity groups (National Cotton Council of America, Cotton Incorporated) with the users of the NCGC and the public (facility tours, publications, online news, etc.) support the NCGC and cotton community germplasm activities. Improvement in the productivity and profitability of cotton for the growers and the rest of the production chain is a key ingredient to maintain the lifeline of budgetary support for the NCGC activities.

Coordination and collaboration with other major cotton collections will be essential to preserve the worldwide status of cotton and *Gossypium* resources. Each of the collections will have their own access to native *Gossypium* and unique cotton pedigrees. Exploration trips within the US borders have been initiated with *G. thurberi* and are planned for *G. hirsutum*. Characterizations of each collection will improve the gap analysis of each collection and highlight those in greatest danger of being lost if not conserved ex situ or in situ.

16.3 Rediscovering *Hesperaloe* as a Fiber Crop

16.3.1 Crop Origin and History of Use Worldwide

Leaves of the genus *Hesperaloe* Engelm. (Asparagaceae) contain long and thin fibers that are a potential source of raw material for paper production. A variety of plant material has been used to manufacture paper, including sisal (*Agave sisalana* Perrine, Agavaceae), abaca (*Musa textilis* Née), mulberry (*Morus papyrifera* L.) bark, papyrus (*Cyperus papyrus* L.), hemp (*Cannabis sativa* L.), flax (*Linum usitatissimum* L.), cotton (*Gossypium hirsutum* L.), cereal straw, and various other timber and nonwoody plants (Dewey 1943; Clark 1965; Hurter and Eng 2001; Pahkala and Pihala 2000; Saijonkari-Pahkala 2001; Ververis et al. 2004; Virk et al. 2012). Sisal and abaca have been used to produce different qualities of paper, for example, banknotes, various filters, cigarettes, carbon paper, tea bags, bags, and heavy-duty sacks, tissues and diapers, and other industrial products such as ropes, twine, and carpets (Corradini 1979; Márquez et al. 1996; Savastano et al. 2004).

The wide applicability of imported sisal inspired the American paper industry in 1985 to seek a domestic supply of sisal fibers (McLaughlin 1996). Sisal originates from tropical regions and could not survive the cold temperatures even in southern Arizona; thus the search was on for other plants in the Agavaceae family that would be climatically adapted and suitable for paper production. In 1986, among the plants evaluated (*Agave* L.*, Dasylirion* Zucc.*, Furcraa* Vent.*, Hesperaloe, Nolina* Michx. and *Yucca* L.), two species of *Hesperaloe* (*H. funifera* (K. Koch) Trel. and *H. nocturna* Gentry) had superior raw material characteristics for production of high-quality paper; their fibers were hard and had the highest fiber ratio of length to width (McLaughlin and Schuck 1991, 1992). Paper made with *Hesperaloe* fibers has a higher tensile and burst strength than that made from sisal but exhibits a lower resistance against tearing (Fairbank and Detrick 2000; McLaughlin 2000, 2003; McLaughlin and Schuck 1991; Reeves et al. 1994), and this might limit the range of products made from *Hesperaloe*. Potentially, lignin from *H. funifera* might be a source of material for biofuel production (Sánchez et al. 2010).

The exact time when *Hesperaloe* started to be used by humans is not known, as various Agavaceae were utilized for fiber in North, Central, and South America. Agave fibers were used by ancient Aztecs and Peruvians for weaving coarse cloth (Rogers 2000). The Papago (current name Tohono O'odham Nation) and Pima tribes (current name Akimel O'odham) traded agave fibers, and the Yavapai, some Apache tribes, and other Native American populations used strips of agave leaves as binding material and to produce cordage and threads (Castetter et al. 1938; Trelease 1902). Trelease (1902), an American botanist, reported that in 1847, Wislizenus, a physician, explorer, and botanist, collected a *Hesperaloe* specimen (named *Yucca* at that time) in the northeast region of Monterrey. Some years later, in 1878, Krauskopf, a businessman from Texas, offered for sale *Hesperaloe* plants collected at the western part of the Nueces River (Starr 1995). Trelease assumed that all *Hesperaloe* cultivated in Europe were derived from Krauskopf's original collection; however, Starr (1997) indicated that Cambridge botanical gardens grew plants of the genus collected by Wright in 1849. In 1900, Trelease spotted red flowered *Hesperaloe* plants in the city of San Antonio, Texas; after some nomenclature considerations, the species was described as *H. parviflora*. The first cultivated plants of *H. nocturna* were observed by Gentry in a garden located in Nogales, Arizona (Gentry 1967). In 1943, *H. funifera* was mentioned as a fiber plant on a list of "long or multiple-celled fibers with the use to make twine and rough sacks" (Dewey 1943).

In the 1990s, scientists from the University of Arizona used wild populations of *Hesperaloe* in selections aimed at improving fiber quality and quantity and enhancing agronomic characteristics (McLaughlin and Schuck 1992). Under experimental cultivation, maximum biomass was harvested in the fifth growing season; a combined plant yield harvested in the third and later in the fifth growing year did not exceed the yield harvested, only once in the fifth year. This is due to the plant biological development; lateral rosettes usually develop in the third year and the maximum leaf growth is observed in the fifth year (McLaughlin 1995). The next harvest was suggested to be done in the seventh cultivation season. The cultivation length of a stand is not known, but it was speculated for 11–15 years. Later, agronomic research recommended the first harvest after five years of cultivation and, following that harvest, every three years (McLaughlin et al. 2000). Flower stalk removal in the fourth and fifth year increased the harvested leaf mass by 27% (McLaughlin et al. 2000; McLaughlin 2003). It was speculated that removing flower stalks would not limit seed availability in the future considering that seeds are used only to establish stands at the beginning of a cultivation cycle and for potential crop commercialization (McLaughlin et al. 2000). After a plant stand is established, *H. funifera* uses water more efficiently than productive C_3 crops, for example, potato, beans, rice, and wheat (McLaughlin 1995; Nelson and McLaughlin 2003; Ravetta and McLaughlin 1996). According to Ravetta and McLaughlin (1993), biomass production and stand establishment are expected to improve with nutrient and water management. No diseases or pests were reported for plants of the genus. One of the major commercialization impediments seems to be the long period between stand establishment and the first and subsequent biomass harvests (McLaughlin 1996). Currently, *Hesperaloe* plants are used as xeric landscape ornamentals due to their low water requirements (McLaughlin 1995; Nelson and McLaughlin 2003). Ornamental cultivars such as "Perpa" with red-colored flowers and "Perfu" with pink-colored flowers (both selected from *H. parviflora* (Torr.) J. M. Coult.) are patented (Gass 2009, 2011). Plants with yellow-colored flowers of the same species are also commercially available (Richwine et al. 1996; Harvey 2014; Caron and Beddes 2016). Cultivars developed for fiber cropping have not yet been commercialized.

H. funifera and *H. nocturna* have a CAM (Crassulacean acid metabolism) photosynthetic pathway which makes them suitable to be grown in arid lands (Ravetta 1994; Ravetta and McLaughlin 1993; Yang et al. 2015). A potential increase in temperature, expected in most regions under climatic change projections, will expand the regions potentially suitable for cultivation of CAM plants such as agave and cacti (Nobel 1996; Yang et al. 2015). Such plants may withstand temperatures up to 55 °C, but do not survive freezing (Nobel and Bobich 2002). An increase of atmospheric CO_2 concentration, also associated with future climate projections, may expand gas uptake between 30% and 70% in CAM species such as *Agave deserti* Engelm., *Ananas comosus* (L.) Merr., *Ferocactus cylindraceus* (Engelm.) Orc, and *Opuntia ficus-indica* (L.) Mill. leading to increased biomass production (Nobel 1991, 1996; Nobel and Hartsocks 1986; Yang et al. 2015). Thus by inference, anticipated temperature and CO_2 increases might lead to enlarging potential growing areas and increasing biomass production of *Hesperaloe* plants. Agavaceae genera can be productive on marginal lands unsuitable for C_3 (e.g., *Beta* L.*, Manihot* Mill., *Triticum* L. species) and C_4 crops (e.g., *Saccharum* L., *Sorghum* Moench*, Zea mays* L.); hence, increased cultivation of *Hesperaloe* can be noncompetitive with other crops (Nobel 1991).

16.3.2 Wild Species, Distribution and Habitat, and Genepool Classification

Hesperaloe plants are evergreen, acaulescent perennials, with slow growth, stiff upright leaves (the leaf architecture varies for species) with a rough texture, and a long flower stalk. The leaves form a rosette from a single meristem; lateral rosettes occur when the primary rosette produces a flower stalk. The secondary (lateral) rosettes bunch together each forming flower stalks at a certain growing time that usually happens around the 3rd to 4th year in plants under cultivation or in the 5th year in wild populations (McLaughlin 1995; McLaughlin and Schuck 1992; Robbins 2017). The flowering time depends on the species, ranging from mid-spring to late fall. *Hesperaloe* plants have bell-shaped flowers that are white-greenish to white, with a shadow of purple in *H. funifera*; greenish-white with a tinge of lilac in *H. nocturna*; and yellow, orange, and to different shades of red in *H. parviflora* (Starr 1995; Trelease 1902). The flowers are self-incompatible. Studies on *H. parviflora* determined hummingbirds to be the primary pollinators (Pellmyr and Augenstein 1997), but *Hesperaloe* flowers are also foraged by bees, and night-blooming species are visited by bats and hawk moths (Rocha et al. 2006; Starr 1995). Seeds are in green capsules turning brown at maturation and not all capsules have viable seeds.

Starr (1997) reports four taxa occurring in the eastern part of the Sierra Madre Occidental, from Texas to San Luis Potosi, Mexico, and two taxa endemic to the western side of the Sierra Madre mountain range, Sonora, Mexico. Specifically, the habitat of wild populations is spread over the Mexican provinces of Sonora (*H. nocturna* and *H. tenufolia* G. Starr), Coahuila (*H. parviflora* and *H. funifera* ssp. *funifera* (Koch) Trelease), San Luis and Potosi (*H. funifera* ssp. *changii* G. D. Starr), Nuevo Leon (*H. campanulata* G. Starr), Southwestern Texas (*H. parviflora* and *H.*

funifera ssp. *funifera*), and over Central-North Texas (*H. parviflora*) (Starr 1997). A survey of known, wild *Hesperaloe* populations in Texas reported *H. parviflora* at Devils River and lower Pecos River of Val Verde County, an area adjacent to Mexico, and *H. engelmanii* Krauskopf ex Baker (a taxon included in *H. parviflora* by Starr in 1997), along the Nueces River in Edwards County, San Saba County, and Central Texas (Turner and Turner 2002). *H. parviflora* was also observed in the Amistad National Recreation Area, Texas (Poole 2013).

Populations of *H. funifera* and *H. nocturna* are the most studied and evaluated and have the highest potential for a successful domestication and commercialization. *H. funifera* (Koch.) Trel. is native to Southern Texas and the Chihuahuan Desert area in Northern Mexico (ASU 2017; Ravetta and McLaughlin 1993). In wild populations, leaves of this species are up to 1.2 m tall; the rosettes are about 1–1.5 m wide with 1.8–3 m tall flower stalk; in cultivation the flower stalk might be 2–5 m tall (McLaughlin et al. 2000). *H. nocturna* Gentry was discovered in north-central and north-eastern Sonora and Sierra El Tigre, Mexico, and has 1.5-m-tall leaves, 1–2-m-wide clumps of rosettes and 1.5–2-m-tall flower stalks (Gentry 1967; Starr 1995; Avila and Jacobs 2008). Starr (1995) speculated that *H. funifera* and *H. nocturna* could have evolved from the same ancestor some 10,000 years ago; both are night bloomers but are found on the opposite sides of the Sierra Madre mountain range. Wild populations of *H. parviflora* (Torr.) J. M., Coult. were found in Central and Western Texas. Plants of the species are 0.9–1.5 m tall and 0.6–1.2 m wide with flower stalks reaching 1.5 m (Plant Database 2017; TNPD 2017).Wild plants of the *Heseraloe* genus occupy arid environments; once established they are tolerant to drought, surviving on less than 12 inches of annual rainfall. The species are also frost tolerant, with *H. funifera* to −9.4 °C, *H. nocturna* to −12.2 °C, and *H. parviflora* to −17.8 °C (Starr 1995). The upright leaves, most prominent in *H. funifera* are assumed to be an adaptation to hot and dry environments (Ravetta and McLaughlin 1993). A species richness map for the genus illustrates where species are most concentrated in North America (Fig. 16.7).

Changes in taxonomy of the *Hesperaloe* genus have a long history. Previous names of *Aloe yuccaefolia* A. Gray*, Yucca parviflora* Torr, and *Yucca funifera* K. Koch were gradually changed. In 1871, Engelmann created the genus name *Hesperaloe*; in 1894, Coulter changed the name *Yucca parviflora* (name that was given by Torrey in 1859) to *Hesperaloe parviflora* and *Y. funifera* for *H. funifera* (Starr 1995). In 1995, Starr described three taxa, previously reported by Gentry (1967): *H. funifera* (Koch) Trelease, *H. nocturna* Gentry, and *H. parviflora* (Torr.) Coulter, as well as two new unnamed accessions described as "Bell Flower *Hesperaloe*" and "Narrow Leaf *Hesperaloe*." Starr's 1997 taxonomic revision of the genus distinguished five species: *H. campanulata* G. D. Starr; *H. funifera* (Koch) Trelease, with two subspecies – *H. funifera* subsp. *funifera* (Koch) Trelease and *H. funifera* (Koch) Trelease subsp. *chiangii* G. D. Starr; *H. nocturna* H. S. Gentry; *H. parviflora* (Torrey) J. M. Coulter [previously named *H. paviflora* (Torrey) Coulter [var.] *engelmanni* (Krauskopf) Trelease]; and *H. tenuifolia* G. D. Starr (Starr 1997). In 2002, Turner and Turner proposed to separate *H. engelmanni* as a separate species. GRIN Taxonomy lists five *Hesperaloe* species (GRIN 2017), identical to those

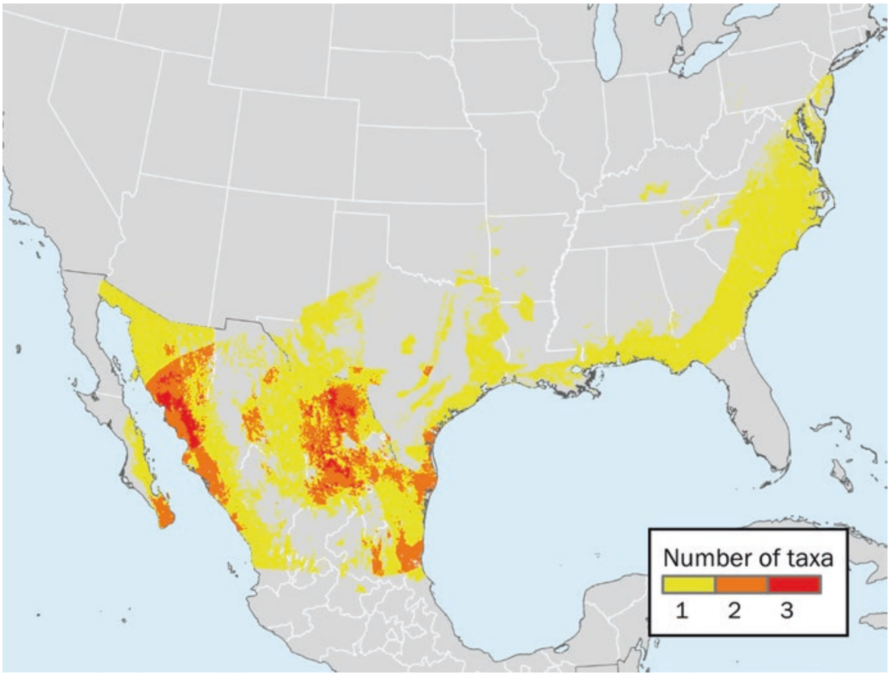

Fig. 16.7 Species richness map of modeled potential distributions of North American *Hesperaloe* taxa, based on climatic and edaphic similarities with herbarium and genebank reference localities. Warmer colors indicate areas where greater numbers of taxa potentially occur in the same geographic localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

revised by Starr in 1997 (Table 16.2). According to phylogenetic studies, the *Hesperaloe* genus is closely related to *Yucca* (Rocha et al. 2006).

Wild populations from various habitats are the major gene sources of traits to be included in cultivar development. University of Arizona made and maintains several breeding selections for the same purpose. Studies on fiber length and width in *H. funifera* showed significant variation between wild populations and less within populations, and fiber length also varies between leaf sections but not with the plant age (Mc Laughlin and Schuck 1992). The last characteristic might be helpful in the crop improvement process because it will not be necessary to delay selection until the fifth growing year to assess the fiber value. Currently, the University of Arizona works on improvement of selected agronomic characteristics such as reliable seed production, establishing breeding systems, and fiber management (Ward 2017). Shortening the time from sowing to the first biomass harvest seems to be important; a shorter time than five years to the first biomass harvest would support the economics and commercialization of *Hesperaloe* as a source of raw material for paper production.

Table 16.2 *Hesperaloe* Engelm. species listed in GRIN Taxonomy

Taxon[a]	Common names	Native to
H. campanulata G. Starr	Bell-flowered hesperaloe[b]	Mexico, Nuevo Leon
H. funifera (K. Koch) Tre.	Giant hesperaloe, New Mexico False yucca, New Mexico False yucca, giant yucca, Coahuilan hesperaloe[c]	Mexico, Coahuila, Nuevo Leon, San Luis Potosi; USA, Texas
H. nocturna gentry	Night-blooming hesperaloe, night-flowering hesperaloe[d]	Mexico, Sonora, Sierra el Tigre
H. parviflora (Torr.) J. M. Coult.	Red Yucca, red hesperaloe, coral yucca, red-flowered false yucca, hummingbird yucca, samandoque[e]	Mexica, Coahuila; USA, Texas
H. tenuifolia G. Starr		Mexico, Sonora

[a] GRIN Taxonomy (2017)
[b] Hochstätter (2017) and SNAWA (2017)
[c] ASU (2017), ITIS (2017), USDA, Natural Conservation Service (2017), and Starr (1995)
[d] Avila and Jacobs (2008), ITIS (2017), and Starr (1995)
[e] TNPD (2017), Plant Database (2017), and Starr (1995)

16.3.3 Conservation Status

With the exception of *H. funifera*, all species in the *Hesperaloe* genus have limited ranges, and due to insufficient surveys, the status of in situ populations is unclear (Hodgson 1997). No information was found on protection status for *Hesperaloe* within the USA or Mexico. *Hesperaloe* plants are of interest to ornamental horticulture, and with the modern discovery of their high-quality fiber characteristics, they are of interest to agriculture. Wild plant populations of the genus are also subject to livestock and wild animal foraging and impacts from tourism; thus population sizes appear to be in decline (Poole 2013; Turner and Turner 2002). According to Turner and Turner (2002), the number of populations and individual plants observed in Texas natural *Hesperaloe* habitats is diminishing. Though the genetic and phenotypic diversity range of the genus is not comprehensively known, in situ conservation on state- and federal-owned land across a range of populations would be a sound beginning for conservation of these species.

The USDA-ARS National Plant Germplasm System maintains a total of 13 accessions of *H. funifera, H. nocturna*, and *H. parviflora* at the National Arid Land Plant Genetic Resources, Parlier, California (NALPGRU 2017) (Table 16.3).

The genetic pool of the NALPGRU collection is narrow, containing only one accession collected in the USA. Seeds maintained at the Parlier genebank are freely distributed for plant breeding and research purposes. Characterization efforts conducted at that site are focused on selected agronomic characteristics. The same three species are on the “Recommended Plant List” of the Desert Botanical Garden in Phoenix, Arizona (2017). The Phoenix garden has *Hesperaloe* plants in its landscape; both forms, i.e., seed distribution and inclusions in cultivation, represent

Table 16.3 *Heseraloe* Engelm. accessions maintained at National Arid Land Plant Genetic Resources, Parlier, California

Taxon	No. of accessions	Collection area
H. funifera (K. Koch) Trel.	11	Mexico
H. nocturna Gentry	1	Mexico
H. parviflora (Torr.) J. M. Coult.	1	USA

viable forms of ex situ conservation. An interesting ex situ conservation concept was presented by West (2004) suggesting establishing urban and residential landscapes with native flora specific to the region. *Hesperaloe*, as a perennial xerophyte and having ornamental characteristics, fits well in that preservation concept. The 1997 botanical gardens "Action Proposal" for conserving genetic diversity included conservation undertaking for the Agavaceae family; however, *Hesperaloe* was not mentioned specifically (Oldfield 1997). Expanding the genetic pool of the ex situ collection, e.g., via seed collection from still existing habitats in the USA and Mexico or seed exchange with Mexican genebanks, would contribute to the *Hesperaloe* germplasm preservation and availability for breeding of cultivars with high fiber quality, research, and repopulation of endemic sites.

One third of the global land area has an arid or semiarid environment. Given the predictions of temperature and atmospheric CO_2 increases, plants of the *Hesperaloe* genus as well as of other genera adapted to arid habitats, especially those with CAM photosynthetic pathways and producing significant aboveground biomass (e.g., *Agave* L. source of fibers and fodder, also used to produce nonalcoholic and alcoholic beverages; *Opuntia* Mill., human food, fodder for cattle, soil erosion control; and *Stenocereus* (A. Berger) Riccob., specialty fruit), have a considerable potential to become economically relevant in the future (Nobel and Hartsocks 1986; Noble 1991, 1996). Hence, existing and proposed conservation efforts at the present are well justified.

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Chapter 17
Native Grass Species for Forage and Turf

Melanie L. Harrison, Vicki L. Bradley, and Michael D. Casler

Abstract North America has an abundance of native grass species including both cool-season and warm-season grasses. These grasses serve a multitude of purposes including use as forage, turf, erosion control, riparian buffer, wildlife habitat, ornamental, and biofuel. Although their importance in agriculture has been somewhat overshadowed by the use of non-native grasses in both forage and turf breeding programs, their value has not been overlooked. As the demand and interest in native grasses have risen in recent decades, germplasm exploration and collection of native grasses have likewise increased. The need to conserve North American native germplasm has become more and more evident as modern agricultural practices, urbanization, and changing climates threaten native populations and highlight the need for preserving high-quality, representative germplasm. Current plant genetic resources, both in situ and ex situ, provide valuable plant germplasm to researchers and plant breeders, but there is a need to better represent the genetic diversity and fill genetic gaps of these important species.

Keywords Grass · Native · North America · Forage · Turf · Germplasm · Genetic resources

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M. L. Harrison (✉)
USDA, Agricultural Research Service, Plant Genetic Resources Conservation Unit, Griffin, GA, USA
e-mail: melanie.harrison@ars.usda.gov

V. L. Bradley
USDA, Agricultural Research Service, Western Regional Plant Introduction Station, Pullman, WA, USA
e-mail: Vicki.Bradley@ARS.USDA.GOV

M. D. Casler
USDA, Agricultural Research Service, U.S. Dairy Forage Research Center, Madison, WI, USA
e-mail: michael.casler@ars.usda.gov

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17.1 Introduction

Grasses are one of the most important families in the Plant Kingdom providing the majority of energy and nutrients to feed the world's population. Besides providing cereal grain directly for human consumption, they are the primary sources of feed for livestock and poultry. In addition, they provide environmental benefits in their use in erosion control, wildlife habitat restoration, and riparian buffers and are used aesthetically as turf and ornamentals. This chapter focuses on their use as forages and turf. Although introduced grass species predominate forage and turf production and use in the USA and Canada, there is an abundance of native species, both warm season and cool season, which are highly desirable. Unfortunately, their use is limited compared to introduced species, and as a result, attention to development and breeding of these native species has been limited as well. Compared to Bermuda grass, fescue, and other major forage and turfgrasses, the native species are still at the stage of being considered wild utilized species. We will only cover the major native grass species currently being utilized as forage and turf that have active breeding programs. These will include warm-season forage grasses; warm-season turf types, seashore paspalum and buffalo grass; and cool-season forages.

17.2 Warm-Season Forage Grasses

Once covering an area of 170 million acres, the tallgrass prairie has been reduced to less than 4% of its original size according to the National Park Service (NPS 2017). The four predominant grass species of this ecosystem include switchgrass (*Panicum virgatum* L.), big bluestem (*Andropogon gerardii* Vitman), little bluestem [*Schizachyrium scoparium* (Michx.) Nash], and Indiangrass [*Sorghastrum nutans* (L.) Nash]. All four species can be found throughout North America from Canada to Mexico; however, their populations are reduced mainly to small remnant prairies and sparse populations outside the tallgrass prairie states. Using MaxEnt, species distribution models built using occurrence points coupled with climatic and soil similarity data demonstrate the broad geographic range of each of these four species (Figs. 17.1, 17.2, 17.3, and 17.4). The USDA Natural Resources Conservation Service (NRCS) has developed lines of each species for use as forage, wildlife habitat restoration, riparian buffers, and erosion control for decades (USDA, NRCS 2016). Efforts have mainly focused on the collection of germplasm and selection of desirable plants from open-pollination crossing blocks at NRCS Plant Materials Centers (PMCs) across the country. The resulting plant releases are closely related to natural populations (Casler et al. 2015). More intensive breeding efforts have focused on switchgrass as a biofuel candidate, and several advanced cultivars have been released including 'Liberty' (Vogel et al. 2014), 'Bomaster,' and 'Performer' (Burns et al. 2008a, b). There is still great potential that has not been utilized in these species for forage and biomass development.

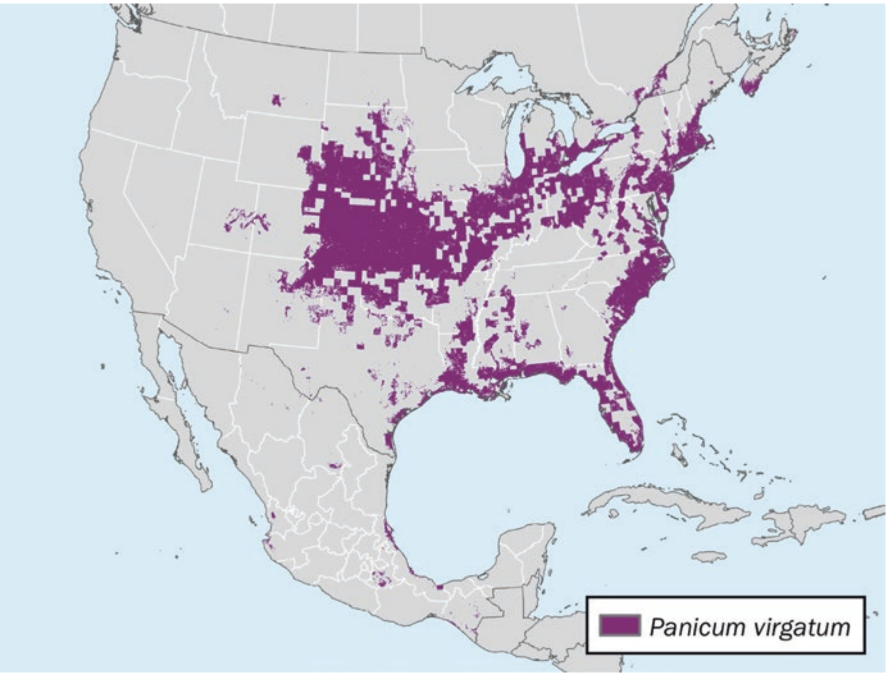

Fig. 17.1 Modeled potential distribution for switchgrass, *Panicum virgatum* L., based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

A number of in situ conservation sites exist for the tallgrass prairie species in both the private and public realm. At 39,000 acres, Joseph H. Williams Tallgrass Prairie Preserve in Oklahoma is reputed to be the largest tract of tallgrass prairie preserved in the world (The Nature Conservancy 2016). The Tallgrass Prairie National Preserve, managed by the National Park Service and co-supported by the Nature Conservancy, protects over 10,000 acres in the Flint Hills region of Kansas (National Park Service 2017). Various other agencies, including federal, state, and local organizations, preserve smaller tracts (Casler et al. 2015). The USDA National Plant Germplasm System (NPGS) preserves all four of these native tallgrass prairie species.

17.2.1 Panicum virgatum L.

There are two main ecotypes of switchgrass: upland and lowland. While the two ecotypes are morphologically and phenologically distinct, they have slightly overlapping geographic distributions, and they show strong evidence for past hybridizations and gene flow (Zhang et al. 2011a, b). Currently, the NPGS switchgrass

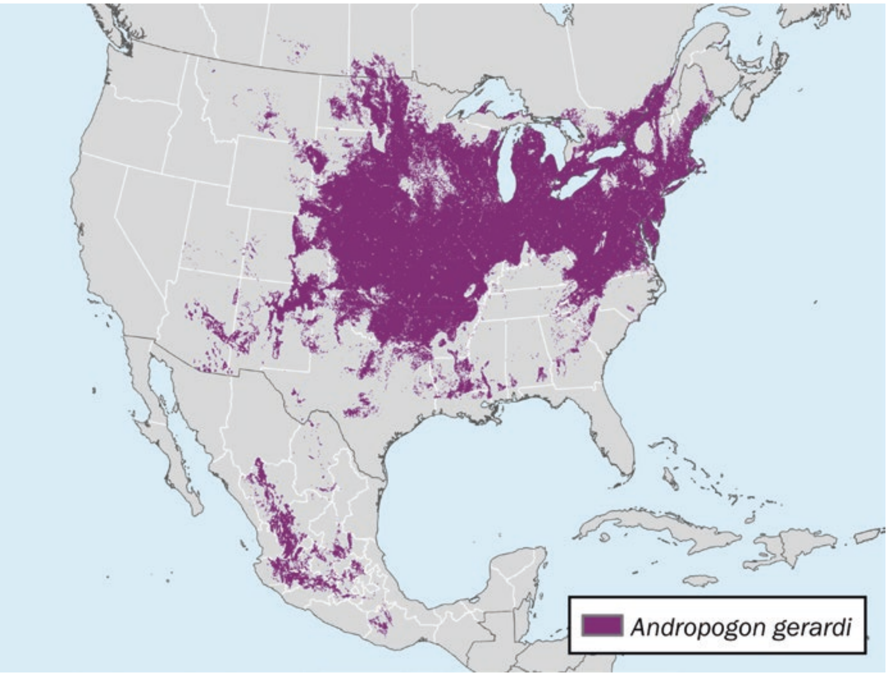

Fig. 17.2 Modeled potential distribution for big bluestem (*Andropogon gerardi* Vitman), based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

collection includes 456 active accessions collected from 25 different states. Effort has been made to increase both the quantity and diversity of switchgrass germplasm in the national collection, particularly as recent DNA sequencing studies have help to identify and delineate specific gene pools and germplasm groupings within each of the two ecotypes (Lu et al. 2013; Evans et al. 2015). A total of six collection trips funded by the USDA Plant Exchange Office (PEO) have been completed since 2006 resulting in the acquisition of 121 accessions from 16 states. These collections have focused on acquiring germplasm in areas where switchgrass germplasm had not been adequately collected including the Southeastern and Northeastern USA. In particular, the Southeastern USA was a target site for germplasm collection since this area is theorized to be a site of high genetic diversity for switchgrass, particularly for the lowland ecotype (Zhang et al. 2011a, b). Mexico and Cuba are included in this high-diversity region but are severely underrepresented in the NPGS switchgrass collection. Donations from NRCS have been made to the NPGS including a large donation of material collected in New York by the NRCS Big Flats Plant Material Center. Switchgrass germplasm collections have also been developed by private industry and state universities, but access to the material is limited, whereas germplasm in the national collection is freely accessible. A thorough review of switchgrass genetic resources was recently published,

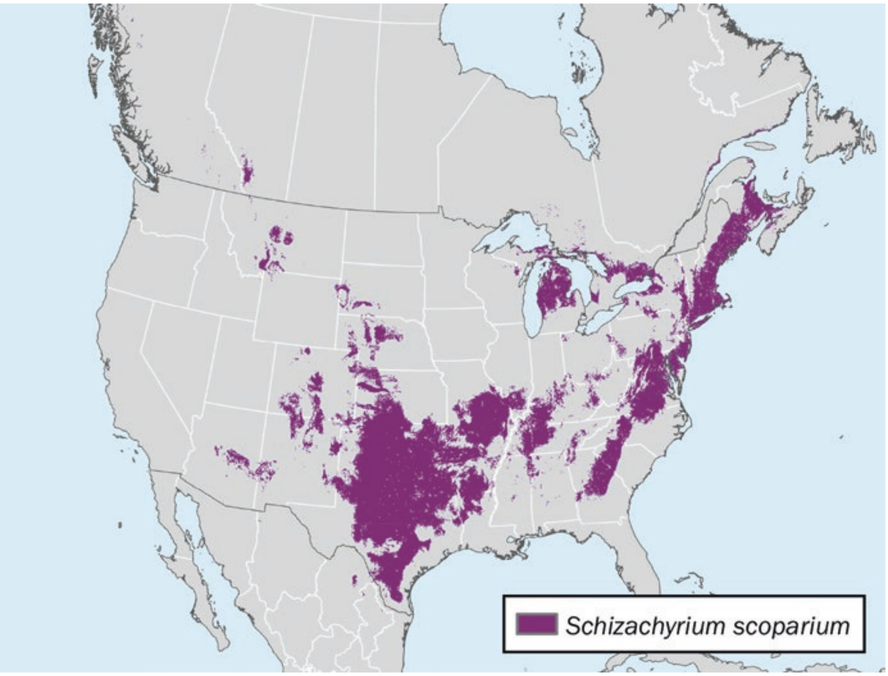

Fig. 17.3 Modeled potential distribution for little bluestem [*Schizachyrium scoparium* (Michx.) Nash], based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

highlighting the need for acquisition and regeneration efforts (Casler et al. 2015). Requests for switchgrass germplasm have risen significantly in recent years with 6307 accessions distributed during 2006–2015 compared to only 444 distributions during 1998–2005.

Wild species related to switchgrass, including bitter beach grass (*Panicum amarum* Elliot), are also being preserved in the national collection although not as extensively. Currently, we are not aware of any effort to incorporate the introgression of these species into switchgrass breeding programs. *Panicum hallii* Vasey is a diploid relative of switchgrass that has been developed as a model species for conducting genetic and genomic studies within the genus (Juenger and Wolfrum 2016). While there are only four accessions of *P. hallii* in the NPGS system, the University of Texas has a fairly large and extensive collection that includes both upland and lowland types that mimic the upland-lowland divergence found in *P. virgatum* (Juenger and Wolfrum 2016). *Panicum rudgei* is the closest known diploid relative of switchgrass (Triplett et al. 2012), and its DNA sequence has been used to realign the switchgrass reference genome, including assignment of chromosome homologs into a “B” and “N” genome to generate the V4.1 version of the reference genome, which will be published later in 2017 on Phytozome (https://phytozome.jgi.doe.gov).

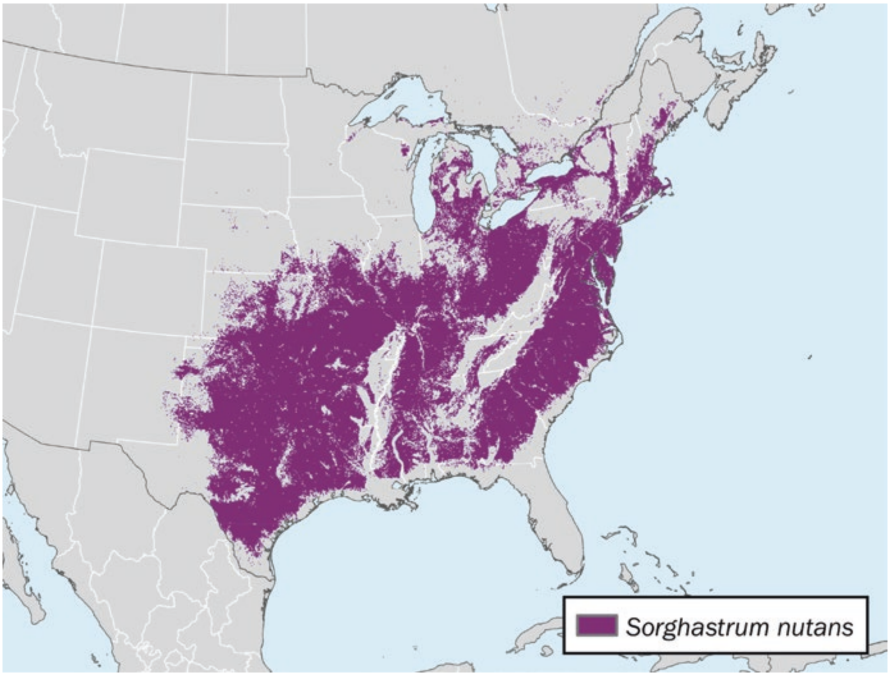

Fig. 17.4 Modeled potential distribution for Indiangrass [*Sorghastrum nutans* (L.) Nash], based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

17.2.2 Schizachyrium scoparium (Michx.) Nash

Little bluestem [*Schizachyrium scoparium* (Michx.) Nash] has a broad geographic range in North America, from the midgrass prairie to the Atlantic Seaboard, including ecotypic variation related to climate and soil fertility (Huff et al. 1998). There are approximately 60 *Schizachyrium* species that have been described, 9 of which are native to North America North of Mexico including *spadiceum* (Swallen) Wipff, *tenerum* Nees, *maritimum* (Chapm.) Nash, *littorale* (Nash) E.P. Bicknell, *cirratum* (Hack.) Wooton & Standl., *sanguineum* (Retz.) Alston, *scoparium* (Michx.) Nash, *niveum* (Swallen) Gould, and *rhizomatum* (Swallen) Gould (Wipff 2003). Until recently, there were only 34 accessions of little bluestem in the NPGS collection, most of which were collected in Texas (22 accessions). Using SSR analysis, Harris-Shultz et al. (2015) found minimal genetic diversity in this original little bluestem collection. To address this issue, germplasm acquisition has been made a priority by the curatorial staff in Griffin, GA. In 2015, 34 populations of little bluestem germplasm were collected from the Northeastern USA in the states of Connecticut, Massachusetts, Maine, New Hampshire, New York, Rhode Island, and Vermont.

There are few other *Schizachyrium* species in the collection. There are three accessions of *S. sanguineum* collected in the USA (Arizona), Mexico, and Paraguay; four accessions of *S. condensatum* (Kunth) Nees; and five accessions of *S. macrostachyum* (Benth) A. Camus, collected from Brazil and Argentina.

17.2.3 Andropogon gerardi Vitman

There are 1257 accessions of *Andropogon* conserved in the NPGS collection, 1222 of which are big bluestem, *Andropogon gerardi*. The majority of the accessions (1059) were collected in North and South Dakota in the 1980s and donated to the collection by Arvid Boe (North Dakota State University, Fargo, ND). Most of this germplasm is maintained in Fort Collins, CO, and is not available for distribution; however, a subset selected to represent the geographical distribution of the Dakota germplasm is being maintained in the working collection in Griffin, GA, and is available for distribution. Recent efforts have greatly expanded the diversity of the big bluestem collection. Donation of 93 accessions in 2009 by Paul Salon (NRCS, Big Flats Plant Materials Center, Corning, NY) collected in Pennsylvania and New York and donation of 14 accessions in 2013 by Michael Casler (USDA, Agricultural Research Service, Madison, WI) collected in Wisconsin significantly increased the geographic coverage of the germplasm. Acquisition of 13 populations from the Northeastern USA including the states of Connecticut, Massachusetts, Maine, New Hampshire, Rhode Island, and Vermont through a USDA, PEO-funded collection trip was completed in 2015.

Thirteen of the approximately 120 described species of *Andropogon* are native to North America, North of Mexico, including *gerardi* Vitman, *hallii* Hack., *gracilis* Spreng., *gyrans* Ashe, *longibarbis* Hack., *virginicus* L., *glomeratus* (Walter) Britton, Sterns, & Poggenb., *ternarius* Mich X., *liebmanni* auct. non Hack, *tracyi* Nash, *brachystachys* Chapm., *arctatus* Chapm., and *floridanus* Scribn (Campbell 2003). Outside of big bluestem, only four of these species are conserved in the NPGS collection. There are 17 accessions of sand bluestem, *A. hallii*, which is a close relative of big bluestem typically found in sandy areas. There are four accessions each of bushy bluestem, *A. glomeratus*, and broomsedge, *A. virginicus* L. No priority has been made to acquire these two species as they are prevalent in their native range, being weedy in areas. There are two accessions of *A. ternarius* Mich X., split bluestem, which is native to the Southeastern USA and Northern Mexico. The remaining *Andropogon* species in the collection, *A. distachyos* L., *A. munroi* C. B. Clarke, *A. paniculatus* Kunth, and *A. ternatus* (Spreng.) Nees are non-native species. Effort is needed to increase the genetic diversity of the big bluestem collection and acquire additional native *Andropogon* species. According to Price et al. (2012), collection of big bluestem germplasm outside the tallgrass prairie region should provide diverse, unique germplasm that would be useful in plant breeding programs.

17.2.4 Sorghastrum nutans (L.) Nash

There are 18 species in the *Sorghastrum* genus of which 3 are considered native to North America including *S. elliottii* (C. Mohr) Nash, *S. secundum* (Elliot), and *S. nutans* (L.) Nash (Davila Aranda and Hatch 2003). Indiangrass, *S. nutans*, is the more prevalent species and has been used as a forage crop, in erosion control, and as an ornamental grass. It has a broad range in North America extending from Canada to Mexico and is found in a variety of diverse environments including woodlands and grasslands. There are 71 accessions of Indiangrass in the NPGS collection collected from 21 states representing a fairly large geographic range. There are only three accessions of *S. elliottii*, slender Indiangrass, collected in Georgia and Texas and no accessions of *S. secundum*, lopsided Indiangrass. Both of these lesser-known species occur in a more limited area confined mainly to the Southeastern USA.

17.3 Native Warm-Season Turf Species

Two major native grass species have been utilized for turf purposes – buffalo grass [*Bouteloua dactyloides* (Nutt.) Engelm] and seashore paspalum (*Paspalum vaginatum* Sw.).

17.3.1 Bouteloua dactyloides (Nutt.) Columbus

Buffalo grass (*Bouteloua dactyloides* (Nutt.) Columbus) is so named because it was the major forage for the American bison, or buffalo (*Bison bison* L.). It was also used in making sod houses for early settlers (Hitchcock and Chase 1971). Currently, it is highly valued for rangeland grazing in the midgrass and short-grass prairies and is used for low-maintenance turfgrass.

Buffalo grass is a warm-season low-growing stoloniferous perennial grass. The leaves are 1–2 mm wide and most often are a gray-green color (Hitchcock and Chase 1971). It is highly drought resistant and tolerates both heat and cold (Beetle 1950). This grass is dioecious for the most part; however, the presence of monoecious plants has been reported (Wu and Harivandi 1995; Beetle 1950). Buffalo grass caryopses are housed in hard burs with as many as six per bur (K. Morris 2016, personal communication). Seed dormancy reduces stand establishment, and burs are routinely treated to increase germination. Seed production is often low, which may be caused in part by few female plants in a stand. However, breeding efforts have produced cultivars that produce a larger amount of seed, and some turf-type cultivars are sold only as plugs or sod, making the number of seeds produced irrelevant. Cultivars such as 'Sundancer' (Amundsen 2014) and 'Bowie'

(Severmutlu et al. 2005), with a more desirable green color for turf, have been developed. Buffalo grass's short-growing season, thus early-fall dormancy and late-spring green-up, is an undesirable trait in a turfgrass that can be mitigated with breeding (Vogel and Moore 1993). The palatability of buffalo grass is good, and it recovers well from hard grazing (Hoover et al. 1948), making it a good candidate for rangeland forage.

Buffalo grass is a primary component of the short-grass prairie (Leithead et al. 1971; Pieper 2005), is an important forage in the mixed grass prairie (Howard 1995), and may also be found on tallgrass prairie sites (Palmer 2007). Buffalo grass is found as far west as Nevada and as far east as Virginia, and its northern reach goes into the Canadian provinces of Manitoba and Saskatchewan (USDA NRCS PLANTS database 2016). Its southern range reaches into Central Mexico (Riordan and Browning 2003), and it is native in the Southern Mexico states of Aguascalientes, Guanajuato, Jalisco, Mexico, Queretaro, and the Federal District (USDA NPGS Genetic Resources Information Network 2017). It is considered native in the US states of Arkansas, Arizona, Colorado, Georgia, Illinois, Iowa, Kansas, Louisiana, Minnesota, Missouri, Montana, Nebraska, New Mexico, Nevada, North Dakota, Oklahoma, South Dakota, Texas, Utah, Wisconsin, and Wyoming and is an exotic in Virginia, according to the NatureServe Explorer database (2015).

Surviving native stands of buffalo grass are fragmented over a vast area encompassing several grassland ecoregions. The short-grass prairie covers approximately 777,000 km^2 of the lower Great Plains, and half of that area has been degraded or converted to other uses, according to the National Fish and Wildlife Foundation (2017). However, in 50% of the central short-grass prairie ecoregion, large blocks of the native prairie remain (Landscope America 2017). The Colorado Shortgrass Prairie Initiative, a long-term collaboration among state and federal agencies and a nonprofit organization, will eventually protect more than 20,000 ha of short-grass prairie in Colorado. Few sites in the 435,000 km^2 Western short grassland are formally protected as most of the area is cropland and grazing lands (World Wildlife Fund 2017). This is also true in the largest of the grassland ecoregions, the 640,000 km^2 Northern short grassland ecoregion (World Wildlife Fund 2017).

The mixed grass prairie, in which buffalo grass is found less frequently than in the short-grass prairie, has also been greatly disturbed. Approximately 5% of the nearly 282,000 km^2 in the Central and Southern mixed grassland ecoregion is considered intact native habitat. Many of these areas are small and fragmented and include unbroken sod on farms in Kansas and Oklahoma (World Wildlife Fund 2017). Another collaborative conservation effort among federal, state, and nonprofit organizations, the Minnesota Prairie Recovery Project, is tasked with protecting the remaining 36,500 ha of native prairie and savanna in Minnesota (The Nature Conservancy 2016).

The NPGS buffalo grass collection consists of 25 accessions. Thirteen are wild-collected material from Colorado, Oklahoma, Texas, and Wyoming. Of these, 11 accessions from Texas and Oklahoma for which plants were collected have been maintained vegetatively in the greenhouse since 2005. Clones of these accessions were combined into four groups by collection location and were field planted in

2013 in order to produce seed. The plants have established, but as of this writing, no seed has been harvested. The other two wild-collected accessions from Wyoming and Colorado were donated in 2010 and 2012, respectively, as part of the Bureau of Land Management Seeds of Success program. Twelve NPGS accessions are cultivars, developed in Nebraska, North Dakota, California, Oklahoma, and Texas. Five of the cultivars are currently protected by intellectual property rights, and another is maintained vegetatively. There are several cultivars and improved materials. Seeded accessions include 'Bison,' 'Bowie,' 'Cody,' and 'Plains,' 'Sharps Improved,' 'Texoka,' and 'Topgun.' Vegetative materials include '609,' 'Density,' 'Legacy,' 'Prairie,' 'Prestige,' and 'Turffalo' (Fresenburg 2015). The University of Nebraska-Lincoln has an ongoing buffalo grass breeding program and maintains a collection of nearly 2000 clones that are distinct from the NPGS collection. Of these, 539 are vegetative selections, and 1377 are progeny from pairwise crosses. They also maintain several segregating breeding populations and crossing blocks. The breeding program focuses on establishment rate, gender expression, classic turf quality traits, inflorescence height, and shade and traffic tolerance (Amundsen 2016, personal communication). There are no accessions of buffalo grass listed in the Plant Genetic Resources of Canada database, GRIN-CA (2015).

The conservation status of buffalo grass is listed as apparently secure globally, although it is critically imperiled in Utah, Arizona, Indiana, Saskatchewan, and Manitoba, imperiled in Illinois, and vulnerable in Wyoming and Minnesota. It has not yet been ranked in 13 of the US states in which it is native (NatureServe 2015). The conservation status in Mexico, of buffalo grass as well as other grasses discussed in this chapter, was unavailable at this writing.

17.3.2 Paspalum vaginatum Sw.

The origin of seashore paspalum has not been conclusively determined: some authors postulate the species to have originated in Asia, Africa, and Europe and others in the Americas (Duncan 2003). This uncertainty is due to the early transport around the world as ballast and bedding in slave ships and as stolons for revegetating salt-affected areas in many parts of the world. The grass grows in brackish waters and is found in coastal areas in both hemispheres in tropical to temperate regions (Duncan and Carrow 1999). In the USA, it is found along the Atlantic coast and has been found frequently at historic off-loading sites for slave boats such as Sea Island and Ft. Pulaski in Georgia and Sullivan Island in South Carolina (Duncan and Carrow 1999). Due to its high salt tolerance and turf-type characteristics, it has been bred and marketed for golf courses and other turf areas in coastal areas and where water restrictions require the use of suboptimal irrigation. The major breeding program for seashore paspalum is located at the University of Georgia, Griffin Campus. Originally established by Ronald Duncan in 1993 and currently being led by Paul Raymer, the program has produced several patented, clonally propagated elite turf cultivars including 'SeaIsle 1,' 'SeaIsle 2000,' 'SeaIsle Supreme,' and 'Sea Star' (University of Georgia 2017). Germplasm from this program has also been used to produce the seeded cultivars 'SeaSpray' and 'Pure Dynasty.'

There are currently 58 accessions of seashore paspalum in the NPGS collection, most of which are maintained clonally. The germplasm was collected in both hemispheres with the majority of germplasm coming from the USA, mainly the states of Hawaii and Georgia. Currently, there are no known in situ conservation sites. Closely related species conserved in the NPGS collection include *P. distichum* L., *P. lividum* Trin. ex Schltdl, and *P. remotum* J. Rémy; however, these species originate in South America with the principal donor countries of Argentina, Bolivia, Brazil, and Uruguay. It has been suggested that *P. distichum* and *P. vaginatum* Elliott be considered a single species based on evidence using SSR markers (Eudy et al. 2017).

17.4 Cool-Season Forages

Several cool-season native grass species are important for forage and rangeland applications. The USDA-NRCS Plant Material Centers (PMCs) and the USDA-ARS Forage and Range Research Laboratory (FRRL) in Logan, Utah, have been major forces in selecting and breeding cool-season native grasses used for reclamation, revegetation, erosion control, and forage. Five of the cool-season native grass taxa on which the FRRL and PMCs have focused are discussed in this chapter: *Achnatherum hymenoides* (Roem. & Schult.) Barkworth, *Elymus elymoides* (Raf.) Swezey, *Pascopyrum smithii* (Rydb.) Barkworth & Dewey, *Poa secunda* J. Presl, and *Pseudoroegneria spicata* (Pursh) A. Löve. Since 1945 30 releases of these taxa have been developed by the FRRL and the NRCS, and 6 were a joint effort between the 2 agencies. These taxa are also among nine grass taxa selected for the Great Basin Native Plant Selection and Increase Project (Shaw et al. 2005). Seed zones have been developed for three of the taxa discussed, *Achnatherum hymenoides*, *Poa secunda*, and *Pseudoroegneria spicata*, to guide restoration toward more locally or regionally adapted germplasm (Johnson et al. 2012).

It has become common to release pre-variety germplasm (PVG) of native grasses as defined in the Association of Official Seed Certifying Agencies (AOSCA) brochure: *The AOSCA Native Plant Connection* (Young et al. 2003). PVGs are designated as cultivars or as wild material in the NPGS database GRIN-Global (GG). For consistency, they are listed as cultivars in this chapter.

17.4.1 *Achnatherum hymenoides* (Roem. & Schult.) Barkworth

The *US Forest Service Range Plant Handbook* (1937) declared "Indian ricegrass is one of the most important native forage grasses on the western desert and semi-desert ranges and is the only one of about 13 species of Oryzopsis in the United States to occur in sufficient abundance and wide distribution on the western ranges to be of outstanding importance." Two states, Nevada and Utah, have officially recognized it as their state grass (Nevada Facts 2016; Utah's Online Library 2016). Indian ricegrass is a self-pollinating cool-season perennial bunchgrass. Plants are 25–70 cm tall with thin convolute leaf blades 0.1–1 mm in diameter. The diffuse panicles are 9–20 cm long (Barkworth 2007). The seeds may be round or elongated and usually have short white callus hairs (Ogle et al. 2013). Indian ricegrass is drought tolerant and very winter hardy and is widely adapted. It does not grow well on poorly drained soils or in shade and does best in sandy, coarse soils (Ogle et al. 2013). It is very sensitive to overgrazing (Hybner 2011). It makes excellent standing winter forage as well as early spring forage (Hafenrichter et al. 1968), and both domestic and wild grazing animals consume it. Several species of rodents and birds utilize the seed in their diets, and jackrabbits graze on the leaves (Tirmenstein 1999a). Historically, Indian ricegrass seeds were used for food by Native Americans (US Forest Service 1937; Barkworth 2007).

Stand establishment of Indian ricegrass is usually difficult and is attributed mostly to seed dormancy (Jones 1990), both mechanical and physiological, that may be reduced in seed less than 2 years old with scarification and stratification (Scianna et al. 2012). Scarification and treatment with gibberellic acid was beneficial in increasing germination for greenhouse-grown plantings but not in overwintering field plantings (Zemetra et al. 1983). Older seeds appear to germinate fairly well with scarification only, as physiological dormancy diminishes with time (Jones 1990; Zemetra et al. 1983; Zemetra and Cuany 1984). Seed germination in Indian ricegrass may also be influenced by seed polymorphism, production environment, and genotype (Jones 1990). Once germinated, seedling vigor is good (USDA, NRCS 2016; Monsen et al. 2004).

Indian ricegrass grows mostly in the western part of North America and Northern Mexico and prefers dry, well-drained soils (Barkworth 2007). It is native in 21 states, including Arizona, Arkansas, California, Colorado, Idaho, Kansas, Minnesota, Missouri, Montana, Nebraska, Nevada, New Mexico, North Dakota, Oklahoma, Oregon, South Dakota, Texas, Utah, Washington, Wisconsin, and Wyoming, and five provinces in Canada: Alberta, British Columbia, Manitoba, Saskatchewan, and the Yukon Territory (NatureServe 2015; USDA NPGS Genetic Resources Information Network 2017).

There are 451 Indian ricegrass accessions in the NPGS collection. Eleven accessions were donated from Canada, and the remaining 440 accessions were collected or developed in the USA (Table 17.1). The NPGS collection does not have accessions from eight US states (Arkansas, Kansas, Minnesota, Missouri, Nebraska, Oklahoma, South Dakota, and Wisconsin) and four provinces (British Columbia, Manitoba, Saskatchewan, and the Yukon Territory) from which it is considered native. Six of the US accessions are cultivars (two accessions of 'Paloma,' 'Nezpar,' 'PM-NM-168,' PM-NM-15,' and 'Mandan 57–2') and two are listed as breeding materials (T-593 ES and Ribstone). In addition to 'Nezpar,' 'Paloma,' and Ribstone, improved materials include 'Rimrock' and Star Lake PVG (Ogle et al. 2013). The FRRL donated a large portion of the NPGS accessions (251), and the staff at the FRRL continues to work with Indian ricegrass to release improved germplasm

Table 17.1 Origin[a] of Indian ricegrass accessions in the NPGS collection. It is considered native in all states and provinces named in the table except Alaska (NatureServe 2015)

Country	State or province	Accessions
USA	Alaska	1
USA	Arizona	19
USA	California	16
USA	Colorado	43
USA	Idaho	14
USA	Montana	1
USA	Nevada	58
USA	New Mexico	30
USA	North Dakota	2
US	Oregon	19
USA	Texas	1
USA	Utah	150
USA	Washington	6
USA	Wyoming	46
USA	State not known	34
Canada	Alberta	8
Canada	Province not known	3
	Total	451

[a] Origin is the state or province from which the accession was collected, developed, or donated. Records as to the exact site from which the accession was collected may not be available in GG. In some instances, the accessions are combinations of germplasm collected in more than one state or province

(J. Staub personal communication 2016). The Great Basin PMC has a small collection of Indian ricegrass from Nevada (C. Bernau 2016, personal communication). There are no accessions of Indian ricegrass listed in GRIN-CA (2015), the database for the Canadian Genebank.

In NatureServe (2015), the global and US national conservation status of Indian ricegrass is secure, whereas the Canadian national status is apparently secure. It is listed as secure in only two US states (Montana and Wyoming) and apparently secure in two Canadian provinces (British Columbia and Saskatchewan) in its native range. It is imperiled in Kansas and the province of Manitoba and critically imperiled in Minnesota and Oklahoma. It is not ranked in other US states or the Yukon Territory.

17.4.2 Elymus elymoides (Raf.) Swezey

Bottlebrush squirreltail is considered a workhorse native grass and is fire resistant (Tilley et al. 2006). It is listed as a high-priority species for restoration in the Great Basin (Shaw et al. 2005) and is used in erosion control and for reclamation/revegetation. It has fair forage potential for domestic livestock both in the spring before seedheads develop and later in the summer once seeds have shattered. The floret awns and glumes are long and sharp and, except when young and tender, may cause injury to grazing animals (Tilley et al. 2006). Bottlebrush squirreltail is a cool-season short-lived perennial bunchgrass that may often be glaucous. The culms grow from 8 to 65 (77) cm tall. Seedheads are 3–20 cm long and have long (15–125 mm) lemma awns that often twist at maturity. The spikelets disarticulate first at the rachis nodes and then beneath each floret. The leaves are fairly thin and (1) 2–4 (6) mm wide and may be smooth or puberulent on the top, while the undersides vary from scabrous to villous (Barkworth et al. 2007). Four subspecies of bottlebrush squirreltail are listed in GRIN-Global: *Elymus elymoides* (Raf.) Swezey subsp. *californicus* (J.G. Sm.) Barkworth, *Elymus elymoides* (Raf.) Swezey subsp. *brevifolius* (J.G. Sm.) Barkworth, *Elymus elymoides* (Raf.) Swezey subsp. *elymoides*, and *Elymus elymoides* (Raf.) Swezey subsp. *hordeoides* (Suksd.) Barkworth. The subspecies' nativity varies in ecological and elevation ranges (Tilley et al. 2006). According to Barkworth et al. (2007), subspecies *hordeoides* is differentiated from the three other subspecies by having rachis nodes with three spikelets with the central spikelet usually having two fertile florets. The florets of the lateral spikelets are rudimentary to awn-like. The lemma awns are 15–30 mm long. Whereas the rachis nodes of the subspecies *brevifolius*, *californicus*, and *elymoides* usually have two spikelets, each spikelet usually has (1) 2–4 (5) fertile florets. The lemma awns of these three subspecies vary from 15 to 120 mm long. The spikelets in subspecies *brevifolius* do not appear to have three glumes, but one or more of the spikelets at most of the nodes in the subspecies *californicus* and *elymoides* appear to have three glumes. The glumes of subspecies *californicus* are entire, whereas one of the glumes at most of the nodes of subspecies *elymoides* has awns split into two or three divisions (Barkworth et al. 2007). A fifth subspecies, *Elymus elymoides* subsp. *"C,"* has been identified through DNA analysis by Larson et al. (2003); however, taxonomic revision is pending. Staub et al. (2016) state that subspecies *"C"* is taller, matures later, and is found more often in high elevations than the subspecies *californicus* and *elymoides*. Although these subspecies are of importance because of their differing patterns of distribution as well as phenological differences, this chapter reports on *Elymus elymoides* in the broad sense unless otherwise noted.

One of the most important qualities of bottlebrush squirreltail is its ability to establish in stands dominated by medusahead (*Taeniatherum caput-medusae* (L.) Nevski) and cheatgrass (*Bromus tectorum* L.) (Hironaka and Sindelar 1973; Arredondo et al. 1998; Clausnitzer et al. 1999). However, suppressing medusahead prior to seeding with bottlebrush squirreltail is recommended as a good management practice (Clausnitzer et al. 1999). Jones (1998) suggested that because bottlebrush squirreltail is fire tolerant and, due to self-pollination, produces seed even when there are few individuals, it is a good candidate for initially reclaiming lands that have been invaded by weedy annuals. Once bottlebrush squirreltail has established, other native perennial plants could be introduced to the area. Bottlebrush squirreltail has good drought resistance and tolerates saline-alkali soils. The traits that make it desirable for land reclamation may also cause it to be a somewhat weedy species in some habitats (Plumb 2010). Seeds and seedheads are easily moved from the mother plant by wind and tend to accumulate en masse at the base of other plants (V. Bradley 2016 personal communication 2016).

Native populations of bottlebrush squirreltail grow from Northern Mexico (Baja Norte) to British Columbia, Alberta, and Saskatchewan and from the Dakotas, Nebraska, Kansas, Oklahoma, and Texas to the West Coast, also including the states Arizona, California, Colorado, Idaho, Kentucky, Missouri, Montana, Nevada, New Mexico, Oregon, Utah, Washington, and Wyoming (NatureServe 2015; USDA NPGS Genetic Resources Information Network 2017).

There are 221 accessions of bottlebrush squirreltail in the NPGS collection (Table 17.2). One hundred thirty-seven of them have been identified to species only, 34 are listed as *Elymus elymoides* subsp. *brevifolius*, 4 are listed as *Elymus elymoides* subsp. *californicus*, and 46 have been identified as *Elymus elymoides* subsp. *elymoides*. There are no accessions identified as *Elymus elymoides* subsp. *"C"* or *Elymus elymoides* subsp. *hordeoides* in the NPGS collection. Two hundred and eighteen accessions were collected or developed in the USA, 5 of which have been released as PVG, while the remaining 213 are listed as wild material. Three accessions were collected in Alberta, Canada. GG does not list any NPGS accessions from the Canadian provinces of British Columbia and Saskatchewan or the US states of Kansas, Kentucky, Missouri, Nebraska, North Dakota, Oklahoma, South Dakota, Texas, and Washington, although bottlebrush squirreltail is reported as being native to those areas. Bottlebrush squirreltail PVGs commercially available are listed in Table 17.3. The Canadian Genebank does not hold any accessions of bottlebrush squirreltail (USDA, NPGS 2017).

Table 17.2 Origin[a] of bottlebrush squirreltail accessions in the NPGS collection. It is considered native in all states and provinces named in the table (NatureServe 2015; USDA NPGS Genetic Resources Information Network 2017)

Country	State or province	Accessions
USA	Arizona	5
USA	California	20
USA	Colorado	21
USA	Idaho	35
USA	Montana	2
USA	Nevada	23
USA	New Mexico	7
USA	Oregon	40
USA	Utah	40
USA	Wyoming	22
USA	State not known	3
Canada	Alberta	3
	Total	221

[a] Origin is the state or province from which the accession was collected, developed, or donated. Records as to the exact site from which the accession was collected may not be available in GG. In some instances, the accessions are combinations of germplasm collected in more than one state or province

Table 17.3 Pre-variety germplasm releases of bottlebrush squirreltail commercially available (Tilley et al. 2006; Staub et al. 2016)

Taxon	Name
Elymus elymoides ssp. *elymoides*	Fish Creek germplasm
	Rattlesnake germplasm
Elymus elymoides ssp. *brevifolius*	Pueblo germplasm
	Tusas germplasm
	Wapiti germplasm
Elymus elymoides ssp. *californicus*	Toe Jam Creek germplasm
Elymus elymoides/Elymus elymoides ssp. *"C"*	Pleasant Valley germplasm
	Antelope Creek germplasm

The NatureServe conservation status of bottlebrush squirreltail is secure, globally, and apparently secure/secure, nationally, in both the USA and Canada. On a state or province level, it is considered secure in Montana and Wyoming, vulnerable in Alberta, and imperiled in Saskatchewan. The status has not been evaluated in British Columbia and the other 17 states in which it is considered native (NatureServe 2015). Researchers at the FRRL are working on developing more releases of bottlebrush squirreltail as well as collecting more materials from native populations (J. Staub personal communication 2016). The Great Basin PMC in Fallon, Nevada, also has a small collection of bottlebrush squirreltail accessions collected in Nevada (C. Bernau personal communication 2016).

17.4.3 *Pascopyrum smithii (Rydb.) Barkworth & D. R. Dewey*

The only species in the genus *Pascopyrum*, western wheatgrass, is an important cool-season perennial forage grass and is used by small mammals such as black-tailed prairie dogs, as well as large mammals like buffalo (Tirmenstein 1999b), elk, deer, sheep, and cattle. Sheeps are quite fond of the seedheads (Leithead et al. 1971; Beetle 1952). It is a rhizomatous plant and grows from 30 to 90 cm tall with glaucous leaf blades 10–20 cm long and with seedheads 5–18 cm long (Leithead et al. 1971; Hoover et al. 1948).

Western wheatgrass is tolerant of alkali soils, is extremely drought resistant, and is very resistant to grazing pressure (Beetle 1952). Mature plants provide nutritious winter grazing (Hoover et al. 1948). Western wheatgrass does not establish quickly from seed; however, the seedlings are drought resistant and compete well with weeds and most grasses. These traits, when combined with conditions that stimulate rhizome development, allow the production of good stands of western wheatgrass (Hoover et al. 1948).

This grass is native to western North America (Lambert 2005), often found in the northern Great Plains, and found less often in the northern Intermountain

Table 17.4 Origin[a] of western wheatgrass accessions in the NPGS collection. It is considered native in all states named, except Mississippi, where it is not known to be present (NatureServe 2015; USDA NPGS Genetic Resources Information Network 2017)

Country	State or province	Accessions
USA	Colorado	4
USA	Iowa	1
USA	Kansas	2
USA	Mississippi	1
USA	Montana	5
USA	New Mexico	5
USA	North Dakota	19
USA	Oklahoma	12
USA	South Dakota	15
USA	Texas	8
USA	Utah	1
USA	Washington	1
USA	Wyoming	3
Canada	Province not known	4
	Total	81

[a] Origin is the state or province from which the accession was collected, developed, or donated. Records as to the exact site from which the accession was collected may not be available in GG. In some instances, the accessions are combinations of germplasm collected in more than one state or province

West (Hafenrichter et al. 1968). It is common on the mixed grass prairie (Pieper 2005). Although found in 32 US states and 6 Canadian provinces (Tirmenstein 1999b), western wheatgrass is considered native to 29 states and 5 provinces, including Alaska, Arizona, Arkansas, California, Colorado, Georgia, Iowa, Idaho, Indiana, Kansas, Massachusetts, Missouri, Montana, North Dakota, Nebraska, New Hampshire, New Mexico, Nevada, New York, Ohio, Oklahoma, Oregon, South Dakota, Tennessee, Texas, Utah, Washington, Wisconsin, Wyoming, Alberta, British Columbia, Manitoba, Ontario, and Saskatchewan (NatureServe 2015).

There are 81 accessions of western wheatgrass in the NPGS collection (Table 17.4). Two accessions are breeding material, and two others are listed as cultivated material. Eight accessions are cultivars: ‘Arriba,’ ‘Barton,’ ‘Rosana,’ ‘PMC 30,’ ‘Rodan,’ ‘Recovery,’ ‘P 727,’ and one unnamed. The other 69 accessions are identified as wild material in GG. Four accessions are from Canada, and the remaining accessions originated in 13 US states. US states from which western wheatgrass is native and is not represented with accessions in the NPGS are Alaska, Arizona, Arkansas, California, Georgia, Idaho, Indiana, Massachusetts, Missouri, Nebraska, New Hampshire, Nevada, New York, Ohio, Oregon, Tennessee, and Wisconsin. There are no accessions from the five Canadian provinces where it is native: Alberta, British Columbia, Manitoba, Ontario, and Saskatchewan. One accession was donated from Mississippi; however, no other information as to the source of this germplasm is available. The provinces from which the four Canadian accessions were donated are not documented. Western wheatgrass cultivars commercially available are ‘Arriba,’ ‘Barton,’ ‘Flintlock,’ ‘Recovery,’ ‘Rodan,’ ‘Rosana,’ and ‘Walsh’ (Ogle et al. 2009). The FRRL is currently working to develop new cultivars of western wheatgrass (J. Staub 2016 personal communication). There are three accessions of western wheatgrass listed in GRIN-CA (2015). They are the cultivars ‘Walsh,’ ‘WR Poole,’ and ‘Rodeo,’ which were all developed in Alberta.

Both the global and US national conservation status of western wheatgrass are secure, and the Canadian national status is listed as questionably secure according to NatureServe (2015). The conservation status has been ranked as secure in only four US states from which it is native (Montana, Iowa, South Dakota, and Wyoming). The other states have not been ranked, whereas the five Canadian provinces from which it is native have been ranked. In British Columbia and Saskatchewan, it is ranked as secure; in Alberta and Manitoba, it is apparently secure; and it is imperiled in Ontario (NatureServe 2015).

17.4.4 Poa secunda J. Presl

Sandberg bluegrass has been described as one of the six most important range grasses in Colorado, Oregon, and Washington (US Forest Service 1937; Majerus and Holzworth 2004). There have been major taxonomic discussions and revisions for this species. Currently, the taxon *Poa secunda* has been synonymized and includes seven species once considered unique from one another, and many taxonomists and researchers refer to it as the *Poa secunda* complex (Majerus et al. 2009; Howard 1997; Halvorson 2011). *Poa ampla* Merrl, *P. canbyi* (Scribn.) Howell, *P. gracillima* Vasey, *P. juncifolia* Scribn., *P. nevadensis* Vasey, *P. sandbergii* Vasey, and *P. scabrella* (Thurb.) Benth were determined to be variants of one species by Kellogg (1985), although another closely related taxon, *P. curtifolia* Scribn., was considered to be a well-defined species and was not placed into the *P. secunda* complex. Other reports include as many as 45 species in the complex (Majerus et al. 2009). Many taxonomists divide the seven species listed above into two subspecies of Sandberg bluegrass: *P. secunda* J. Presl ssp. *secunda* (*P. canbyi*, *P. gracillima*, *P. sandbergii*, and *P. scabrella*) and *P. secunda* ssp. *juncifolia* (Scribn.) Soreng, which includes *P. ampla* and *P. nevadensis* (Soreng 2007; Winslow 2013). This chapter discusses Sandberg bluegrass in the broad sense including the seven species listed above.

Sandberg bluegrass is a perennial cool-season bunchgrass that rarely produces rhizomes. Most of the narrow (0.5–1.5 mm) leaves, which are 3–5 cm long, are at the base of the plant and have the prow-shaped tip common to bluegrass (Monsen et al. 2004; Soreng 2007). Plants often produce anthocyanins that give them a reddish or purple tinge (Kellogg 1985; Monsen et al. 2004; Soreng 2007; Halvorson 2011). Culms vary from (10) 15 to 120 cm tall, and the panicles, usually erect or somewhat lax, are 2–25 (30) cm in length (Soreng 2007).

Sandberg bluegrass is one of the first native grasses to begin growing in the spring. Although forage is not usually abundant, it is of excellent quality and palatability that lasts into early summer (Monsen et al. 2004), when it goes dormant as soils dry (Halvorson 2011). It is a valuable bunchgrass for soil stabilization and spring grazing of livestock and wildlife (Staub et al. 2016) and is adapted to diverse climates, growing at elevations from 100 to 3650 m in numerous soil types (Majerus et al. 2009). It is commonly found on dry, rocky, or sandy soils but will thrive in rich clay loam as well (US Forest Service 1937). The plants have deeply growing, fibrous roots which contribute to their drought tolerance and resistance to grazing and trampling (Majerus et al. 2009).

Sandberg bluegrass occurs throughout the Western USA, a few Central and Southern US states, and most of Canada. Sandberg bluegrass is native to the 19 US states of Alaska, Arizona, California, Colorado, Idaho, Michigan, Minnesota, Mississippi, Montana, Nebraska, Nevada, New Mexico, North Dakota, Oklahoma, Oregon, South Dakota, Utah, Washington, and Wyoming, as well as Alberta, British Columbia, Ontario, Manitoba, Quebec, Saskatchewan, and the Northwest Territories in Canada (NatureServe 2015). GG indicates Sandberg bluegrass is native to Mexico as well as Chile and the Argentine provinces of Chubut, Neuquen, and Santa Cruz.

There are 115 accessions of Sandberg bluegrass in the NPGS collection (Table 17.5). One accession is from Argentina, and one, given an "uncertain improvement status," is from Sweden, and there are five wild accessions and one cultivar ('Service') from Canada. The remaining accessions are from the USA and are mostly wild material (99 accessions). There are two US accessions with the designation of breeding material, two designated as cultivars ('Canbar' and 'Sherman'), three are cultivated material, and one other has been given an "uncertain Improvement status" designation. The NPGS cool-season grass collection does not hold any accessions of Sandberg bluegrass from the eight Canadian provinces or the ten US states of Alaska, Arizona, Michigan, Minnesota, Mississippi, Nebraska, New Mexico, North Dakota, Oklahoma, and South Dakota, from which it is reported as being native. Commercially available cultivars include 'Service,' 'Sherman,' and 'Canbar'. Other releases available include Opportunity, High Plains, and Reliable Selected Germplasm; Hanford, Duffy Creek, and Wallowa Source Identified Germplasm; and Mountain Home Germplasm (Majerus et al. 2009). A local collection of Sandberg bluegrass is being developed by the Great Basin PMC (C. Bernau personal communication 2016), and the FRRL is continuing to evaluate their collections of Sandberg bluegrass as well (J. Staub personal communication 2016). The NRCS Bridger PMC at Bridger, Montana, is working with *Poa juncifolia* (*Poa secunda* ssp. *juncifolia*); they have collected for evaluation for salt-affected sites (J. Scianna personal communication 2016). One hundred and five accessions of Sandberg bluegrass, collected in the intermountain west states of California, Idaho, Oregon, Nevada, Utah, and Washington, will soon be added to the NPGS collection. GRIN-CA (2015) lists one accession of Sandberg bluegrass: the cultivar 'Sherman.'

The NatureServe (2015) global and national conservation status for Sandberg bluegrass in the USA and Canada is ranked as secure. In the USA, Arizona, Montana, and Wyoming have a ranking of secure, and in Canada, Saskatchewan

Table 17.5 Origin[a] of Sandberg bluegrass accessions in the NPGS collection. It is considered native in all countries, states, and provinces named in the table except Sweden (NatureServe 2016; USDA NPGS Genetic Resources Information Network 2017)

Country	State or province	Accessions
USA	California	9
USA	Colorado	6
USA	Idaho	9
USA	Montana	3
USA	Nevada	8
USA	Oregon	14
USA	Utah	22
USA	Washington	3
USA	Wyoming	20
USA	State not known	13
Argentina	Santa Cruz	1
Canada	Province not known	6
Sweden	Province not known	1
	Total	115

[a] Origin is the state or province from which the accession was collected, developed, or donated. Records as to the exact site from which the accession was collected may not be available in GG. In some instances, the accessions are combinations of germplasm collected in more than one state or province

is ranked as apparently secure, but Ontario and Quebec are ranked as critically imperiled. The other US states and Canadian provinces from which this grass is native have not been ranked.

17.4.5 Pseudoroegneria spicata (Pursh) Á. Löve

Bluebunch wheatgrass is a very important native bunchgrass that is palatable to both wild and domestic grazing animals (Monsen et al. 2004). Bluebunch wheatgrass is a perennial, cool-season, bunchgrass (Tilley and St. John 2013; Sedivec et al. 2007; Lambert 2005) but may occasionally have rhizomes (Carlson 2007; Asay and Jensen 1996). The plants grow 30–100 cm tall. Leaves are 2–6 mm wide and may be blue green instead of "grass" green. Seed spikes are 8–15 cm long and fairly slender (3–8 mm wide) excluding the awns, if present. Awns may be as long as 25 mm and are strongly divergent (Carlson 2007). A subspecies (or forma) of this taxon, *Pseudoroegneria spicata* (Pursh) A. Löve subsp. *inermis* (Scribn. & J. G. Sm.) A. Löve, has long been recognized by some as beardless wheatgrass and appears to differ from bluebunch wheatgrass only in the absence of divergent awns (Nelson 1903).

Bluebunch wheatgrass leaves remain green during most of the growing season and continue to be palatable after growth has stopped (Hoover et al. 1948). The recommended grazing season for this grass on the Northern Plains is from

Table 17.6 Origin[a] of bluebunch wheatgrass accessions in the NPGS collection. It is considered native in all states and provinces named in the table (NatureServe 2015; USDA NPGS Genetic Resources Information Network 2017)

Country	State or province	Accessions
USA	Alaska	4
USA	California	3
USA	Colorado	4
USA	Idaho	31
USA	Montana	10
USA	Nevada	14
USA	New Mexico	1
USA	Oregon	49
USA	Utah	18
USA	Washington	62
USA	Wyoming	19
USA	State not known	13
Canada	Alberta	4
Canada	British Columbia	5
Canada	Province not known	3
	Total	240

[a] Origin is the state or province from which the accession was collected, developed, or donated. Records as to the exact site from which the accession was collected may not be available in GG. In some instances, the accessions are combinations of germplasm collected in more than one state or province

early June through early October (Sedivec et al. 2007). Unlike buffalo grass, it does not recover well from overgrazing. It is highly drought resistant and has an extensive root system (Tilley and St. John 2013). Seedlings develop slowly, making it difficult for bluebunch wheatgrass to establish when aggressive or weedy plants are present. Once established, it is able to compete with, and even suppress, annual weedy grasses such as cheatgrass (*Bromus tectorum* L.), but it does not compete well with crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.] (Zlatnik 1999).

Bluebunch wheatgrass is native to the Intermountain Region, the Rocky Mountains, and the western Great Plains of the USA (Staub et al. 2016) and is found in many habitat types (Zlatnik 1999). US states and Canadian provinces from which this grass is considered native are Alaska, Arizona, California, Colorado, Idaho, Michigan, Montana, Nebraska, Nevada, New Mexico, North Dakota, Oregon, South Dakota, Texas, Utah, Washington, Wyoming, Alberta, British Columbia, Saskatchewan, and the Yukon Territory (Natureserve 2015).

There are 240 accessions of bluebunch wheatgrass in the NPGS collection (Table 17.6). Twelve of the accessions were collected in Canada, and the remainder were collected or developed in the USA. All but six US accessions are listed as wild material. These six include the cultivars ‘Goldar,’ ‘Anatone,’ P-7 Selected Germplasm, PMC29 from New Mexico, and 9,081,457 from Montana. The US states and Canadian provinces where bluebunch wheatgrass is considered native and from which there are no accessions in the NPGS collection are Arizona, Michigan, Nebraska, North Dakota, South Dakota, Texas, Saskatchewan, and the Yukon Territory. At this time GG does not identify any of the NPGS accessions as beardless wheatgrass, although ‘Whitmar’ (PI 421022) is listed as such by its developers. Bluebunch wheatgrass cultivars and pre-variety germplasm commercially available are ‘Anatone,’ P-7 Germplasm, ‘Goldar,’ ‘Secar,’ ‘Whitmar’ (Beardless) (Sedivec et al. 2007), and Columbia Germplasm (Staub et al. 2016). The FRRL includes bluebunch wheatgrass in their native grass development program (J. Staub 2016, personal communication). There are four accessions of bluebunch wheatgrass listed in the GRIN-CA (2015) database. Each is from a different US state (Utah, New Mexico, Idaho, and Wyoming). The Wyoming accession is a duplicate of an NPGS accession, PI 232134.

NatureServe (2015) lists both the global and Canadian national status of bluebunch wheatgrass as secure. The US national status has not been ranked. It was presumed to be extirpated in Michigan and critically imperiled in Nebraska. It is considered to be secure in Montana and Wyoming, but it has not been ranked in the 13 other US states in its native range. In Canada, it is vulnerable in Alberta and the Yukon Territory but apparently secure in Saskatchewan. Both the FRRL and the Bridger PMC are currently working with bluebunch wheatgrass (J. Staub 2016, J. Scianna 2016 personal communications).

17.4.6 Ex Situ Status of Five Cool-Season Native Grasses

The number of accessions in the NPGS cool-season grass collection for Indian ricegrass (451), bottlebrush squirreltail (221), western wheatgrass (81), Sandberg bluegrass (115), and bluebunch wheatgrass (240) may appear to be adequate when considering only the numbers of accessions. However, each of the taxa in the collection is missing accessions from a number of states or provinces from which they are native (Fig. 17.5). There have been no collections or donations from 12 of the states or provinces from which Indian ricegrass is native. The bottlebrush squirreltail collection lacks accessions from 11 states or provinces; western wheatgrass, 17; Sandberg bluegrass, 18; and bluebunch wheatgrass, 8.

Maintaining and increasing genetic diversity in the cool-season grass collection is a priority. Expansion of the collection to include more accessions of these grass taxa is needed to capture more diversity. It appears that a promising effort may be to collect in Saskatchewan, North Dakota, South Dakota, and Nebraska, as four to five taxa do not have representative accessions from each of these states or provinces. However, timing of the collections could be problematic due to variations in seed maturity dates, and finding populations of the desired grasses may be difficult as wild lands are disturbed by development. Another approach is to collect a single taxa, such as western wheatgrass, a small collection (81 accessions) lacking accessions from 17 states or provinces. This would entail collecting over a vast area of North America if representatives from each missing area were targeted,

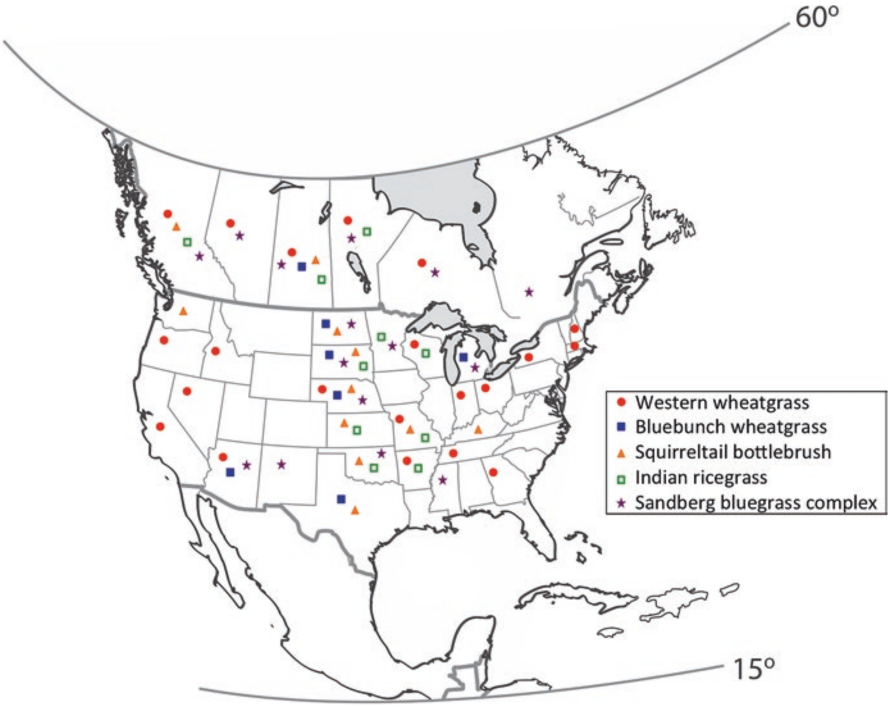

Fig. 17.5 North American map showing states and provinces that are not represented in the USDA-NPGS collections of five native cool-season grasses. Not shown on the map are the Yukon Territory (bluebunch wheatgrass, Indian ricegrass, Sandberg bluegrass), Northwest Territories (Sandberg bluegrass), and Alaska (western wheatgrass and Sandberg bluegrass)

and limitations may have to be set. Whichever approach is used, the value of the NPGS cool-season grass collection will increase as accessions from these important native grass taxa are added.

17.4.7 Further Reading

Plant guides and plant fact sheets prepared by NRCS PMCs are a valuable source of information. To find those for a specific species, perform an Internet search using the common name of the plant and “plant guide” or “plant fact sheet.” Each PMC webpage has a list of the publications that have been developed by their staff. A listing of webpages for the PMCs is available from https://www.nrcs.usda.gov/wps/portal/nrcs/detail/plantmaterials/technical/publications/?cid=stelprdb1042086.

Information about all NRCS conservation plant releases, including grasses, may be found at https://www.nrcs.usda.gov/wps/portal/nrcs/releases/plantmaterials/technical/cp/release/.

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Chapter 18
Genetic Resources of Herbaceous Ornamentals in North America

Pablo Jourdan

Abstract Herbaceous ornamental plants represent a crop category that includes hundreds of species used in diverse ways. Such plants have been an important component of constructed landscapes and represent a significant economic activity. There are many North American native species that are used as herbaceous ornamentals although worldwide trade tends to be dominated by species native elsewhere. While there are some North American herbaceous ornamentals that fit conventional definitions of a crop, and would thus benefit from availability of crop wild relatives for enhancement through breeding, many more are basically nearly wild utilized species that are readily propagated and fit the demands of the marketplace. The study and preservation of herbaceous ornamentals genetic resources significantly lags that of food and industrial crops as evidenced by scant germplasm collections and very limited representations in the collections that do exist. This chapter highlights general issues associated with crop wild relatives and wild utilized species of herbaceous ornamentals and provides examples of current status of and work with three genera: *Coreopsis* L., *Rudbeckia* L., and *Phlox* L. These are three priority genera for germplasm development and conservation at the Ornamental Plant Germplasm Center in Columbus, Ohio. The prospects for utilization of genetic resources of native herbaceous taxa are very good, but the limited resources and relatively low priority of this group of plants present considerable challenges to comprehensive conservation.

Keywords Ornamentals · Germplasm · Conservation · *Coreopsis* · *Phlox* · *Rudbeckia*

P. Jourdan (✉)
Ornamental Plant Germplasm Center, Department of Horticulture and Crop Science,
The Ohio State University, Columbus, OH, USA
e-mail: jourdan.1@osu.edu

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18.1 Overview of Herbaceous Ornamentals

18.1.1 Introduction

18.1.1.1 Origin and History of Use Worldwide

Plants that are described as ornamental play a significant role in daily life and are arguably essential for the health and well-being of people in the twenty-first century. Although the term ornamental implies “decoration,” the plants are much more than just decorative. Ornamental plants enhance our surroundings and are central to cultural landscapes. As more than half of the world population now lives in urban areas (UN 2014), the use of plants in designed/constructed landscapes will likely play an increasingly significant role in providing environmental benefits and ecological services (Wilde et al. 2015). Addressing challenges of climate change in urban areas will require creative, functional, and aesthetic use of plants to, for example, ameliorate anticipated higher temperatures through shading, reduction in glare, and moisture retention to manage storm water runoff.

Herbaceous ornamental plants represent a crop *category*, rather than a single crop, that includes many species from all over the world, with a significant representation of species native to North America. Approximately 2000 genera that include 15,000 taxa of both woody and herbaceous plants, native and nonnative, have been described for cultivation as ornamentals in the diverse climatic zones of North America (Brickell 2004). The majority of these taxa are herbaceous plants. The species within this crop category are defined not only by the type of usage but also by botanical and horticultural traits such as life cycle, habit, flowering response (seasonality, flower abundance, color), management requirements, and overall aesthetic appeal.

18.1.1.2 Modern Day Use

The primary uses of herbaceous ornamentals parallel the classification followed by the United States Department of Agriculture (USDA) of the crop category, where annual bedding/garden plants, potted flowering plants, and herbaceous perennials are grown primarily outdoors either in containers or in the ground. Indoor uses include foliage plants and indoor/patio, cut flowers, and cut cultivated greens (USDA 2016). Herbaceous ornamentals are used as part of modern urban/suburban life in small-scale residential contexts (balcony or patio plants in pots), in larger-scale residential settings with a wide range of formal and informal gardens, in commercial/industrial settings where constructed landscapes are used to enhance the image of an organization, and in much larger-scale plantings that may be components of restoration projects, highway beautifications, and even primarily functional plantings such as rain gardens and retention catchments (Fig. 18.1). Within the last couple of decades, there has also been an expansion of intense urban-setting plantings, such as green roofs and green walls, both for aesthetic and functional purposes (Rowe 2011).

Fig. 18.1 Examples of herbaceous ornamental plantings used in different landscape contexts. (**a**) Winter-tender herbaceous plants grown in containers. (**b**) Enhancement of an urban setting with a combination of herbaceous perennials and woody plants. (**c**) Native North American herbaceous perennials that include the genera *Coreopsis* L., *Echinacea* Moench, *Phlox* L., and *Rudbeckia* L.

Fig. 18.1 (continued)

Herbaceous ornamentals are the defining crops of the floriculture industry and a significant component of the nursery industry, which also includes woody plants. Worldwide trade in ornamental plants accounts for approximately US$16 billion (UN Comtrade 2016), but overall use outside of trade doubles the value to nearly US$35 billion; the USA and Canada account for only 15–20% of this worldwide activity (Hanks 2016). The majority of the international trade is based on only a couple of hundred species; and for cut flowers, a few genera predominate, such as tulips, gerberas, chrysanthemums, and carnations (Table 18.1).

Current activities in breeding and cultivar development are naturally focused on the largest segments of the floriculture/nursery industry: annual bedding and garden plants, potted flowering plants, herbaceous perennials, and cut flowers. An example of the range of genera of bedding plants that have active breeding programs can be seen in the entries for new cultivars at the Annuals Trials of the Ohio State University (https://ohiofloriculture.osu.edu/cultivar-trials; Table 18.2). Similar trials are held

Table 18.1 Major crops of herbaceous plant genera based on sales volume in the USA (USDA 2016)

Potted plants	Cut flowers
Begonia L.	*Alstroemeria* L.
Petunia Juss.	*Dianthus* L. (carnations)
Tagetes L. (marigold)	*Chrysanthemum* L.
Viola L. (pansy)	*Delphinium* L. (larkspurs)
Impatiens L.	*Gerbera* L. (daisies)
Pelargonium L'Hér. (geranium)	*Gladiolus* L.
Lilium L. (Easter lilies)	*Iris* L.
Euphorbia L. (poinsettias)	*Lilium* L.
Chrysanthemum L. (mums)	*Eustoma* Salisb. (lisianthus)
Hosta Tratt.	*Rosa* L. (roses)
Orchids	*Antirrhinum* L. (snapdragons)
Ferns	*Tulipa* L. (tulips)

Table 18.2 Genera of herbaceous ornamentals entered into the OSU Annuals Trials in 2015[a]

Agapanthus L'Hér.	***Cosmos*** Cav.[b]	***Melampodium*** L.[b]
Agastache J. Clayton ex Gronov.[b]	***Dahlia*** Cav.[c]	*Nemesia* Vent.
Angelonia Humb. and Bonpl.[c]	*Dianthus* L.	*Nepeta* L.
Antirrhinum L.	*Diascia* Link & Otto	*Petunia* Juss.
Argyranthemum Webb ex Sch. Bip.	***Euphorbia*** L.[b]	***Phlox*** L.[b]
Begonia L.	***Fuchsia*** L.[c]	*Portulaca* L.
Bidens L.[b]	***Gaura*** (*Oenothera* L.)[b]	***Salvia*** L.[c]
Bracteantha (*Xerochrysum* Tzvelev)	***Geranium*** L.[b]	*Scaevola* L.
Caladium Vent.	*Gerbera* L.	*Stachys* L.
Calibrachoa Cerv.	*Hibiscus* L.	***Tagetes*** L.[b] (marigold)
Capsicum L.[c] (orn. pepper)	***Impatiens*** L.[b]	*Verbena* (*Glandularia* J. F. Gmel.)
Canna L.[b]	*Ipomoea* L.	*Vinca* L.
Celosia L.[c]	*Lobelia* L.	***Zinnia*** L.[b]
Coleus Lour. (*Plectranthus* L'Hér.)	*Lobularia* Desv.	
Coreopsis L.[b]	***Mandevilla*** Lindl.[b]	

[a] Genera in bold include species native to North America

[b] Genus consists of species native in parts of North America that include USA

[c] Genus consists of species native primarily in Mexico

throughout the USA and Canada with an equivalent range of genera. Genera native to North America are identified in the table, where they constitute slightly less than half of the total.

Another example of the extent of breeding activity in herbaceous ornamentals can be seen in the annual Spring Trials held in California every year (http://www.springtrials.org). This week-long event showcases newly introduced cultivars and provides a broad perspective on the most economically important herbaceous ornamentals. Thousands of cultivars have been introduced in the past 5 years alone; the greatest numbers of new introductions are found in petunia, poinsettia, geranium (*Pelargonium* L'Hér.), begonia, calibrachoa, pansy (*Viola* L.), verbena (*Glandularia* J. F. Gmel.), chrysanthemum, impatiens, and gerbera.

Whereas worldwide trade in herbaceous ornamentals is dominated by non-US native species, there is significant commerce in the native genera such as *Agastache* J. Clayton ex Gronov., *Coreopsis* L., *Gaillardia* Foug., *Gaura (Oenothera* L.*)*, *Lobelia* L., *Penstemon* Schmidel, *Phlox* L., and *Rudbeckia* L., as evidenced by the offerings in many of the larger floriculture and nursery catalogs. A popular nursery lists 13 *Heuchera* L., 4 *Echinacea* Moench, and 3 ×*Heucherella* H. R. Wehrh. cultivars among its top 25 sellers; all these originate from native North American species (Terra Nova Nurseries 2016). Of the major herbaceous ornamentals in the trade, marigolds (*Tagetes* L.) and poinsettia (*Euphorbia pulcherrima* Willd. ex Klotzsch) are native to Mexico, a country also rich in genetic resources for other ornamentals such as *Salvia* L., *Zinnia* L., *Dahlia* Cav., *Capsicum* L. (ornamental peppers), *Begonia* L., *Plectranthus* L'Hér., *Agave* L., *Yucca* L., etc. (USDA, ARS 2017b).

There are more than 170 genera of North American native herbaceous ornamental plants (wildflowers, grasses, ferns, and orchids) that can be used in American gardens (Table 18.3), although the list is dominated by woodland species (Armitage 2006; Borland 2006). Armitage's compendium only lists plants available in the marketplace; thus, there are likely more species of herbaceous ornamentals that could be used for landscapes but that have not yet found their place in commerce.

18.1.1.3 Challenges in Cultivation and Use

The challenges to cultivation of herbaceous ornamentals vary by species, although there are issues in common with the production of any plant in controlled environments and with the use of plants in constructed landscapes. The high diversity of herbaceous ornamentals precludes any reasonable assessment of cultivation challenges that may be faced by each species. However, as with most crops, there are some common challenges during the production phase, such as diseases and pests. There are also challenges during the utilization phase of these plants since herbaceous perennials are grown for long periods in constructed landscapes; such challenges are associated with overall performance, resilience, drought tolerance, diseases, and occasional pests. The more typical production challenges lie in managing diseases and pests. Among the various diseases that can affect production are

Table 18.3 Genera of herbaceous ornamentals with species native to North America; including crops and WUS (Armitage 2006)

Aconitum L.	*Coreopsis* L.	*Hydrophyllum* L.	*Salvia* L.
Actaea L.	*Cornus* L.	*Hymenocallis* Salisb.	*Sanguinaria* L.
Adiantum L.	*Corydalis* DC.	*Hypoxis* L.	*Sanguisorba* L.
Adlumia Raf. ex DC.	*Crinum* L.	*Hyssopus* L.	*Saururus* L.
Agastache J. Clayton ex Gronov.	*Cynoglossum* L.	*Hystrix* (*Leymus* Hochst.)	*Schizachyrium* Nees
Ageratina Spach	*Cypripedium* L.	*Impatiens* L.	*Scutellaria* L.
Amsonia Walter	*Darmera* Voss	*Iris* L.	*Sedum* L.
Andropogon L.	*Delphinium* L.	*Isopyrum* L.	*Senecio* L.
Anemone L.	*Deschampsia* P. Beauv.	*Jeffersonia* Barton	*Shortia* Torr. & A. Gray
Antennaria Gaerth.	*Dicentra* Bernh.	*Liatris* Gaertn. ex Schreb.	*Silene* L.
Ampelaster G. L. Nesom	*Diphylleia* Michx.	*Lilium* L.	*Silphium* L.
Aquilegia L.	*Disporum* Salisb.	*Lobelia* L.	*Sisyrinchium* L.
Arisaema Mart.	*Doellingeria* Nees.	*Lupinus* L.	*Solidago* L.
Aruncus L.	*Dodecatheon* L. (*Primula* L.)	*Lysichiton* Schott	*Spigelia* L.
Asarum L.	*Dryopteris* Adans.	*Maianthemum* F. H. Wigg.	*Spiranthes* Rich.
Asclepias L.	*Echinacea* Moench	*Marshallia* Schreb.	*Sporobolus* R. Br.
Astilbe Buch.-Ham. ex D. Don	*Elymus* L.	*Mertensia* Roth	*Stipa* L.
Athyrium Roth	*Enemion* Raf.	*Mitella* L.	*Stokesia* L'Hér.
Baptisia Vent.	*Epilobium* L.	*Monarda* L.	*Streptopus* Michx.
Berlandiera DC.	*Equisetum* L.	*Muhlenbergia* Schreb.	*Stylophorum* Nutt.
Bidens L.	*Eragrostis* Wolf	*Nassella* (Trin.) É. Desv.	*Symphyotrichum* Nees
Blephilia Raf.	*Eryngium* L.	*Nemophila* Nutt.	*Symplocarpus* Salisb. ex W. P. C. Barton
Boltonia L'Hér.	*Erythronium* L.	*Oenothera* L.	*Tagetes* L.
Bothriochloa Kuntze	*Eupatorium* L.	*Onoclea* L.	*Talinum* Adans.
Bouteloua Lag.	*Euphorbia* L.	*Osmunda* L.	*Thalia* L.
Callirhoe Nutt.	*Eurybia* (Cass.) Cass.	*Pachysandra* Michx.	*Thalictrum* L.
Callisia Loefl.	*Filipendula* Mill.	*Packera* Á. Löve & D. Löve	*Thermopsis* R. Br.
Camassia Lindl.	*Gaillardia* Foug.	*Panicum* L.	*Tiarella* L.
Campanula L.	*Galax* Sims	*Parthenium* L.	*Tradescantia* L.
Cardamine L.	*Gentiana* L.	*Penstemon* Schmidel	*Trillium* L.
Caulophyllum Michx.	*Gentianopsis* Ma	*Phacelia* Juss.	*Trollius* L.
Centaurea L.	*Geranium* L.	*Phlox* L.	*Uvularia* L.

(continued)

Table 18.3 (continued)

Chamaelirium Willd.	*Geum* L.	*Physostegia* Benth.	*Veratrum* L.
Chasmanthium Link	*Gillenia* Moench	*Pityopsis* Nutt.	*Verbena* L.
Chelone L.	*Glandularia* J.F. Gmel.	*Podophyllum* L.	*Vernonia* Schreb.
Chrysogonum L.	*Helenium* L.	*Polemonium* L.	*Veronicastrum* Heist. ex Fabr.
Chrysopsis (Nutt.) Elliott	*Helianthus* L.	*Polygonatum* Mill.	*Viola* L.
Cimicifuga Wernisch. (*Actaea* L.)	*Heliopsis* Pers.	*Porteranthus* Britton (*Gillenia* Moench)	*Woodwardia* Sm.
Claytonia L.	*Heterotheca* Cass.	*Pycnanthemum* Michx.	*Yucca* L.
Clematis L.	*Heuchera* L.	*Ratibida* Raf.	*Zephyranthes* Herb.
Clintonia Raf.	*Hibiscus* L.	*Rudbeckia* L.	*Zinnia* L.
Conoclinium DC.	*Hydrastis* J. Ellis	*Ruellia* L.	

powdery mildew, botrytis blight, root rot diseases (*Rhizoctonia* D.C., *Phytophthora* de Bary, *Pythium* Pringsh., *Thielaviopsis* Went), damping off, and bacterial blight of geranium, verticillium wilt, and viruses (Daughtrey and Benson 2005). The challenges in the utilization of herbaceous ornamentals vary by the type of use in constructed landscapes, but in general, reliable performance with minimal maintenance, absence of diseases and pests, and adaptability to environmental extremes are the principal factors that influence plant quality.

18.1.2 Crop Wild Relatives and Wild Utilized Species

18.1.2.1 Genepool Classifications and Wild Species

Crop wild relatives (CWR) are defined in relation to the domesticated crops. In most food and industrial crops, there is a fully domesticated species that can benefit from traits that may be introduced from relatives. In the case of many herbaceous ornamentals, there is a less-defined demarcation between a wild and a domesticated form. Thus, both CWR and wild utilized species (WUS) will be treated together in this chapter. In the context of this chapter, WUS refers to species that are grown as ornamentals in their unimproved form, rather than those that are collected from the wild and used immediately, as is common for plants used as food and medicine. As stated by Meilleur and Hodgkin (2004): “Ambiguity remains on the status as ‘crops’ of many forestry, forage, medicinal and ornamental species, especially those recently domesticated or potentially ‘domesticable’, and thus on the status of their wild relatives as CWR.” The genepool concept of Harlan and de Wet (1971) is based on interspecific sexual compatibility between a crop and its wild relatives. Studies to delineate such compatibility have not been undertaken for most herbaceous ornamental species. The alternative genepool categories of Maxted et al. (2006), and expanded by Wiersema et al. (2012), are based on taxonomic and evolutionary relationships, and these may be of greater applicability to herbaceous ornamentals.

North America includes many species that currently are, or could be, considered herbaceous ornamentals. There are approximately 16,000 vascular plant species in 1900 genera native to the USA and Canada (Qian 1999) and more continue to be discovered (Flora of North America 2016). Mexico alone has approximately 26,000 species of flowering plants (Rhoda and Burton 2010; SciDevNet 2016). Among these thousands of North American native species are many genetic resources important for agriculture in general, such as for food and industrial crops, but the largest group of CWR and WUS from the USA is primarily used for ornamental, restoration, and medicinal purposes (Khoury et al. 2013). Regardless of the distinction between CWR and WUS, the genetic resources available in North America, as determined in the most recent survey (Khoury et al. 2013), include ten families (Asteraceae, Ericaceae, Fabaceae, Oleaceae, Papaveraceae, Plantaginaceae, Poaceae, Ranunculaceae, Rosaceae, and Salicaceae) and over 800 taxa. A representative sample of herbaceous ornamentals native to USA, presented in Table 18.4, provides a sense of the diversity of native genera that contribute to constructed landscapes. This list was selected by the author based on personal experience with the plants found in the trade and includes 29 genera and 1031 taxa.

There is no systematic or comprehensive assessment of the CWR or WUS for nearly all of the genera listed in Table 18.4. The diversity of native herbaceous ornamentals provides ample opportunity for introduction of new crops and development of new ornamental forms. The genus *Penstemon*, for example, is the third most speciose genus of native North American taxa (Kartesz 2015), representing a large reservoir of genetic diversity that has been exploited only to a very limited extent. The Ornamental Plant Germplasm Center (OPGC), a genebank at The Ohio State University that is part of the National Plant Germplasm System (NPGS), has been developing genetic resources for herbaceous ornamentals. The collection includes over 5000 accessions of more than 1000 species in over 200 genera. Some of these genera are native to North America. Among the six genera selected as priority for germplasm development, there are four with species native to North America: *Coreopsis*, *Lilium* L., *Phlox*, and *Rudbeckia*. The scope of this treatise does not allow for a detailed assessment of each native herbaceous ornamental genus. Instead, three genera, *Coreopsis*, *Rudbeckia*, and *Phlox*, will be used to illustrate the type of information being gathered to build the genetic resources for conservation and utilization.

18.1.2.2 Utilization and Potential for Expanded Use

A driving force in the use of herbaceous ornamentals is novelty. The commercial life of any new bedding plant cultivar is estimated to be only 3–5 years, so there is intense effort to develop novel flower/foliage colors or habits within established and well-known crops such as petunia and begonia. There are different breeding

Table 18.4 Genetic resources and commercially available cultivars of selected North American native herbaceous ornamentals[a]

Genus	Number of taxa	Threatened or endangered taxa		Number of OPGC active accessions	Commercially available cultivars
		Federal	State		
Agastache J. Clayton ex Gronov.	15	0	3	92	3
Asclepias L.	46	2	19	111	29
Baptisia Vent.	24	1	8	68	25
Bidens L.	20	2	10	14	20
Coreopsis **L.**	**41**	**0**	**7**	**133**	**140**
Echinacea Moench	13	2	5	188	165
Euphorbia L.	76	2	7	53	1
Gaillardia Foug.	12	0	0	29	69
Glandularia J. F. Gmel.**	21	0	1	11	150+
Helenium L.	15	1	2	18	27
Heliopsis Pers.	2	0	0	12	18
Heuchera L.	20	0	3	14	228
Iris L.	32	1	7	1	30
Liatris Gaertn. ex Schreb.	32	2	11	100	13
Lilium L.	32	2	10	7	1
Lobelia L.	17	4	14	20	6
Monarda L.	14	0	5	76	65
Oenothera L.*	93	3	19	440	71*
Panicum L.	12	2	11	717	33
Penstemon Schmidel	199	3	20	312	124
Phlox **L.**	**114**	**2**	**15**	**378**	**247**
Rudbeckia **L.**	**42**	**0**	**10**	**267**	**62**
Salvia L.	51	0	3	129	30
Schizachyrium Nees	3	0	2	391	17
Silene L.	43	6	13	30	8
Tagetes L.	17	0	0	160	200
Tiarella L.	3	0	1	3	27
Vernonia Schreb.	10	1	4	21	7
Zinnia L.	12	0	0	141	150
Total (29)	1031		210	3936	905

[a] Included in this table are the total number of taxa for North America; the accessions also represent those that could be identified as originating in the USA, though not all of these may be native taxa. The three genera in **bold** are discussed in this chapter

[b] Data from USDA, ARS (2017b)

[c] Threatened taxa obtained from ECOS (2016)

[d] Data from USDA, ARS (2017a)

[e] Data from Ball Horticulture (2016)

approaches and strategies, ranging from sophisticated systems for many of the annual bedding plants to simple selection of unique forms in the wild for many herbaceous perennials. Some herbaceous ornamentals have been studied thoroughly as exemplified by petunia (Bombarely et al. 2016), snapdragon (Hudson et al. 2016; Schwarz-Sommer et al. 2003), geraniums, and lilies (Craig 2003). Arguably the most significant breeding tool has been interspecific hybridization. A premier example of such hybrids has been the development of the zonal geranium, *Pelargonium* x *hortorum* L. H Bailey, a hybrid of *P. zonale* (L.) L'Hér. and *P. inquinans* (L.) L'Hér. (USDA, ARS 2017b), and also the regal geranium, *P*. x *domesticum* L. H. Bailey, a complex hybrid involving *P. grandiflorum* (Andrews) Willd., *P. cucullatum* (L.) L'Hér., and others.

New germplasm, especially from wild species, is desired as a source of variation in traits of interest, including flower color, altered growth habit (e.g., trailing instead of upright, for use in hanging baskets), and disease resistance, mainly because much of the current breeding uses existing cultivars for incremental changes in the crop. In addition, clonal cultivars have little of the desirable variation. A significant challenge is the development of new ornamental plants essentially through domestication of wild species that requires some breeding so the plants meet market expectations and can be produced with relative ease. For example, many of the North American prairie forbs, such as species of *Helenium* L., *Rudbeckia*, *Silphium* L., *Sorghastrum* Nash, and *Vernonia* Schreb., tend to be tall plants that do not fit the more compact habit desirable for mass market and would need to be bred for more marketable characteristics.

The increasing interest and desire for enhanced biodiversity in landscapes and plants that provide ecological services as well as aesthetics indicates that native species are likely to play a more significant role in gardens (Tallamy 2009; Wilde et al. 2015). As recommended by McKinney (2002) and Parker et al. (2014), native plant species should be cultivated in order to maintain native biodiversity in increasingly urbanized communities. Thus, expanded use of native North American species is very possible, and greater availability and selection of such species is desirable.

In parallel with the diverse use of herbaceous ornamentals, breeding goals also vary, but there are common threads. Aesthetic value of a plant is central, and it includes traits such as flower color, number of flowers, altered flower morphology (e.g., double flowers), blooming period, and repeat blooming, as well as flower vase life. Overall habit and branching pattern are also critical; some uses emphasize a more upright habit and others a more trailing habit. General adaptability, as reflected in disease resistance, drought tolerance, and efficient nutrient uptake are also highly desirable performance traits. However, all of these aesthetic and growth attributes must be matched by ease of propagation, environmentally friendly production, minimal post-production "shrinkage" (a loss in quality in the time between the crops is produced and purchased by the end user), and high marketability (Horn 2004; Wilde et al. 2015).

A general challenge to greater use of either CWR or WUS of native herbaceous ornamentals is lack of availability of diverse and well-characterized genetic resources. Conservation of CWR and WUS of herbaceous ornamentals significantly lags the conservation of food crops; these plants are poorly represented in genebanks worldwide (Heywood 2003; Jaenicke 2013). There is only one genebank focused on herbaceous ornamentals, the OPGC, mentioned previously (Tay 2003, 2007). This relative dearth of available wild germplasm, with some notable exceptions, such as *Echinacea*, limits their more widespread use in breeding.

A second challenge to the increased use of wild species is the lack of relevant information about them. Very little is known about the potential for hybridization between these species. There is likely to be wide variation in the ability of different species to hybridize. Some appear to be relatively easy (e.g., *Coreopsis*, *Heuchera*), but others are likely to be much more challenging (e.g., *Rudbeckia*). There is also limited knowledge of ploidy and its variation within populations. For many species, such as the perennial forms of *Phlox*, there are no reliable seed germination protocols and even less knowledge about dormancy mechanisms. In addition, culture requirements have not been defined. However, increased availability of germplasm will likely lead to more studies that can provide insights into many of these issues.

A third challenge has been limited marketing of the native herbaceous ornamentals. There is a link between marketing and availability; the more demand there is for a species, the more likely is its availability. The limited use of some native species may be related to insufficient availability, but their marketing has also been very limited. A few programs exist, such as the American Beauties Native Plants® label (http://www.abnativeplants.com), that are making inroads into the market and popularizing native species.

18.1.3 Conservation Status of Herbaceous Ornamental CWR and WUS in North America

18.1.3.1 In Situ Conservation

Of the native North American genera listed in Table 18.4, about half (16 of 29) have at least one taxon on the US Fish and Wildlife Service (USFWS) list of endangered and threatened plants (ECOS 2016), and 25 of the genera have species with threatened/endangered designation in at least one state in the USA. Approximately 16% of the taxa within these listed genera are at risk in some regions of the country. A review of these taxa in NatureServe (2017) shows that 20 of the 29 genera have one or more species as either critically imperiled (G1) or imperiled (G2). Species endemic to Hawaii such as *Bidens*, *Euphorbia*, *Panicum*, and *Silene* are, not surprisingly, among the most imperiled. Information on the federally listed threatened and endangered species in Mexico can be found on the official list for the country (SEGOB 2015). Nevertheless, although it is likely that the majority of currently used or potential herbaceous ornamental taxa are not threatened or endangered in their native habitats, a thorough assessment of their conservation statuses is needed and requires detailed ecogeographical information (distribution, population size, and possible threats).

While in situ conservation is an important complement to ex situ conservation for CWR, there are very few examples of the use of this approach, even for food crops (Maxted et al. 2016). It is not surprising that in situ conservation activities related to ornamental plants are minimal. At present, the major effort lies in establishing priorities, setting targets, identifying challenges (BGCI 2016; Kramer et al. 2011; NatureServe 2017), and the summaries and gap analysis generated by Khoury et al. (2013) point the way forward. There is passive conservation of many potential herbaceous ornamental plants in protected areas and such sites can be one of the best sources of germplasm for ex situ conservation, but focused in situ conservation efforts for specific herbaceous ornamentals are rare.

The large diversity of taxa that fall under the herbaceous ornamental category makes it impossible to summarize species-specific needs and opportunities, but strategies and activities that lead to diverse habitat conservation are likely to contribute to conservation of many desired taxa. A key need is to develop an ecogeographic inventory of the herbaceous ornamental taxa at risk; this effort depends strongly on prioritizing the genera that should be surveyed to identify taxa that need protection (Meilleur and Hodgkin 2004). A good starting point would be the selection of the important genera among those listed in Table 18.3. The North American Botanic Garden Strategy for Plant Conservation includes relevant objectives for ornamental plants. For example, objective B4 pertaining to conserving plant diversity states that “Botanic gardens will contribute to the conservation and preservation of economically and culturally important plants, including crop wild relatives.” Two targets associated with this objective include the following: (1) “Botanic gardens will increase efforts to identify priorities, set targets and take action for preserving economically and culturally important plants in North America and other regions where they work.” (2) “Conservation programs for ornamental plant varieties will be developed, especially heirloom plants and plants of historical or cultural importance including those derived from non-native species” (BGCI 2016).

In situ preservation of herbaceous ornamental CWR and WUS is challenged on many fronts, most of which are no different from those of any other species. These include limited financial resources, differences in mission and objectives between organizations, and insufficient coordination between conservation activities. A specific challenge is that public perception of ornamental plants as not “critical” likely will limit funding to study and evaluate conservation needs of plants that have a primarily nonconsumptive value, regardless of the many other important benefits they provide. Herbaceous ornamentals are likely to be protected in a more passive way as part of a landscape ecology strategy that preserves critical natural habitats. There are threatened species that require targeted conservation actions, but diverse genotypes of the many species used as ornamentals will be best preserved in overall healthy natural habitats. The sheer diversity of native herbaceous species with potential for ornamental use also presents a challenge for conservation, emphasizing the need for establishing priorities based on criteria that are relevant to the use of such plants in landscapes.

18.1.3.2 Ex Situ Conservation

Genebanks with ornamental taxa in their collections are very few and primarily include the NPGS in the USA, the Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (IPK-Gatersleben) in Germany, the Center for Genetic Resources in the Netherlands, the National Agriculture and Food Research Organization (NARO) genebank in Japan, and the National GeneBank of China. However, botanical gardens and arboreta play a critical role in conservation of native North American taxa, including many ornamental plants. The Plant Collections Network (formerly NAPCC) is a national group of public gardens that promotes strategies for germplasm conservation and management; its major collections are of trees and shrubs, but valuable herbaceous plant collections exist at a few institutions (Plant Collections Network 2016). Examples include *Penstemon* at the Arboretum at Flagstaff and the Idaho Botanical Garden, alpine plants at the Denver Botanical Garden, *Geranium* L. at the Chicago Botanical Garden, *Sarracenia* L. at the Atlanta Botanical Garden, and ornamental grasses at the Minnesota Landscape Arboretum. Significant seed collections are stored at the Rancho Santa Ana Botanic Garden in California, the R. S. Berry Seed Bank at Portland State University in Oregon, and the Desert Botanical Garden in Arizona (Kramer et al. 2011). The Center for Plant Conservation focuses on 700 endangered species, the majority herbaceous plants, which are conserved by participating institutions (Center for Plant Conservation 2016). These are endangered species, not necessarily plants with potential use as ornamentals. On an international level, the Millennium Seed Bank of Kew Gardens in Great Britain also houses a large seed collection of native herbaceous North American species.

The OPGC conserves approximately 200 genera of herbaceous ornamentals and nearly 60% of these include species native to North America. However, many of these genera are represented by a single accession. Table 18.4 lists approximately 2400 accessions of native herbaceous taxa within 25 genera in the NPGS, but the representation of these accessions varies widely. None of the genera can be said to have a comprehensive coverage, although the most extensive collections (number in parenthesis) can be found in *Coreopsis* (133), *Penstemon* (320), *Phlox* (382), and *Rudbeckia* (267). There are collections of genetic resources that have use both as ornamentals and as medicinals (e.g., *Echinacea*, *Calendula* L.), or as industrial crops (e.g., *Salvia*). Tropical ornamentals have limited representation within the NPGS, where the Subtropical Horticulture Research Station in Florida and the Daniel K. Inouye US Pacific Basin Agricultural Research Center in Hawaii conserve some (mainly woody) ornamental plants.

As part of its mission, the OPGC actively explores and collects relevant germplasm of its priority genera in the USA including *Phlox*, *Rudbeckia*, and *Coreopsis*. Since 2006, there has been a concerted effort to develop genetic resources for these three genera, but other genera have been collected as well. Regeneration activities have also been ongoing and include work with the aforementioned genera as well as *Penstemon*, *Stokesia* L'Hér., *Tradescantia* L., and *Ratibida* Raf. The Seeds of Success program of the Bureau of Land Management (SOS 2016) has been a major contributor of new accessions of principally western USA taxa. Botanic gardens, such as Mt. Cuba Center in Delaware, have contributed germplasm of *Baptisia* Vent., *Clematis* L., *Coreopsis*, *Lilium*, *Monarda* L., and *Rudbeckia*.

There is a need for more comprehensive sampling of the priority genera at the OPGC and to expand the list of native genera targeted for conservation. Developing further collaboration with different botanic gardens in exploration and exchange is also desirable. From a technical standpoint, studies on the seed quality, dormancy, germination, and longevity of many of the native genera are of utmost importance. Limited information is available on seed management of many wild species, and this creates an opportunity for research and development, which is hampered by scant financial resources. An important tool that requires further development is the establishment of in vitro preservation protocols for selected genera because such tools are essential for the generation of disease-free material that can then be used for seed production under controlled conditions.

18.1.3.3 Suggestions on Ways to Improve Conservation

Conservation efforts may be enhanced with greater collaboration between germplasm centers and organizations, such as botanical gardens and arboreta, that have regional collections of herbaceous ornamentals. The perception that utilization of germplasm for commercial purposes is inconsistent with conservation efforts sometimes limits opportunities for collaboration. Some of this concern arises from situations where unscrupulous collectors, often with economic incentives, have decimated native populations or rare plants. However, as some have indicated, propagation may be a powerful tool for conservation; making desirable plants more readily available could be a strategy to minimize their loss in natural areas.

18.2 Examples of Herbaceous Ornamental Crop Wild Relatives and Wild Utilized Species in North America

18.2.1 Coreopsis L.

18.2.1.1 Introduction

Coreopsis is a long-standing, popular, and generally reliable garden plant grown for bright flower colors, long-blooming period, and ease of cultivation. *Coreopsis* species and cultivars are versatile: they can be used in mixed or herbaceous borders, as bedding, in containers, in naturalistic landscapes, and as components of green roofs. Of the 28 species of *Coreopsis* in North America, fewer than half have been used to any extent in constructed landscapes. The principal cultivated species (with a representative number of named cultivars in parentheses) include *C. auriculata* L. (2), *C. grandiflora* Hogg ex Sweet (10), *C. lanceolata* L. (1), *C. major* Walter, *C. palmata* Nutt., *C. pubescens* Elliott (1), *C. rosea* Nutt. (4), *C. tripteris* L., *C. tinctoria* Nutt. (2), and *C. verticillata* L. (5). However, in addition to these 25 or so cultivars of individual species, there are probably 30 or more other cultivars that are interspecific hybrids, most of mixed parentage (Armitage 2011; Padhye and Cameron 2005). There has been continuous introduction of new *Coreopsis* cultivars, most of them interspecific hybrids, developed by breeders in the USA, Europe, and Israel. One nursery (Darwin Perennials) offers 18 selections of *Coreopsis*, whereas another (Terra Nova) offers 26.

18.2.1.2 Crop Wild Relatives and Wild Utilized Species in North America

18.2.1.2.1 Genepool Classifications

Coreopsis taxonomy is organized into an eastern and a western clade (Table 18.5), although some treatments have transferred the western clade into the genus *Leptosyne* (Jepson Flora Project 2016). The extensive development of interspecific hybrids in *Coreopsis* is a consequence of the broad sexual compatibility that appears to exist within members of the eastern clade. Studies by Archibald et al. (2005) demonstrated

Table 18.5 Germplasm accessions of *Coreopsis* L. in the OPGC[a]

Region	Section	Taxon	Number of accessions	Number of cultivars
Eastern NA	*Silphidium*	*C. latifolia* Michx.	0	
	Gyrophyllum	*C. delphiniifolia* Lam.	2	
		C. major Walter	12	
		C. palmata Nutt.	7	
		C. pulchra F. E. Boynton	2	
		C. triperis L.	13	1
		C. tripteris x *C. verticillata*	1	
		C. verticillata L.	10	7
	Calliopsis	*C. leavenworthii* Torr. & A. Gray	3	
		C. paludosa M. E. Jones	0	
		C. tinctoria Nutt.	6	1
	Eublepharis	*C. falcata* F. E. Boynton	1	
		C. floridana E. B. Sm	0	
		C. gladiata Walter	3	
		C. integrifolia Poir.	1	
		C. linifolia Nutt.	0	
		C. nudata Nutt.	0	
		C. rosea Nutt.	5	5
	Coreopsis	*C. auriculata* L.	6	5
		C. basalis (A. Dietr.) S. F. Blake	1	
		C. grandiflora Hogg ex Sweet	18	17
		C. intermedia Sherff	0	
		C. lanceolata L.	12	2
		C. nuecensis A. Heller	2	
		C. nuecensoides E. B. Sm.	0	
		C. pubescens Elliott	4	1
		C. wrightii (A. Gray) H. M. Parker	4	
	Unknown	*Coreopsis* sp.	22	17

(continued)

Table 18.5 (continued)

Region	Section	Taxon	Number of accessions	Number of cultivars
Western NA	*Electra*	*C. cuneifolia* Greenm.	0	
Mexico		*C. mutica* DC.	0	
	Anathysana	*C. cyclocarpa* S. F. Blake	0	
	Tuckermannia	*C. gigantea* (Kellogg) H. M. Hall	1	
		C. maritima (Nutt.) Hook. f.	0	
	Pugiopappus	*C. bigelovii* (A. Gray) Voss	2	
		C. calliopsidea (DC.) A. Gray	0	
		C. hamiltonii (Elmer) H. Sharsm.	0	
	Leptosyne	*C. californica* (Nutt.) H. Scharsm.	0	
		C. douglasii (DC.) H. M. Hall	0	
		C. stillmanii (A. Gray) S. F. Blake	0	
	Pseudoagarista	*C. mcvaughii* D. J. Crawford	0	
		C. petrophila A. Gray	0	
		C. petrophiloides B. L. Rob. & Greenm.	0	
		C. rudis (Benth.) Hemsl.	0	
		Total	133	56

[a]Data from USDA, ARS (2017a)

the successful production of interspecific hybrids between most species of the eastern clade, although pollen viability in the hybrids ranged from 0 to 100%. Thus, there are possible limitations to the production of fertile hybrids in some crosses, but the entire clade can potentially be considered as part of GP1 or GP2 (Harlan and de Wet 1971). The barriers to interspecific hybridization that do exist have yet to be carefully delineated. The potential for crop improvement and development of new forms within the economically important *Coreopsis* is relatively high.

18.2.1.2.2 Distribution/Habitat/Abundance

Coreopsis is found throughout the continental USA (Fig. 18.2), but the eastern clade is most abundant in the southeastern region (Kartesz 2015). Only *C. palmata*, *C. intermedia* Sherff, *C. nuecensis* A. Heller, and *C. nuecensoides* E. B. Sm. are generally absent from much of this region. The most widely distributed species are *C. tinctoria*, *C. grandiflora*, *C. lanceolata*, and *C. tripteris*. The western clade species are mostly restricted to southern California. The different species occur in a wide range of soil types (heavy loams, moist clay soils, sandy or rocky soils, moist sands, alkaline flats, granite and sandstone outcrops, shale, and serpentine slopes) and habitats (prairies, open woods, pine barrens, swamps, marsh edges, peaty bogs, coastal bluffs, dunes, alkaline playas, ditches, low woodlands, flood plains, disturbed sites, roadsides, and various oak woodlands).

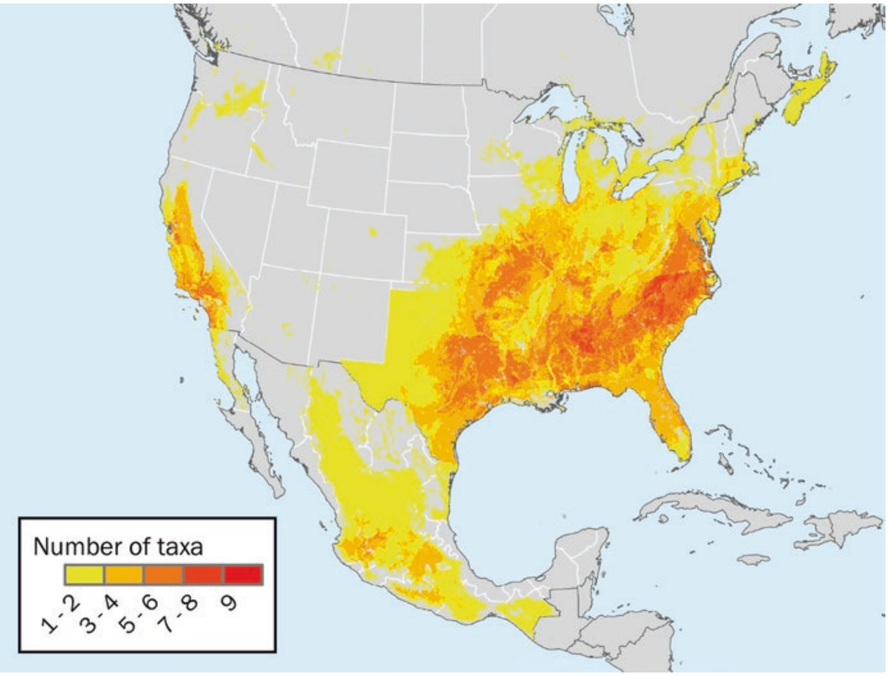

Fig. 18.2 Species richness of modeled potential distributions of North American *Coreopsis* taxa, based on climatic and edaphic similarities with herbarium and genebank reference localities. Warmer colors indicate areas where greater numbers of taxa potentially occur in the same geographic localities. Full methods for generation of maps and data providers are given in Appendix 1

18.2.1.2.3 Utilization and Potential for Expanded Use

Breeding of *Coreopsis* cultivars is relatively active, as indicated by the many new cultivars introduced within the last 15 years. The salient feature of the majority of new cultivars is new combinations of flower colors; another feature is more compact and dense habit. Cultivars with yellow foliage have also been introduced. The diversity in inflorescence colors arose from a concerted effort to combine traits from wild forms of different species with the cultivated forms. A plant patent granted in 2012 for the cultivar *Coreopsis* 'Star Cluster' states: "The inventor collected seed in the wild from five different species that are not commercialized and made six generations of crosses to produce interspecific hybrids to utilize in his breeding work" (Probst 2012). While the species are not mentioned, they likely include the colorful annual *C. tinctoria*, the white and pink-flowered forms of *C. rosea*, and other species.

The characters that are typically sought in *Coreopsis* cultivars include compact habit, alternative growth forms (prostrate, upright), variable foliage textures, variable inflorescence colors, long flowering period, lack of seed production, winter hardiness to at least USDA Plant Hardiness Zone 5, and disease resistance. The most common diseases for which resistances are sought are *Alternaria* Nees, *Botrytis* P. Micheli ex Haller, *Cercospora* Fresen. ex Fuckel, downy mildew, powdery mildew, and *Verticillium* Nees; of these, powdery mildew is the most prevalent (Daughtrey and Benson 2005), although it can be managed to a certain extent by cultural practices and fungicide treatments.

The most likely challenge to increased use of *Coreopsis* germplasm is availability of a comprehensive and well-documented collection that can expedite the introduction of new traits. Availability of such germplasm would allow other breeders to explore new combinations of traits for the crop. Many breeding programs do not have the option of extensive exploration for new germplasm in the plants' native habitats. The potential for expanded use rests with the market for *Coreopsis* in general. Superior plants with good performance, robust winter hardiness, and variable flower colors are likely to find successful placement within a range of contexts, including the native plants market.

18.2.1.3 Conservation Status of *Coreopsis* Crop Wild Relatives and Wild Utilized Species in North America

18.2.1.3.1 In Situ Conservation

The USFWS does not list any *Coreopsis* taxa as federally threatened or endangered (ECOS 2016). However, *C. latifolia* Michx. is in the Center for Plant Conservation's National Collection of Endangered Plants (Center for Plant Conservation 2016). NatureServe (2017) includes *C. hamiltonii* (Elmer) H. Sharsm., *C. integrifolia* Poir., and *C. pulchra* F. E. Boynton as either critically imperiled or imperiled at both a global and state level. *Coreopsis rosea* is listed as endangered in Canada (COSEWIC 2012) and is protected in the Pine Barrens of New Jersey (New Jersey Pinelands Commission 2012). It is listed as vulnerable by NatureServe (2017). *Coreopsis nudata* Nutt., while not uncommon in northern Florida, is considered critically imperiled in Alabama and rare or threatened in other southern states (NatureServe 2017). *Coreopsis integrifolia*, *C. pulchra*, and *C. rosea* are generally considered rare plants wherever they occur (Cosner and Crawford 1994).

The author is not aware of any in situ conservation programs that include taxa of *Coreopsis* as a specific conservation goal. For *C. rosea*, there are efforts in Canada and Massachusetts to protect habitats where the plants occur. For example, the Domero Cortelli Reserve near Plymouth, Massachusetts, includes habitat ideal for *C. rosea*; a healthy population of this species was noted at this site during a visit by the author in 2015.

In situ conservation for the rare species may benefit from a more up-to-date assessment of current efforts. Collaboration between local organizations that protect habitats and organizations, such as the OPGC, that seek to conserve the germplasm ex situ, may yield mutually beneficial outcomes. There remains resistance on the part of some in the conservation community to working with germplasm centers that provide materials to the horticulture industry; unfortunately, the industry is sometimes viewed as contributing to the decline of some rare species.

18.2.1.3.2 Ex Situ Conservation

Ex situ preservation of *Coreopsis* can be very successful since seeds of most species tend to be relatively easy to obtain and display normal, desiccation-tolerant behavior. The only genebank in North America with significant numbers of accessions of native taxa of *Coreopsis* is the OPGC, which has approximately 80 accessions of wild germplasm for 21 of the 43 taxa listed for the genus in Table 18.5. Of these, 11 have three or fewer accessions. Five taxa have ten or more accessions, but the extent of coverage within the native distribution of these species is not comprehensive. Since 2008, the OPGC has conducted four exploration/collection trips for *Coreopsis* and more are planned for the future, targeting both more comprehensive coverage of the major taxa but also aiming to include representation of all species.

Characterization of the collection is a continuous process. In a survey of 99 accessions of 18 of the 27 known eastern clade species of *Coreopsis* (67 wild accessions and 32 cultivars), it was found that the majority had DNA content equivalent to diploid chromosome numbers (Jourdan et al. 2015). In addition to the natural tetraploid *C. delphinifolia* Lam. (Smith 1975), probable tetraploids were found in cultivars of *C. rosea*, *C. verticillata*, and *C. grandiflora*.

There is a need for expansion of the ex situ collection by additional exploration, particularly for the species that are underrepresented in the collection. Sampling germplasm along the perimeter of the distribution range for the more widely distributed species, such as the northernmost range, may provide material with desirable attributes, such as cold hardiness. There is also an urgent need to obtain wild germplasm of all the western species and of the more rare species, such as *C. hamiltonii*, *C. integrifolia*, *C. nudata*, and *C. pulchra*. The use of some species in highway seed mixes and the potential for escape from cultivation makes it critical to ensure that collections are of truly wild local germplasm. The major challenge is one of limited resources primarily because of the broad mandate in the conservation of many herbaceous ornamental plants.

18.2.2 ***Rudbeckia*** **L.**

18.2.2.1 Introduction

Widely known as black-eyed Susan or coneflower, *Rudbeckia* species can be found throughout the USA growing along roadsides, forest and stream edges, and in open fields. For many in North America, the black-eyed Susan (*R. fulgida* Aiton) may be the quintessential wildflower species (Harkess and Lyons 1994). The cultivated forms are easy to grow, have showy inflorescences in shades of yellow and orange, are tolerant of a wide range of constructed landscape conditions, have few insect or disease problems, and require only minimal care for a show of color from summer through autumn.

The taxonomy of *Rudbeckia* is relatively well established (Urbatsch et al. 2000), although there has been reassessment of the status of some subspecific taxa, particularly for the widely distributed *R. fulgida* (Campbell and Seymour 2013). There are 23 species organized into three sections (Table 18.6). The two principal species that have important cultivars are *R. hirta* L. and *R. fulgida*. The former is grown as an annual and is widely used in beddings and containers and as a cut flower. There are both diploid and tetraploid cultivars (Palmer et al. 2009). The latter species is the most commonly grown of the perennial *Rudbeckia* species, principally the long-popular cultivar 'Goldsturm.' However, selections and cultivars exist of *R. maxima* Nutt., *R. laciniata* L., *R. nitida* Nutt., *R. subtomentosa* Pursh, and *R. triloba* L. There are both diploid and tetraploid cytotypes of *R. hirta* and *R. fulgida*, although

Table 18.6 Germplasm accessions of *Rudbeckia* in the OPGC[a]

Section	Species	Total number of accessions	Number of cultivars
Dracopis	*R. amplexicaulis* Vahl	1	
Macrocline	*R. alpicola* Piper	1	
	R. auriculata (Perdue) Kral	2	
	R. californica A. Gray	1	
	R. glaucescens Eastw.	3	
	R. klamathensis P. B. Cox & Urbatsch	0	
	R. laciniata L.	24	3
	R. maxima Nutt.	6	1
	R. mohrii A. Gray	4	
	R. montana A. Gray	0	
	R. nitida Nutt.	3	1
	R. occidentalis Nutt.	13	2
	R. scabrifolia L. E. Br.	1	
	R. texana (Perdue) P. B. Cox & Urbatsch	3	
Rudbeckia	*R. fulgida* Aiton	52	5
	R. graminifolia (Torr. & A. Gray) C. L. Boyonton & Beadle	1	
	R. grandiflora (Sweet) C. C. Gmel. ex DC.	6	1
	R. heliopsidis Torr. & A. Gray	1	
	R. hirta L.	88	24
	R. missouriensis Engelm. ex C. L. Boynton & Beadle	3	
	R. mollis Elliott	2	
	R. subtomentosa Pursh	7	1
	R. triloba L.	30	1
Unknown	*Rudbeckia* sp.	15	3
	Total	267	41

[a] Data from USDA, ARS (2017a)

tetraploids of *R. fulgida* seem to be most common (Jourdan et al. 2015; Palmer et al. 2009). *Rudbeckia* inflorescences, particularly those of *R. hirta*, are found in colors ranging from lemon yellow to gold, chestnut, mahogany, and bronze, and flowers come in single and double forms; some cultivars have quill-shaped rolled ligules.

18.2.2.2 Crop Wild Relatives and Wild Utilized Species in North America

18.2.2.2.1 Genepool Classifications

The primary genepool (GP-1) for both *R. hirta* and *R. fulgida* is the wild accessions of the same species. Both are widely distributed throughout the Eastern USA and have also become naturalized in most regions of the country where growing conditions are suitable (Urbatsch et al. 2000). The potential for the other species to be within GP-2 and GP-3 is limited by low sexual compatibility. Some interspecific hybrids appear possible, albeit with great difficulty (Palmer et al. 2009); however, attempts at such hybridization have thus far been few, so the extent to which interspecific combinations are possible needs more careful evaluation. There is one report of a somatic hybrid between *R. hirta* and *R. laciniata* (Al-Atabee et al. 1990).

18.2.2.2.2 Distribution/Habitat/Abundance

The species of *Rudbeckia* include annuals, biennials, and perennials. Four of the species (*R. fulgida, R. hirta, R. laciniata*, and *R. triloba*) are widely distributed in the continental USA, especially in the eastern half; the rest tend to have more restricted distributions in southeastern or western states (Fig. 18.3). Native stands of *R. hirta* have been found in virtually every state in the continental USA. The soil types and habitats where the different species occur vary, but moist to wet sites are preferred. Habitats include open meadows, old fields, mesic pastures, edges of woods, thickets, wet prairies, along streams, wet pine savannahs, bogs, seeps, serpentines, rocky prairies, limestone glades, and sandy soils (Flora of North America 2016).

18.2.2.2.3 Utilization and Potential for Expanded Use

The most extensive breeding effort has been made with *R. hirta*, which became an important annual crop after introduction of improved cultivars by Goldsmith Seeds in the 1960s (M. Miller, personal communication). There are tetraploid cultivars that are vegetatively propagated and diploid cultivars that are seed propagated. In contrast to the relative ease of hybridization between species in *Coreopsis*, significant barriers to interspecific hybridization occur in *Rudbeckia* (Oates et al. 2012; Palmer et al. 2009). For example, only one hybrid between *R. subtomentosa* and *R. hirta* was identified among 844 seedlings obtained from the cross. The genus has

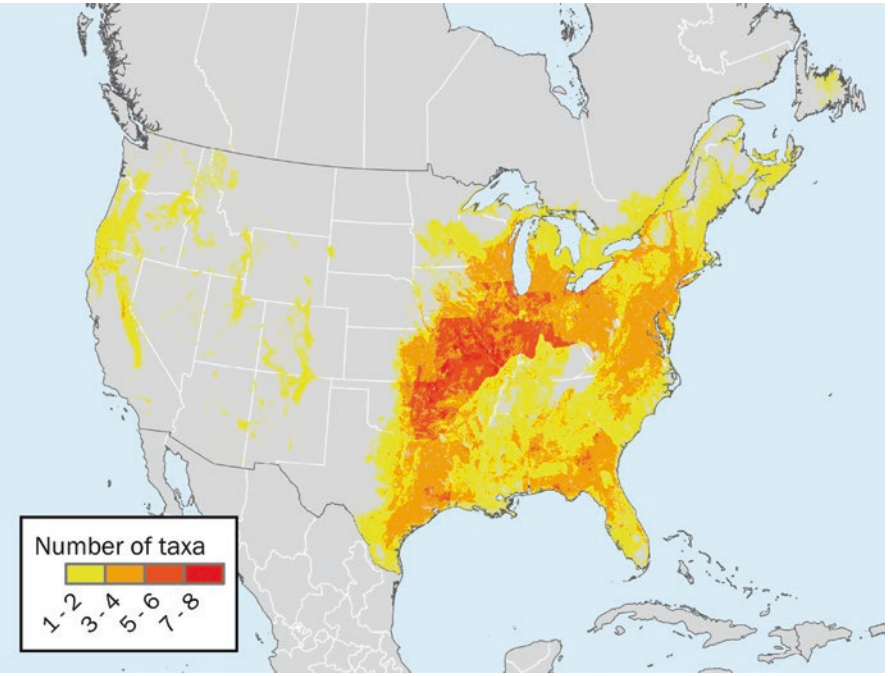

Fig. 18.3 Species richness of modeled potential distributions of North American *Rudbeckia* taxa, based on climatic and edaphic similarities with herbarium and genebank reference localities. Warmer colors indicate areas where greater numbers of taxa potentially occur in the same geographic localities. Full methods for generation of maps and data providers are given in Appendix 1

strong self-incompatibility and pseudogamy, a form of apomixis, that appears to be a common reproductive pathway (Palmer et al. 2009).

The typical traits previously described for ornamental plants are relevant for *Rudbeckia*. Novelty in flower color continues to be desirable. For some of the species (*R. laciniata*, *R. nitida*, *R. maxima*, *R. triloba*), compact habit is of great interest as this would broaden the options for use in more confined urban settings. Disease resistance in *R. fulgida* is also desirable as occasional problems occur with *Septoria* Sacc. and *Ramularia* Unger leaf spot, as well as powdery mildew and aster yellows (Daughtrey and Benson 2005).

> Increased use of *Rudbeckia* in constructed landscapes will depend on more intense domestication of species other than *R. hirta* and *R. fulgida*. Expansion of the available germplasm as well as more intensive screening for desirable traits is needed. Some compact forms have been found among the tall species, but the stability of the trait and ease of growth is still undetermined (S. Stieve, personal communication). Additional efforts at interspecific hybridization, even by protoplast fusion, could be beneficial, although prior attempts have encountered limited success. Similarly, ploidy manipulation may open possibilities that have not yet been fully examined.

18.2.2.3 Conservation Status of *Rudbeckia* Crop Wild Relatives and Wild Utilized Species in North America

18.2.2.3.1 In Situ Conservation

Some taxa are abundant throughout their native range (e.g., *R. hirta*), whereas others have a restricted distribution and lower abundance (e.g., *R. klamathensis* P. B. Cox and Urbatsch) (Kartesz 2015). *Rudbeckia auriculata* (Perdue) Kral is a rare and threatened plant restricted to the coastal plain (Diamond and Boyd 2004). NatureServe (2017) lists its conservation status as critically imperiled (S1) in Florida and Georgia and imperiled (S2) in Alabama. *Rudbeckia heliopsidis* Torr. & A. Gray and *R. auriculata* are currently under review by the USFWS for possible threatened/endangered listing (ECOS 2016). The Flora of North America (2016) describes conservation concern also for *R. alpicola* Piper, *R. klamathensis*, and *R. nitida*, as well as indicating that *R. scabrifolia* L. E. Br. is in the Center for Plant Conservation's National Collection of Endangered Plants. However, none of these species have a formal in situ conservation programs. The Nature Conservancy protects habitats of some rare species, like *R. scabrifolia* in Texas (Poole 2007). Conservation management plans for even the more abundant *R. fulgida* var. *sullivantii* have been proposed to ensure persistence of healthy populations of the species (USDA Forest Service 2003). A more comprehensive and updated study of the status of the threatened taxa is clearly needed. Making the genus a priority for conservation and identifying clear targets for conservation are necessary in order to encourage in situ conservation efforts.

18.2.2.3.2 Ex Situ Conservation

The OPGC collection of *Rudbeckia* consists of approximately 270 accessions, with about 15% of them as cultivars (Table 18.6). There is a reasonably good numerical representation of wild accessions in *R. hirta*, *R. fulgida*, *R. triloba*, and *R. laciniata*, but the geographic coverage is still limited, considering the extent of distribution of the taxa. In contrast, eight taxa have only one or two accessions, and there are no accessions of two other taxa; these accessions were not collected from the wild and represent a minimal sampling of the genetic diversity that may be available. The overall collection consists primarily of seeds, but one quarter of the taxa are represented by a single plant, obtained from commercial sources.

Exploration for *Rudbeckia* germplasm by OPGC personnel has been ongoing since 2008; three collection trips have been conducted in the USA. Additional explorations are needed both for more comprehensive coverage of the distribution of species and for more complete representation of genetic diversity within all taxa. Characterization efforts have included genome size measurements (Jourdan et al. 2015); there are both diploid and polyploid forms of some species, but polyploids were more frequent among the cultivars. The widely distributed *R. fulgida* displayed a nearly continuous variation in genome size, indicating a complexity that needs further examination to assess its significance. To be fully comprehensive, the collection must have additional representation of germplasm from diverse habitats of the widely distributed species. In addition, more sampling of the western USA taxa, including *R. alpicola, R. californica* A. Gray, *R. klamathensis*, and *R. occidentalis* Nutt., is needed. The same holds true for some of the eastern species, such as *R. auriculata*, *R. heliopsidis*, *R. mollis* Elliott, and *R. scabrifolia*. Greater availability of diverse germplasm for these species may permit a more thorough analysis of interspecific compatibilities between them.

18.2.3 Phlox L.

18.2.3.1 Introduction

The genus *Phlox* provides another example of a native North American herbaceous ornamental with current diverse utility and potential for further development and use (Locklear 2011). There are approximately 65 species that have two broad centers of distribution in the eastern and western USA (Wherry 1955). All of the important cultivated taxa are from the eastern group. The species *P. drummondii* Hook., an annual, as well as *P. subulata* L. and *P. paniculata* L., both long-lived perennials, can be considered the principal crops and are some of the most easily recognized and widely cultivated flowering plants in temperate regions of the world (Locklear 2011). There are numerous cultivars of the three principal crop species. In fact, the garden phlox, *P. paniculata*, is reported to have over 500 cultivars (Bendtsen 2009), although only a fraction of them are in the general trade; however, a specialty nursery lists 136 cultivars for sale (Perennial Pleasures 2016). Most major nursery catalogs list only a dozen or so cultivars. Both *P. subulata* and *P. drummondii* also have approximately a dozen cultivars regularly available in commerce. Other species straddle the line between a crop and a WUS; these include *P. divaricata* L., *P. carolina* L., *P. glaberrima* L., *P. maculata* L., and *P. stolonifera* Sims. *Phlox pilosa* L. is sometimes used in wildflower mixes. A popular cultivar of a perennial phlox is ‘Minnie Pearl.’ Initially considered an interspecific hybrid, it is actually a wild form of *P. carolina* that was found by Karen Partlow along a road in Kemper, Mississippi, and introduced into the trade by Plant Delights Nursery (T. Avent, personal communication). Thus, ‘Minnie Pearl’ is basically a WUS that has been vegetatively propagated and maintained; similar circumstances likely led to many cultivars of *Phlox* (Zale 2014).

18.2.3.2 Crop Wild Relatives and Wild Utilized Species in North America

18.2.3.2.1 Genepool Classifications

Interspecific sexual compatibility exists among some species of *Phlox* (Levin 1963, 1968, 1973, 1975; Levin and Smith 1966; Levy and Levin 1974; Wherry 1955), but a more comprehensive assessment of species-crossing relationships from a breeding standpoint has only recently been initiated (Zale 2014). There are reports of interspecific hybrids, some of natural occurrence, such as *Phlox* ×*procumbens* (Lehmann) Wherry (*P. stolonifera* × *P. subulata*), *P.* ×*glutinosa* Buckley (*P. divaricata* × *P. pilosa*), and *P.* ×*rugelii* Brand (*P. divaricata* × *P. amoena*) (Locklear 2011); other interspecific hybrids have been reported but poorly documented. In addition to phylogenetic distance, one possible barrier to interspecific hybridization is ploidy differences within and among species. Studies by Ferguson's group (Chansler et al. 2016; Fehlberg and Ferguson 2012a, b; Worcester et al. 2012) and by Zale (2014) have shown that cytotype variation within species may be quite frequent, although this ploidy variation may not always be readily expressed in phenotype (Chansler et al. 2016). Thus, an important need for *Phlox* genetic resources is the assessment of the ploidy of wild materials that may be used in breeding efforts.

The phylogeny of *Phlox* is still in a state of flux, but there are broad outlines that provide a guide for possible sexual compatibility between species based on phylogenetic proximity (Ferguson et al. 1999; Ferguson and Jansen 2002). For example, the status of some species, such as those of the *P. carolina/P. glaberrima* complex, as well as *P. pilosa*, is still unclear. Many of the species designations remain unresolved (The Plant List 2013). Most species exhibit extensive phenotypic and genetic diversity among populations that has resulted in a confusing taxonomic history (Zale 2014). Table 18.7 lists the principal eastern USA species arranged by subsections; also included are some western USA species. Given that interspecific hybrids have been identified, it is likely that the subsection groupings in the genus include species with sexual compatibility, at least for those within the same ploidy level (Zale 2014). However, hybridization between species of different subsections is also possible, suggesting that much of the genus may be within GP2 (C. Valin, personal communication; Zale 2014).

18.2.3.2.2 Distribution/Habitat/Abundance

Of the 65 species of *Phlox,* about 45 species occur in the western USA, and 20–23 species in the east, including much of Texas (Wherry 1955). Within the eastern region, states with the highest diversity of taxa include Tennessee, North Carolina, Virginia, Alabama, Texas, Kentucky, and Georgia (Fig. 18.4) (Zale 2014). Taxa such as *P. amplifolia* Britton, *P. floridana* Benth., *P. villosissima* (A. Gray) Small, *P. pilosa* ssp. *deamii* D. A. Levin, and others tend to be geographically remote endemics or relicts with restricted natural distributions in places of low population density and may be rare in the wild (Wherry 1955; Zale 2014). Wherry's monograph of 1955 still presents the most comprehensive assessment of the distribution of *Phlox* species; a more up-to-date evaluation of the ecogeographic patterns is clearly warranted. A detailed representation of the distribution of selected *Phlox* species is provided in Fig. 18.5 which groups species phylogenetically by subsection.

Table 18.7 Germplasm accessions of *Phlox* in the OPGC[a]

Section	Subsection	Species	Total number of accessions	Number of cultivars
Annuae	*Divaricatae*	*P. amoena* Sims	17	
		P. cuspidata Scheele	1	
		P. divaricata L.	35	9
		P. drummondii Hook.	19	13
		P. floridana Benth.	1	
		P. longipilosa Waterf.	2	
		P. nana Nutt.*	2	
		P. pattersonii Prather*	1	
		P. pilosa L.	17	4
		P. pulcherrima (Lundell) Lundell	7	
		P. roemeriana Scheele	3	
		P. villosissima (A. Gray) Small	3	
Phlox	*Cluteanae*	*P. buckleyi* Wherry	8	
	Longifoliae	*P. stansburyi* (Torr.) A. Heller*	1	
	Phlox	*P. carolina* L.	14	1
		P. glaberrima L.	14	5
		P. maculata L.	17	6
		P. ovata L.	12	0
		P. pulchra (Wherry) Wherry	6	2
	Paniculatae	*P. amplifolia* Britton	9	4
		P. paniculata L.	117	95
	Stoloniferae	*P. adsurgens* Torr. ex A. Gray*	3	1
		P. stolonifera Sims	18	6
	Subulatae	*P. bifida* L. C. Beck	13	4
		P. nivalis Lodd. et al. ex Sweet	2	1
		P. subulata L.	32	10
Occidentales	*Albomarginatae*	*P. alyssifolia* Greene*	2	
	Canescentes	*P. austromontana* Coville*	3	
		P. muscoides Nutt.*	1	
		P. opalensis Dorn*	1	
		P. pungens Dorn*	1	
		Total	382	161

[a] The emphasis of the list is on species primarily distributed in the eastern/central USA, except for the western species marked with an asterisk (*). There are 22 species (and up to 20 additional subspecies) within the eastern/central USA group (Zale 2014). Data from USDA, ARS (2017a)

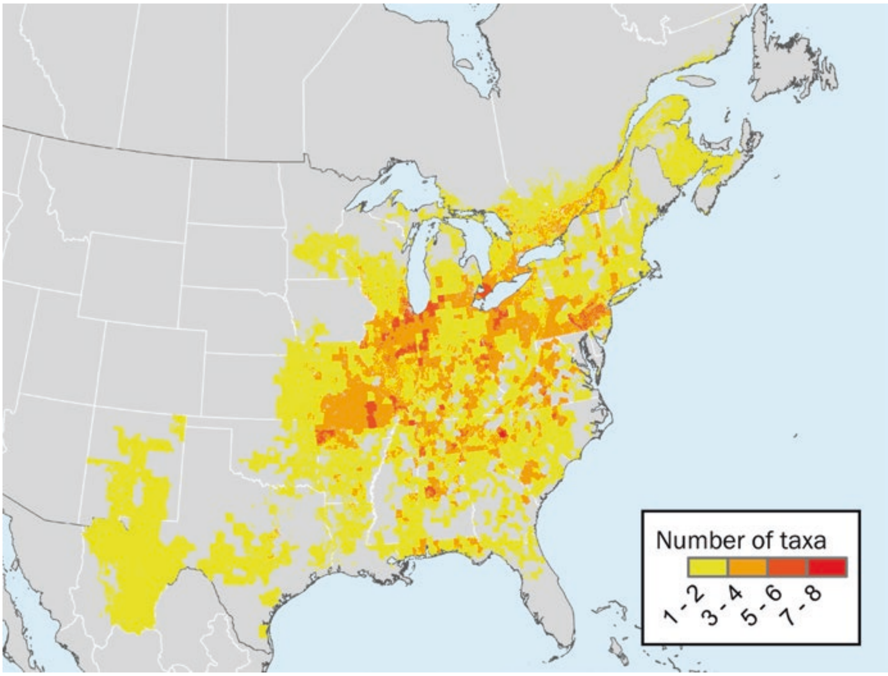

Fig. 18.4 Species richness of modeled potential distributions of *Phlox* taxa for eastern North America, based on climatic and edaphic similarities with herbarium and genebank reference localities. Warmer colors indicate areas where greater numbers of taxa potentially occur in the same geographic localities. Full methods for generation of maps and data providers are given in Appendix 1

18.2.3.2.3 Utilization and Potential for Expanded Use

The first commercial *Phlox* cultivar was released in 1824 (Symons-Jeune 1953). Since then, intensive breeding and selection has resulted in the introduction of hundreds of cultivars, primarily of *P. paniculata* and also of *P. drummondii* and *P. subulata*, but the scope of breeding efforts has been relatively limited (Zale 2014). Most of the breeding has occurred at the diploid level since the majority of cultivars in the trade are diploid (Zale and Jourdan 2015; Zale et al. 2016). Interspecific hybridization appears to have played some role in phlox cultivar development, but there is renewed interest in exploring new interspecies combinations using the germplasm that is increasingly available (Zale 2014).

The most salient feature of cultivated *Phlox* is the vivid color and abundance of flowers. Characteristics that enhance the flowering effect by providing different colors, more abundant flowers in a compact plant, and extending flower longevity are continuous goals. However, one important characteristic in need of development is resistance or reduced susceptibility to powdery mildew. The ultimate combination of traits is superior flowering with disease resistance. For some species, such as

P. paniculata, reduction in height to produce more compact plants and increasing the sturdiness of stems are also highly desirable characteristics. For *P. drummondii*, greater adaptability to more humid environments, both for landscape use and for production systems, would be desirable. For *P. subulata*, extending the flowering period or developing reblooming forms is of great interest.

As with any flowering herbaceous ornamental, novel flower colors in phlox are much sought out. The current palette centers on pinks, mauves, purples, and whites, with some gradation toward red and blue. What is lacking are strong yellows and oranges. Any germplasm that provides a way to develop these colors would be highly valued. The potential for such colors exists in the genus. Two cultivars of *P. mesoleuca* Greene, considered by some a variant of *P. nana* Nutt., showed both vivid yellow (‘Paul Maslin’) and fiery orange/red (‘Mary Maslin’) flowers; these color variants were found in the Chihuahua region of northern Mexico (Kelaidis 1984). Unfortunately, both cultivars seem to have been lost from cultivation and may even be lost in the wild (Kelaidis 2012). The principal flower pigments in phlox are anthocyanins (Bohorquez-Restrepo 2015), but carotenoids are present in some taxa, such as *P. roemeriana* Scheele and the golden-eye phlox, and it is likely that carotenoids accounted for the yellows and oranges of *P. mesoleuca*.

The potential for expanded use of phlox in constructed landscapes is significant. New plants introduced into the trade must have the desirable attributes of flower abundance and vibrant color, high quality foliage, and ease of production. *Phlox* display remarkable plasticity in growth characteristics based on growing conditions; plants that look spindly and insignificant in native habitats can display striking flowering response in cultivation. Preliminary evaluations of phlox germplasm at the OPGC suggest the combination of such traits may be possible either through different selections of wild germplasm or by interspecific hybridization. For example, *Phlox amoena* Sims and *P. bifida* subsp. *stellaria* (A. Gray) Wherry are taxa with potentially interesting horticultural attributes that could be of some value in diverse landscape settings, but more thorough evaluation of ornamental characteristics, as well as efficient propagation systems, needs to be developed to expand their use. At present, the principal challenge is the lack of availability of different accessions of the various species. Such availability will facilitate assessment of novel plants for the trade.

18.2.3.3 Conservation Status of *Phlox* Crop Wild Relatives and Wild Utilized Species in North America

18.2.3.3.1 In Situ Conservation

Most of the eastern *Phlox* taxa appear to be relatively abundant throughout their native range, but a few have restricted distributions and lower abundance, and, as a consequence, are more likely to be at risk. Among the eastern taxa, *P. buckleyi* Wherry and *P. pulchra* (Wherry) Wherry are ranked as globally imperiled and locally imperiled in their respective regions (NatureServe 2017). Two other taxa,

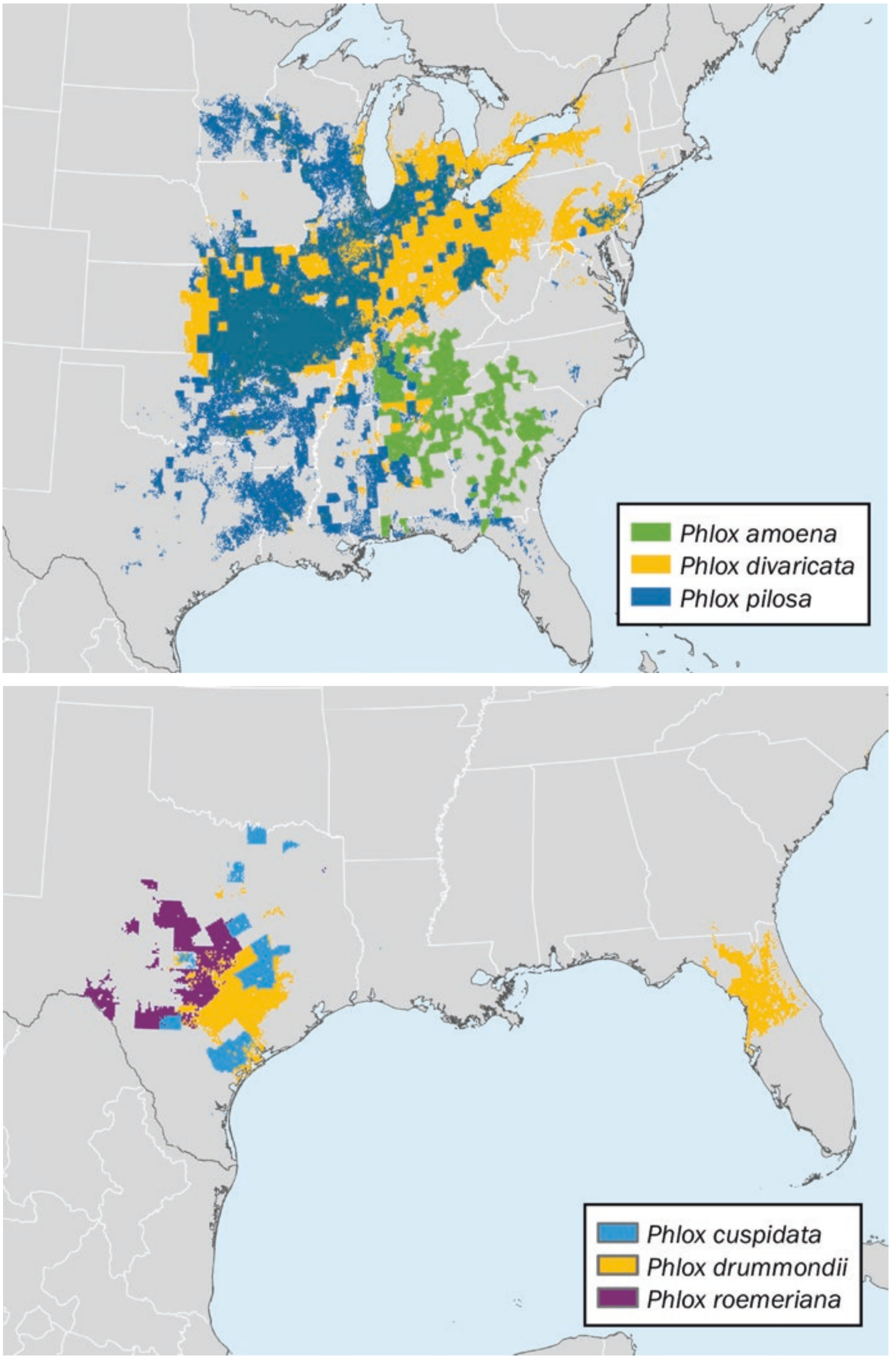

Fig. 18.5 Geographic distribution of selected *Phlox* taxa, grouped phylogenetically by subsection. (**a**) and (**b**) Subsection *Divaricatae*. (**c**) Subsection *Phlox*. (**d**) Subsection *Paniculatae.* Full methods for generation of maps and data providers are given in Appendix 1

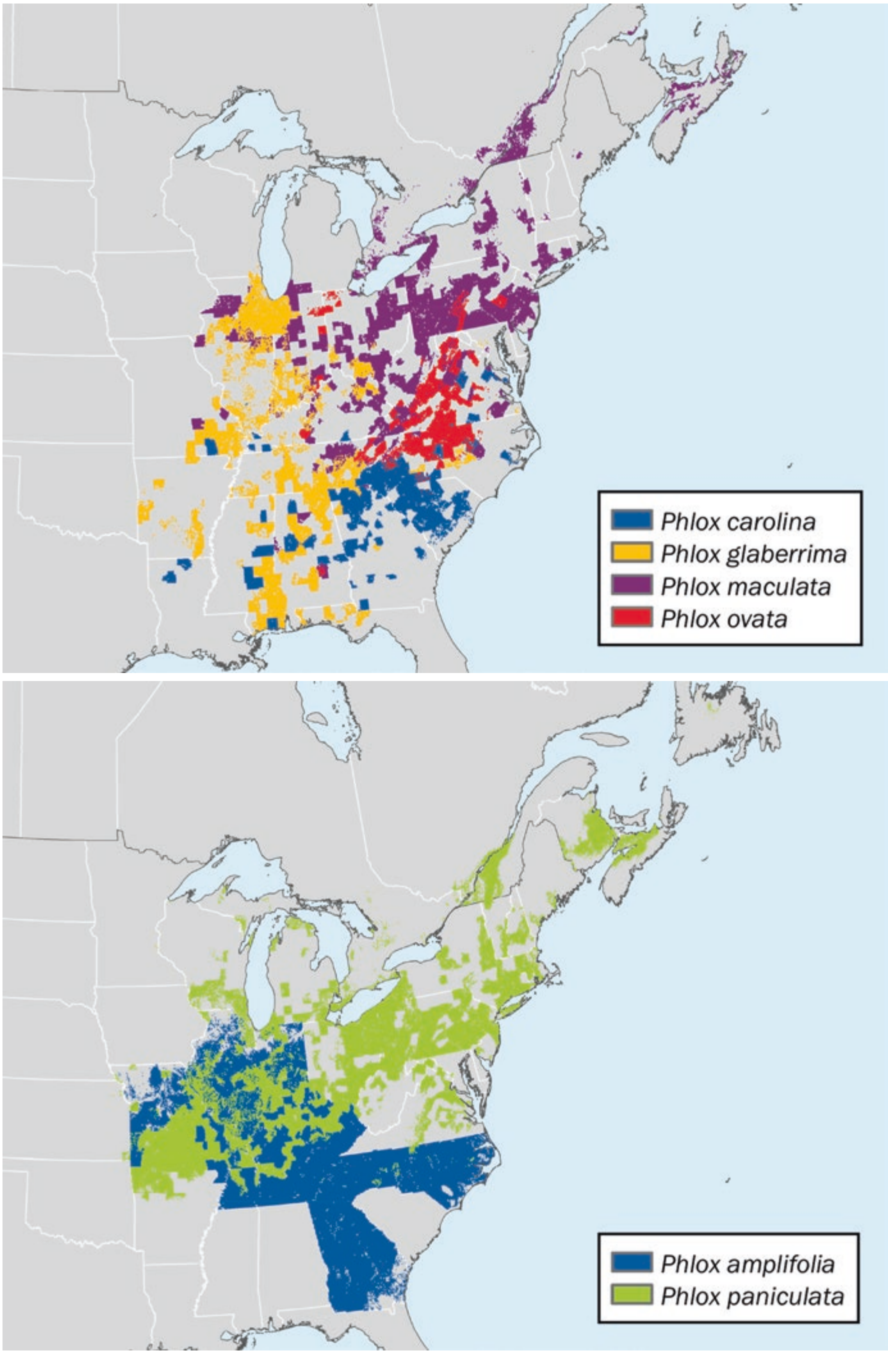

Fig. 18.5 (continued)

P. hirsuta E. E. Nelson, the Yreka phlox, and *P. nivalis* ssp. *texensis* Lundell, Texas trailing phlox, are listed as endangered by the USFWS, and recovery plans involving several agencies and organizations are in place (California Department of Fish and Wildlife 2016; ECOS 2016). The former is found in only five locations near Yreka, California (Ruane et al. 2015), and the latter is limited to fewer than 20 populations in three counties in eastern Texas (Texas Park and Wildlife 2016). *Phlox idahonis* Wherry and *P. pilosa* subsp. *sangamonensis* D. A. Levin & D. M. Sm. are included among taxa that need special conservation (Kramer et al. 2011). *Phlox idahonis* is ranked by NatureServe (2017) as critically imperiled in Idaho and *P. pilosa* subsp. *sangamonensis* as critically imperiled in Illinois. Both are also ranked as critically imperiled globally. In situ conservation efforts for *Phlox* appear to be limited to *P. hirsuta* and *P. nivalis* subsp. *texensis*. The Texas trailing phlox is under protective management at the Roy E. Larsen Sandyland Sanctuary (Texas Park and Wildlife 2016).

More extensive ecogeographic studies of phlox species are needed in order to guide possible protection of other taxa at risk. As indicated earlier, the most recent assessment of phlox distribution in the USA is more than 60 years old (Wherry 1955); thus, we do not know the extent to which changes in many populations have occurred since that time.

The yellow- and orange-flowered forms of *P. mesoleuca* indigenous to northern Mexico mentioned earlier could provide genes for pigments that may open an entire new color palette for the genus. Whether such plants still exist in the wild is uncertain, but if still present, the possibility of habitat protection is unknown. The best hope may be for ex situ conservation if it is possible under national and local laws.

18.2.3.3.2 Ex Situ Conservation

The OPGC collection of eastern *Phlox* species includes about 200 accessions obtained from natural habitats (Table 18.7). The taxa with the most accessions of wild origin include *P. divaricata, P. paniculata, P. subulata, P. amoena, P. pilosa, P. carolina, P. ovata* L., *P. stolonifera, P. maculata, P. glaberrima*, *and P. bifida* L.C. Beck. Beginning in 2010, the OPGC initiated development of a comprehensive collection of *Phlox* germplasm, an ongoing effort that will require additional years of exploration and collection to achieve. The focus has been on eastern USA species, but selected western species are also targeted for specific traits. Because of unique characteristics of *Phlox*, the collection strategy depends not only on obtaining seed from wild sources, the preferred method, but also on collecting vegetative samples that are propagated and grown in Ohio to produce seed under controlled conditions. This strategy is needed because many taxa flower over an extended period of time and the ripened fruit readily shatter to release the seed; thus, collecting sufficient seed from some populations is restricted to a relatively narrow window of time that is easily missed. Regeneration and seed increase efforts depend on availability of various Lepidoptera pollinators because *Phlox* flowers are not pollinated by bees, a situation that challenges efforts at controlled pollinations.

There is a need for more detailed studies of phlox seed biology, including quality assessments, germination, and potential for long-term storage; this is particularly true for the perennial species. Similarly, more effective systems for controlled pollination using butterflies are needed. The analysis of genome size for the germplasm collection suggests that polyploids may be more frequent at the margins of the distribution of a species (Zale 2014). Populations of different ploidy may provide new sources of desirable traits for breeding material. Such information indicates that more comprehensive sampling of *Phlox* taxa throughout their native range is important and desirable.

The principal challenges for ex situ conservation for many of the taxa lie in the difficulty in obtaining sufficient seed of high quality that can be safely stored. The reasonable longevity in storage and germination efficiency of the annual phlox, *P. drummondii*, suggests that more effort to produce seed and study their properties in the perennial species is justified.

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Chapter 19
Species for Medicinal and Social Use with an Emphasis on *Theobroma cacao* L. (Cacao), *Nicotiana tabacum* L. (Tobacco), *Actaea racemosa* L. (Black Cohosh), and *Humulus lupulus* L. (Hops)

Joe-Ann McCoy, Johanna H. Young, Jessica M. Nifong, Kim Hummer, Jeanine DeNoma, Carlos H. Avendaño-Arrazate, Stephanie L. Greene, and Michael B. Kantar

Abstract This chapter explores plants that are used for medicinal and social uses. It first gives a brief overview of taxa that are found throughout North America, how and where they are conserved and how they are distributed. It then looks at four economically important taxa, *Theobroma cacao* L. (cacao), *Nicotiana tabacum* L. (tobacco), *Actaea racemosa* L. (black cohosh), *Humulus lupulus* L. (Hops), as case

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J.-A. McCoy (✉) · J. H. Young
The North Carolina Arboretum Germplasm Repository, Asheville, NC, USA
e-mail: jmccoy@ncarboretum.org; j.young@ncarboretum.org

J. M. Nifong
US Nicotiana Germplasm Collection, Department of Crop and Soil Sciences,
NC State University, Raleigh, NC, USA

K. Hummer · J. DeNoma
USDA, Agricultural Research Service, Research Leader and Small Fruit Curator
at the USDA National Clonal Germplasm Repository, Corvallis, OR, USA
e-mail: Kim.Hummer@ars.usda.gov; Jeanine.DeNoma@ars.usda.gov

C. H. Avendaño-Arrazate
Cocoa Program, Experimental Field Rosario Izapa-INIFAP, Tuxtla chico, Chiapas, Mexico
e-mail: avendano.carlos@inifap.gob.mx

S. L. Greene
USDA, Agricultural Research Service, Center for Agricultural Resources Research,
National Laboratory for Genetic Resources Preservation, Fort Collins, CO, USA
e-mail: stephanie.greene@ars.usda.gov

M. B. Kantar
Tropical Plant and Soil Science, University of Hawaii at Manoa,
Honolulu, HI, USA
e-mail: kant0063@umn.edu

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studies of how medicinal and social plants have been used over the centuries and how their wild relatives have been conserved and how we can expect these plant to be used in the future.

Keywords Medicinal crop · Wild collected · Social-use crop · Crop wild relative

19.1 Overview of Species Used for Medicinal and Social Use

19.1.1 Historic and Modern Use Worldwide

Plants have been central to human culture since antiquity. This chapter will focus on species that have played a role in medicinal and social settings. Worldwide, more than 80% of the population in developing countries relies on herbal medicine, and its use in developed countries is increasing (Canter et al. 2005). Historically, a wide range of plant species have been used by a multitude of cultures across the world, reflecting a diversity of traditional pharmacopeia. An estimated 50,000–80,000 plant species are used currently for medicinal purposes around the world (Chen et al. 2016). Both the United States and Mexico fall among the top ten countries, in terms of number of medicinal plant species; the United States having slightly less than 3000 species, representing about 12% of its flora, and Mexico having about 2500 species, representing 9% of its flora (Chen et al. 2016). Even in boreal Canada, at least 546 taxa were used by First Nations (Uprety et al. 2012). Approximately two-thirds of medicinal species are collected from the wild, which is creating sustainability concerns (Canter et al. 2005). Recommendations have been made for the conservation and sustainable use of medicinal plants (Hamilton 2004) and include field cultivation, breeding, and molecular fingerprinting, as well as tissue culture and genetic transformation.

19.1.2 Challenges to Cultivation and Crop Improvement

Medicinal and social-use crops span the production gamut from large-scale commercial production, small acreage, and backyard production to direct harvest of wild species from managed or unmanaged natural landscapes. Medicinal and social-use crops may also be used for multiple purposes. Plant part, plant preparation, and agronomics can differ depending on the use, adding to the complexities of cultivation. Although the challenges of cultivation vary by species, all share the common element of dealing with biotic stress (disease, insects) and abiotic stress (drought, heat), particularly in the face of climate change and the resulting changes occurring in pest distributions and weather patterns. Although it is not possible in this chapter to adequately address the cultivation challenges faced by all North American species utilized for medicinal and social purposes, a common thread among all species is that challenges in cultivation and commercialization can be addressed by capitalizing on the inherent diversity found in naturally occurring populations. The genetic resources available to improve medicinal and social-use crops span a range of germplasm that includes cultivated and wild forms (i.e., wild utilized species) of the crop species, as well as species related to the crop (crop wild relatives, CWR). This broad range of germplasm has great potential as a source of variation for many different traits. A general challenge in using diverse germplasm is lack of availability of diverse and well-characterized genetic resources, especially for crops used for specific cultural or ceremonial purposes. A challenge to the increased use of related wild species is the lack of knowledge about the potential for hybridization between CWR and the specific crop. A final challenge is to ensure that these resources, especially those found in the wild, are effectively conserved both in situ and ex situ.

19.1.3 Conservation and Sustainable Use

Globally, approximately two-thirds of medicinal species are obtained directly from the wild (Canter et al. 2005). Many medicinal and social-use plants occur on endangered and threatened plant lists. Table 19.1 lists medicinal species listed in the US crop wild relative inventory of Khoury et al. (2013), ranked as vulnerable or imperiled by (NatureServe 2017).

As with many wild plant species, habitat loss is a major factor contributing to vulnerability (e.g., *Echinacea*; Kindscher 2006). Other factors that contribute to species rarity include habitat specificity, distribution range, population size, species diversity, growth rate, and reproductive system (Chen et al. 2016). Overharvesting is a cyclical problem depending on demand. Although not officially listed, many medicinal species are at risk from overharvesting, and close monitoring is needed to ensure sustainable harvest. A ranking tool has been developed to quantify the vulnerability of temperate North American species to overharvest (Castle et al. 2014). The ranking tool supports a species watch list published by the United Plant Savers (https://www.unitedplantsavers.org) (United Plant Savers 2017). RootReport (http://www.rootreport.frec.vt.edu) is a collaborative website housed at Virginia Technical University, Virginia, that tracks US native medicinal plant harvest, production, and markets and provides resources to support the sustainable harvest and production of medicinal plants. In addition to monitoring for the negative impacts of overharvest, in situ and ex situ conservation are important strategies.

19.1.3.1 Ex Situ and In Situ Conservation

Medicinal and social-use taxa are present in many genebanks; significant collections include the NPGS (USA), the Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung (Germany), and the National Agriculture and Food Research Organization (NARO) genebank in Japan. The NPGS medicinal plant collection is housed at the USDA, Agricultural Research Service, North Central Regional

Table 19.1 Vulnerable or threatened medicinal plant species occurring in crop wild inventory of the United States (Khoury et al. 2013)

Taxon	Common name	Rank[a]
Abies fraseri (Pursh) Poir.	Fraser fir	G2
Artemisia australis Less.	Hinahina	G3
Artemisia palmeri A. Gray	San Diego sagewort	G3
Artemisia porteri Cronquist	Porter's wormwood	G2
Croton alabamensis E.A. Sm. ex Chapm. var. Alabamensis	Alabama croton	G3 T3
Croton alabamensis E.A. Sm. ex Chapm var. Texensis	Texabama croton	G3 T2
Echinacea angustifolia var. strigosa	Narrowleaf purple coneflower	G4HQ
Echinacea atrorubens Nutt.	Topeka purple coneflower	G3
Echinacea laevigata (C.L. Boynt. & Beadle) S.F. Blake	Smooth coneflower	G2G3
Echinacea paradoxa (Norton) Britton var. neglecta R.L. McGregor	Bush's purple coneflower	G2T1
Echinacea paradoxa (Norton) Britton var. Paradoxa	Ozark coneflower	G2 T2
Echinacea sanguínea Nutt.	Sanguine coneflower	G3G5
Echinacea tennesseensis (Beadle) Small	Tennessee coneflower	G2
Eurybia furcata (Burgess) G.L. Nesom	Forked aster	G3
Guaiacum sanctum L.	Holywood lignum vitae	G2
Hypericum adpressum W.P.C. Barton	Creeping St. John's wort	G3
Hypericum chapmanii P. Adams	Apalachicola St. John's wort	G3
Hypericum cumulicola (Small) W. P. Adams	Highlands scrub St. John's wort	G2
Hypericum graveolens Buckley	Mountain St. John's wort	G3
Hypericum harperi	Sharp-lobe St. John's-wort	G3G4
Hypericum lissophloeus P. Adams	Smooth-barked St. John's wort	G2
Hypericum mitchellianum Rydb.	Blue ridge St. John's wort	G3
Lindera melissifolia (Walter) Blume	Pondberry	G2G3
Panax quinquefolius L.	American ginseng	G3G4
Papaver alboroseum Hultén	Pale poppy	G3G4

[a] NatureServe rank (NatureServe 2017); *G2* imperiled, at high risk of extinction due to very restricted range, very few populations (often 20 or fewer), steep declines, or other factors; *G3* vulnerable, at moderate risk of extinction due to a restricted range, relatively few populations (often 80 or fewer), recent and widespread declines, or other factors; *G#G#* range rank, a numeric range rank (e.g., G2G3) is used to indicate the range of uncertainty in the status of a species or community

Plant Introduction Station (NCRPIS), located in Ames, Iowa, and conserves ~210 medicinal taxa. Many taxa are also conserved in botanical gardens and arboreta. In Mexico, the IB-UNAM Botanic Garden has been active in sharing knowledge about indigenous plants, and the Oaxaca Botanic Garden has been promoting their use in public landscapes (Hawkins 2008). Although Maunder et al. (2001) found that European botanical gardens housed a number of medicinal species, few systematic conservation plans were in place, and efforts tended to be skewed toward ornamental species. However, the Botanical Garden Consortium International has since developed a global priority species list and action plan for conserving medicinal plants (Hawkins 2008). In temperate North America, the United Plant Savers has established a network of over 100 botanical sanctuaries that preserve habitat that harbors a diversity of wild medicinal species (http://www.unitedplantsavers.org). Public lands also afford a level of protection for medicinal and social use species that are commercially harvested. In the United States, USFS and BLM regulate collection, but there is room for improvement (Robbins 2000). In Canada there is no formalized system to protect native stands of commercially harvested species (Westfall and Glickman 2004). In Mexico a collaborative effort between the National Autonomous University of Mexico (UNAM), the National Commission for the Knowledge and Use of Biodiversity (CONBIO), and the KEW Royal Botanical Gardens has resulted in the collection and security of ex situ storage of useful native Mexican species, including many medicinal and social-use species (Rodríguez-Arévalo et al. 2017).

19.2 Case Studies

While it is possible to talk about the general status of medicinal and social-use genetic resources, it is impossible in this chapter to cover all species. Instead, we explore individual case studies of some of the most economically important species within this broad category. To this end, this chapter presents snapshots of cacao, tobacco, hops, and black cohosh – all important medicinal and social-use crops with important genetic resources in North America.

19.2.1 Cocoa (Theobroma cacao L.)

19.2.1.1 Summary

Cocoa is one of the most recognized products across the world due its major commercial product of chocolate. Chocolate holds a special place in many cultures across the world. Although cocoa is a crop of historic, economic, social, and ecological importance, there is still limited information about the distribution of native wild-type cocoa and no legal protection of native varieties. There is an urgent need to invest in the preservation of cacao germplasm resources to ensure that this crop will continue to thrive.

19.2.1.2 Origin of the Crop and Brief History of Use Worldwide

The genus *Theobroma* comprises 21 species, and includes *Theobroma cacao* L. (Cuatrecasas 1964). Most species of this genus are distributed exclusively in South and Central America; however, *Theobroma cacao* L. and *Theobroma bicolor*

Humb. & Bonpl. are distributed in southeastern Mexico, with *T. bicolor* being locally known as "pataxte" (CacaoNet 2012). Cocoa was important to the Mayan culture; it was used as currency, and therefore drinking chocolate represented the height of luxury. Historic information from antiquity is represented in a series of painted or engraved vessels found in the tombs of the Mayan nobles (Ogata 2002). Cocoa seeds are fat-rich and are used as a source of cocoa solids and butter for chocolate making and for the cosmetic industry. The center of origin has been well studied (Cuatrecasas 1964; Cheesman 1944; Dias 2001; Miranda 1962), with recent work suggesting cocoa originated in South America and was brought north by humans (Bartley 2005; Motamayor et al. 2002).

19.2.1.3 Modern-Day Use

Cocoa *(Theobroma cacao* L.) has great economic importance, being cultivated by greater than 2 million producers in greater than 50 countries. Each year, in the humid tropics, more than three million metric tons of dried cocoa beans are produced to be consumed in developed countries. Cocoa was exclusively a New World crop until 1890, when cultivation began in Africa (Ogata et al. 2006), where today the highest volume of production occurs. More than 20 million people around the world depend directly on the cultivation of cocoa for their livelihood with ~90% of cocoa production coming from small farms of less than five hectares. In 2015 in Mexico, cocoa was cultivated on 61,397 hectares with a production of 28,006 tons worth $1,034,792,000 Mexican pesos (SIAP 2016). Cocoa is cultivated in the states of Chiapas, Tabasco, and Guerrero (Avendaño-Arrazate et al. 2011). In Tabasco, cocoa is grown in the Chontalpa region, which includes the municipalities of Paraiso and Cardenas, in the central region that includes Nacajuca and Jalpa, and in the mountainous regions of Teapa, Jalapa, and Tacotalpa. In the state of Chiapas, it is cultivated in the northern region in the municipalities of Pichucalco, Ostuacan, Reforma, and Juarez and in the southern regions of Tapachula, Huixtla, Tuxtla Chico, Tuzantan, Cacahoatan, and Huehuetan (Fig. 19.1; SIAP 2016; Gutiérrez-López et al. 2016; Avendaño-Arrazate et al. 2011).

19.2.1.4 Challenges in Cultivation

While Mexico is a large cocoa producer, the average yield of the main producing states (Tabasco and Chiapas) of 470 kg/ha (SIAP 2016) is low compared to other exporting countries where yield is approximately 1 ton per hectare. Low yields of cocoa in Mexico are mainly due to the following:

(a) Advanced age of plantations with 40–80% older than 25 years (Avendaño-Arrazate et al. 2011)
(b) The poor performance of old cultivars having low yield potentials (Hernández-Gómez et al. 2015)
(c) Low planting densities

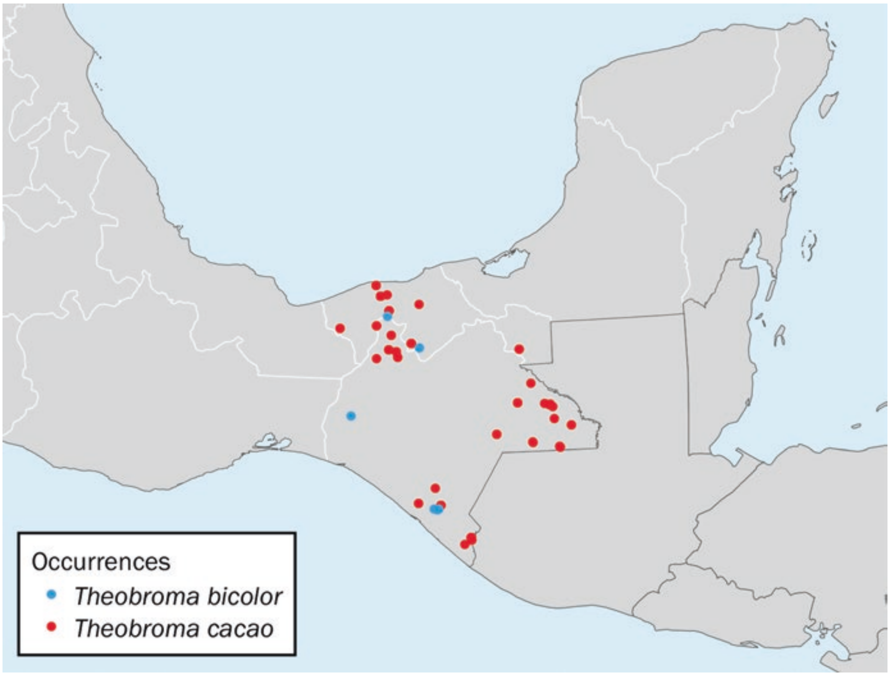

Fig. 19.1 Distribution of *Theobroma bicolor* L. and *Theobroma cacao* L. occurrence points located within areas of Mexico listed as native to the species by GRIN Taxonomy (USDA ARS National Plant Germplasm System 2017). Occurrence locations also exist for both species in many parts of central and southern Mexico, but their status as wild types is uncertain

(d) The cumulative damage of pests and diseases, with the major diseases being black pod disease caused by *Phytophthora palmivora* Butler, progressive tree death caused by *Ceratocystis fimbriata* Ellis & Halst, and recently moniliasis, caused by *Moniliophthora roreri* (Cif.) H.C. Evans, Stalpers, Samson & Benny, which has decreased yields in Soconusco, Chiapas, by up to 80% (Phillips-Mora et al. 2006; Phillips 2003)

(e) Little or incorrect management of plantations, which includes no shade management or pruning, inadequate fertilization, and inefficient control of pests and diseases

(f) Poor postharvest management (no controlled fermentation), leading to reduced quality and market price

19.2.1.5 Nutritional Use

Cocoa contains ~300 volatile compounds, including esters, hydrocarbolactones, monocarbonyls, and pyrroles, among others. The important flavor components are aliphatic esters, polyphenols, unsaturated aromatic carbonyls, diketopiperazines, pyrazines, and theobromine (Kalvatchev et al. 1998). Cocoa products and their uses are described in Table 19.2.

Table 19.2 Cocoa products and their uses

Products	Uses
Cocoa	Chocolate
Cocoa butter	Moisturizing creams, soaps
Cocoa pulp	Production of alcoholic and nonalcoholic beverages
Peel of the fruit	Animal feed, compost
Ashes of the shell	Soap, fertilizer
Cocoa juice	Preparation of jellies and jams
Cocoa powder	Ingredient in chocolate drinks and desserts, such as ice cream, mousses, sauces, cakes, and biscuits
Nutraceutical roles	(1) Treating patients to regain their weight; (2) stimulating nervous system of patients with hepatitis, exhaustion, or weakness; and (3) improving digestion, as cocoa/chocolate counteracts the effects of stunted or weak stomachs, stimulates the kidneys, and improves bowel function. In addition, chocolate/cocoa treatments have been performed for anemia, lack of appetite, mental fatigue, low breast milk production, tuberculosis, fever, gout, kidney stones, low sexual appetite, and low virility
Other	Antibacterial, antimycotic, and antiviral activity, the latter may be related to cocoa flavonoids

Source: Kalvatchev et al. (1998), Dillinger et al. (2000), Kalvatchev et al. (1998)

19.2.1.6 Crop Wild Relatives of the Crop

Theobroma cacao L. (2n = 2x = 20) belongs to the Malvaceae family and is classified into three main morphogeographic groups: outsider, criollo type, and trinitarian (Cheesman 1944). Cocoa populations from the Amazon basin belong to the outsider group, which can be further subdivided into an outlying group from the upper Amazon region and the outsider group from the lower Amazon region. The wild-type (criollo) group contains populations present from Central America to northern Venezuela and Colombia, while the trinitarian group is considered to be a group of hybrid materials between the outsider and the wild type (Bartley 2005).

The criollo type is characterized by elongated fruits with a pronounced asymmetry and acute point. The pod surface is usually rough, green, and often with splashes of red to purple, and seed embryos are large and white. This material produces the highest-quality chocolate (Cuatrecasas 1964; Ogata 2003). However, criollo type individuals are poor in performance and susceptible to disease. For these reasons, criollo type cocoa has been displaced from plantations by more productive varieties resistant to disease, but with lower quality (Avendaño-Arrazate et al. 2011). In Mexico, there is a wide diversity of criollo type cocoa genotypes that have not yet been exploited due to the lack of systematic studies (Avendaño-Arrazate et al. 2010). In Mexico, criollo cocoa has practically disappeared from commercial plantations. Only 5% of the interviewed producers reported having exclusively native cocoa, while 13% reported having native cocoa associated with other types (Avendaño-Arrazate et al. 2011).

19.2.1.7 Utilization

The evaluation and selection of clones began between 1945 and 1948 with the selection of 350 trees on farms from the municipalities of Tuxtla Chico and Cacahoatan, Chiapas. Clones were multiplied and established at Rosario Izapa Experimental Field of the National Institute of Forestry, Agriculture and Livestock Research (INIFAP), and the preliminary evaluation was initiated. Of these collections, 26 clones were selected in 1962, from which, 13 clones with superior production were selected as a basis for the genetic improvement program. The establishment of a germplasm bank occurred in 1980 with collections from Mexico and Central and South America. A collection of ~175 accessions was obtained, of which 125 clones have been characterized morphologically. Varietal descriptors of cocoa were created for the International Union for the Protection of Plant Varieties (UPOV), and these were adopted worldwide as a reference for the registration of improved cocoa varieties (Avendaño et al. 2014). Further evaluation and selection of interclonal crosses were carried out in field experiments in Rosario Izapa and other localities of Tabasco and northern Chiapas. Interclonal crosses involving Mexican clones and introductions from other countries were evaluated for production, adaptation, and resistance to *P. palmivora* and *Moniliophthora roreri* under natural conditions. In these studies, the progeny of clone "Pound 7" has been identified as most outstanding. Interclonal hybrids generally perform better than the "Amelonado" variety traditionally grown in the region of Tabasco and northern Chiapas.

Starting in 2009 in the region of Soconusco, Chiapas, INIFAP began the participative genetic improvement project that includes a very close collaboration between researchers and producers (Martin and Sherington 1997). Specifically, producers are involved in the breeding program, including setting objectives, generating variability, selecting and testing, as well as seed production and distribution (Rios et al. 2000). The methodology consists of (a) socialization of the project and definition of the criteria of selection of trees with the participating producers; (b) searching for, selecting, and labeling trees; (c) in situ morphological characterization and agronomic behavior of the selected trees; (d) evaluation of the response to pathogens; and (e) propagation of basal suckers and evaluation of the disease resistance in at least three environments of Soconusco, Chiapas. More than ten producers participated in the project. The criteria for selection were disease tolerance (moniliasis), high yield, quality, and aroma (wild-type characteristics). Five trees were selected and resistance testing was performed. Of these, two varieties were found to be tolerant to moniliasis, "Regalo de Dios" and "Arcoiris," and three with characteristics of wild type, "Rojo Samuel," "Rojo Gustavo," and "Verde Gustavo" (Avendaño-Arrazate et al. 2013).

19.2.1.8 Wild Utilized Species

Pataxte (*Theobroma bicolor*) is the most important relative of commercial cocoa. Pataxte is classified in Mexico as a semidomesticated species which has its own market (Ogata 2002). The major uses of pataxte are the same as for cocoa – drinks, candies, and marmalades (García et al. 2002). Dried pataxte seeds are a snack in South America (Avendaño-Arrazate et al. 2010). The pataxte pulp and beans are mainly used to manufacture confectioneries (marzipan, nougat, and marshmallow), chocolate (mixture of seeds of *T. cacao* and *T. bicolor*), fresh drinks (gruel, pozol, powder, and popo), and as fresh fruit (García et al. 2002; Bressani and Furlan 1997). A common preparation in the state of Oaxaca is a drink known as "popo" that in Nahuatl means "smoke," perhaps in reference to the foam produced when the drink is whipped with a wooden blender, traditionally made from a branch of *Quararibea funebris* (Key) Vischer, where flowers of pataxte are also used for other beverage known as "tejate." The drink "popo," also known by foreigners as "capuchino oaxaqueño," is made with slight modifications by the Nahuas, Mixe-Popolucas, Zoque-Popolucas, Mazatecos, and Chinantecos (Galvez-Marroquín et al. 2016). Recent work mentions its utility as a better source of antioxidants than *T. cacao* (Kalvatchev et al. 1998), and several studies recommend the use of *T. bicolor* as a substitute for cocoa butter alone or in combination, although in comparison with commercial cocoa it contains less fat. The fruit in general contains 127 volatile compounds, with high concentrations of ethylene acetate (36%).

Today, pataxte is associated with cocoa production systems, serving as a shade tree or as part of backyard orchards, with a wide variation of fruit shapes and sizes (Fig. 19.2). However, like cocoa, fruits of this species are susceptible to moniliasis *(Moniliophthora roreri* [Cif. & Par.] Evans), providing an alternate host for the pathogen. It is for this reason that producers are eliminating it, and in some regions it is disappearing (Mendoza-López et al. 2012). In the Soconusco and Chiapas northern regions, it is associated with cocoa; however, both regions lack management, and the few existing trees are being cut down (Gálvez-Marroquin et al. 2016). In the 1980s a considerable area was planted in the Chinantla region of Oaxaca, particularly Valle Nacional, San Felipe León, San Mateo Yetla, San Juan Lalana, Ojitlan, Usila, and San Jose Chiltepec. The state of Oaxaca is the only Mexican state that consumes large amounts of pataxte, and this demand represents a profitable opportunity for producers motivated by the price at the regional level (Mendoza-Lopez et al. 2012). Pataxte represents an alternative crop to improve the income of producers in southeastern Mexico; however, the lack of availability of improved varieties, including those with resistance to moniliasis, lessens its appeal. That is why it is necessary to generate technological packages that allow its cultivation in a sustainable way for the producer and in this way help to preserve it.

19.2.1.9 Conservation Status of CWR and WUS

Criollo-type cocoa is still found in the natural protected area of Montes Azules (Lacandon Jungle, Chiapas), a federal reserve where cocoa is preserved. There is a need for in situ conservation in cocoa and for promoting this strategy among producers of cocoa and for developing varieties that the market needs. By creating participatory breeding programs, where the transfer and use of varieties are more effective, producers can have additional income and avoid displacement from the

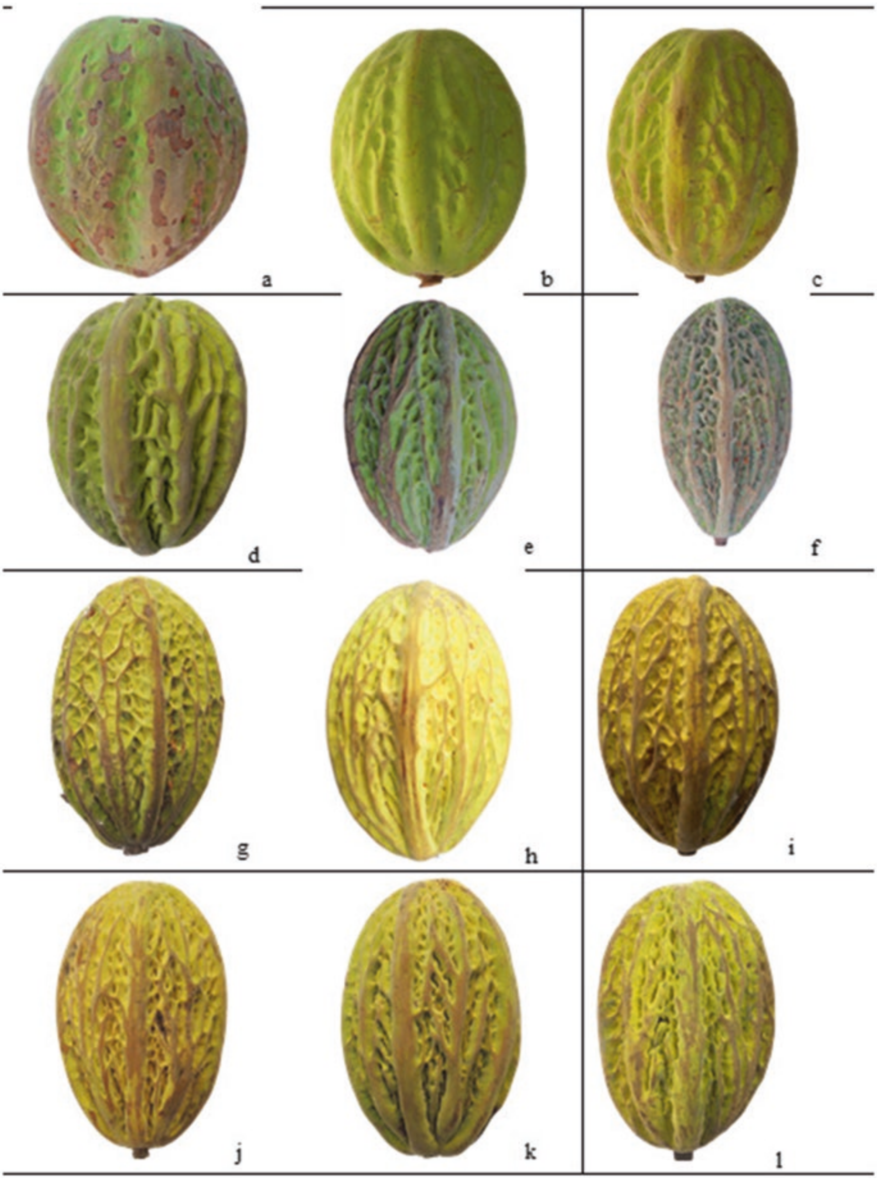

Fig. 19.2 Diversity of fruit forms of pataxte *(T. bicolor* L.*)* distributed in Mexico. (Source: Galvez-Marroquín et al. 2016)

countryside or, in this case, the replacement of the cultivation of cocoa by other crops. Finally, the protected natural areas of Mexico, mainly the Montes Azules in Chiapas where native cocoa is still found, should be invested in heavily to educate both technicians and producers for the conservation and sustainable use of this resource. An associated ethnic group, the Chol, live in the city of Palenque, Chiapas, and are supported by the National Commission of Natural Protected Areas, although this does not necessarily imply that in situ species conservation is being performed (Avendaño-Arrazate et al. 2011). As wild-type cocoa is highly valued by market niches in Europe, this can be an incentive to continue the conservation and sustainable use of wild-type cocoa. The challenge is to provide institutions that promote in situ conservation with financial resources for training and capacity building, so that the various players in the value chain of cocoa increase their awareness of preserving and maintaining Mexican wild-type cocoa. In the case of *T. bicolor*, its conservation is promoted in cocoa plots, because on average each plot has five to ten trees of *T. bicolor*.

In 1942 Mexico initiated collection and census of clonal nurseries of the collected germplasm, selecting local germplasm, and introduced germplasm in the Experimental Field Rosario Izapa-INIFAP. Likewise, INIFAP has reported that most of the genetic material protected in its germplasm banks is wild in origin (López et al. 1990). From these clonal nurseries and in their selection programs, important genotypes have been derived including Amelonado, Calabacillo, RIM (Rosario Izapa, Mexico), Guayaquil, Ceylan, wild type, Colegio de Postgraduados Germoplasma (CP1, CP6, (INIFAP 68 and 67 derived from wild type)), and INIFAP (INIFAP 75 and 76 derived from Amelonado). The “Rosario Izapa” germplasm collection is one of the two national collections of INIFAP cocoa germplasm, with a total of 176 accessions of trinitarians, outsiders, and a collection of Mexican wild-type cocoa. The other collection is located in the Huimanguillo Experimental Field of INIFAP in Tabasco. The cocoa collection at the Rosario Izapa Experimental Field was established in the early 1980s and currently has accessions from eight countries in Latin America and Mexico: Costa Rica (UF, CC, CATIE, Santa Clara, Diamantes), Colombia (ICS), Venezuela (Ocumare, Chuao, Porcelana), Guatemala (SPA), Brazil (SIAL, RB, Catongo, EEG) (SGU) and Mexico (RIM, La esmida pentagona, PICH, TAB, P, CHI, OST, Santa Ana), *T. mammosum*, T. *bicolor* and *Herrania* spp., and 70 wild type accessions reproduced through buds (materials from Yucatan, Tabasco, Chiapas, Oaxaca, and Veracruz mainly). In addition, it has 30 accessions of materials reproduced by seeds from the Lacandon Jungle of Chiapas. The collection has been an important resource in the search for resistance to *Phytophthora palmivora* Butler, *P. capsici* Leonian, *Colletotrichum gloeosporioides* M. B. Dickman, *Ceratocystis fimbriata* Ellis & Halst., and *Moniliophthora roreri* (Cif.) H. C. Evans, Stalpers, Samson, & Benny. In addition to different characteristics of commercial interest, there has been extensive characterization of the germplasm (Avendaño et al. 2014; UPOV 2011). The germplasm bank has helped produce cocoa germplasm that is tolerant to *P. palmivora*, such as INIFAP-H12 and INIFAP H-13 and tolerant to moniliasis (CAERI-1, CAERI-2); varieties of high performance and quality, such as RIM-24, RIM-44, RIM-56, RIM-88, and RIM-105; and wild-type varieties such as CAERI and Lacandon.

There has been less effort to collect *T. bicolor*, although during 2012 and 2013, collections were made in southern Mexico, and currently a genebank has been established in the Experimental Field Rosario Izapa-INIFAP with 20 accessions derived from seed. There are fewer economic resources to keep the collection alive and to have a permanent breeding program. The best rationale for funding is that there is a need to characterize native cocoa germplasm for quality and aroma that can be used for gourmet chocolates.

One of the main challenges to conservation is keeping the collection alive, as collections must be maintained as clonally propagated trees (Cheesman 1944; Cuatrecasas 1964). In living collections, there is limited water availability, and there is the potential for natural disasters. Another challenge is the possible arrival of diseases, such as witches broom caused by *Moniliophthora perniciosa*. The future of cocoa worldwide depends on the use of germplasm for the generation of new varieties with resistance to pests and diseases, quality characteristics, and good adaptation to climatic changes (Zhang and Motilal 2016).

19.2.1.10 Suggestions on How to Improve Conservation

Although cocoa is a crop of ancestral, economic, social, and ecological importance in Mexico, there is still no systematized information about the distribution of native wild-type cocoa. The information found in the herbaria is old and in most cases, the places where collections were made are now pastures (as in the case of the jungle region of Chiapas). In addition, there is no legal protection of native varieties. Germplasm conservation is located in a single institution, INIFAP, and accessions have not yet been fully characterized. Most research is dedicated to genetic improvement, health, and postharvest. Phytosanitary problems such as moniliasis, little or no management of plantations, and the advanced age of producers and plantations are leading to the abandonment and demolition of plantations and, as a consequence, the loss of genetic diversity. Therefore, it is urgent and necessary to continue with the national collection and morphological, physiological, biochemical, and molecular characterization. Advances in rescuing wild-type cocoa from Mexico and the conservation of genotypes in germplasm banks have not been concluded, and there is a risk of losing the great genetic and cultural richness of the species. The safeguard and disposal of the high organoleptic quality of the Mexican wild-type cocoa represent a significant advance for the future of cocoa. An area that needs further exploration and research is cryopreservation of clonal plant parts or seed, as an alternative to the ex situ conservation of genetic diversity of wild-type cocoa of Mexico.

19.2.2 Tobacco (Nicotiana L.)

19.2.2.1 Summary

Tobacco (*Nicotiana* spp.) use dates back thousands of years ago in North America; it has been used medicinally, socially, and ceremonially for much of this timeframe. Tobacco has been a major economic species worldwide for over 500 years. There has been widespread use of CWR in tobacco as well the genus being a workhorse for basic plant science.

19.2.2.2 Origin of the Crop and Brief Use History

Although tobacco (*Nicotiana* spp.) is not a food crop, its use likely stretches back to the very origins of agriculture, with the earliest known evidence dating to 2500–1800 BC in northern Peru (Rafferty 2002). It subsequently spread throughout the American continents such that usage of various *Nicotiana* species by Native Americans was widespread at the time of European arrival to the New World. At the time of contact, *N. tabacum* L. was being grown in the northern regions of South America, the Caribbean, and Mexico (although it is unclear in this region if the "tobacco" noted was *N. tabacum* L., *N. rustica* L., or both). *Nicotiana rustica* L. was the preferred species of the Mississippian tribes of eastern North America, while Native peoples of western North America made use of locally available species such as *N. attenuata* Torr. ex S. Watson and *N. quadrivalvis* Pursh. Among Native Americans, plants were either actively or passively grown depending on the tribe, and the leaves (or calyces in the case of *N. quadrivalvis*) were dried and smoked or ground and mixed with lime to form a type of lozenge (Linton 1924).

Large-scale cultivation of *N. tabacum*, modern commercial tobacco, was initiated in the Caribbean by Spaniards in the late 1500s. Tobacco use and cultivation was rapidly spread by European sailors as they traveled along trade routes to Europe, Asia, and Africa during the early 1600s (Collins 2013). Over the centuries many different market classes of tobacco were developed with different smoke flavor profiles and leaf textures. The current classes are burley, flue-cured, dark fire- and air-cured, cigar wrapper and filler, and oriental. While tobacco has been consumed in many different forms since antiquity, today the primary uses of tobacco leaf are for the manufacture of cigarettes, cigars, and smokeless tobacco (i.e., chewing tobacco). The nicotine dispensed by electronic cigarettes primarily comes from cheap waste materials discarded from the manufacture of other tobacco products. According to the Food and Agriculture Organization of the United Nations, 7.4 million tons of cured tobacco leaf was harvested from 4.2 million hectares of land in 2013, generating a gross production value of over USD 19 billion (FAOSTAT 2017). The total value of manufactured tobacco products on the global market in 2013 was USD 605.1 billion, with cigarettes accounting for over 90% of all revenue (USDA, ERS).

19.2.2.3 Cultivation

19.2.2.3.1 Agronomic Practices

Nicotiana tabacum is a tropical perennial species that is grown as an annual crop. Agronomic practices involve the germination and growth of seedlings, the transplanting of young plants into the field, growth of plants to maturity, harvesting, and curing. Each market class of tobacco has its own unique set of practices regarding row and plant spacing, fertilization, when or if the inflorescence is removed (topping), whether the leaves are harvested individually (priming) or if the whole plant is harvested by cutting the stalk, and how the leaves are ultimately dried during the curing process (reviewed in Johnson and Reed 1994). Tobacco is primarily grown on silt or sandy loam soils, where the soil is actively cultivated into large ridge rows around the base of plants in order to prevent lodging and for drainage. For flue-cured tobacco, the predominant market class, the inflorescence is removed shortly after the initiation of flowering. This allows for increased development of the leaves, particularly those of the upper stalk positions, and also triggers desirable chemical changes in the leaves (including an increase in nicotine content). Approximately 2 weeks after topping, harvest will begin as the lower leaves start to yellow due to nitrogen starvation. Collected leaves are subjected to a very specific regimen of heat and humidity control during curing, which will result in the leaf turning a golden hue and having a sweet aroma.

19.2.2.3.2 Pests, Diseases, and Climatic Limitations

While many pathogens impact tobacco production (reviewed by Lucas 1975), the two most economically important pathogens in North America are *Phytophthora nicotianae* Breda de Haan and *Ralstonia solanacearum* (Archibald) Robbs, the casual agents of the black shank and bacterial wilt diseases of tobacco, respectively. These two pathogens are particularly devastating because they often lead to complete plant death before harvest. A number of different viral diseases also are important globally, including *Tobacco mosaic virus* (TMV), *Potato virus Y* (PVY), *Tobacco etch virus* (TEV), and *Tomato spotted wilt virus* (TSWV). Due to the natural insecticidal properties of nicotine, few herbivorous insects consume significant tobacco leaf tissue, but there are two species, the tobacco hornworm (*Manduca sexta* L.) and budworms (*Heliothis virescens* (Fabricius)), which can cause considerable damage. Aphids are also a problem as their exudates promote mold growth during curing that reduces quality and value.

Tobacco is amenable to a wide array of soil and climatic conditions, and it is actively grown on all arable continents, with China, Brazil, and Zimbabwe being the major producers along with the United States. It has historically been grown in North America in Mexico, throughout the Caribbean, in the United States from Florida up into Pennsylvania and Wisconsin, and as far north as Canada. A cultivar which grows well in Florida will often grow equally well in Pennsylvania, as latitude and altitude tend to have little impact on phenotype. This is at least partly due to the fact that almost all tobacco varieties are day-neutral, despite being the species in which photoperiodism was first described (Garner and Allard 1920). While tobacco is known to be drought tolerant, requiring only about 1 in of precipitation per week, fields are often irrigated during long dry spells to preserve yield. Conversely, tobacco does not grow as well in soils that retain a lot of moisture, and its growth is limited in extreme latitudes (and altitudes) where a sufficient window of time does not exist between the last and first frost dates.

19.2.2.4 Crop Wild Relatives (CWR)/Wild Utilized Species (WUS) of the Crop

19.2.2.4.1 General Description of Genus

Nicotiana L., a member of the Solanaceae family, is comprised ~75 naturally occurring species, the exact number being debatable as species once considered distinct have been consolidated by various authorities but not by others. In his treatise of *Nicotiana*, Goodspeed (1954) provided the following description of the genus:

> Tall, soft-woody subarborescent shrubs to diminutive annuals. Indument varied, often moist- or viscid-glandular, seldom lacking. Leaves alternate, petioled or sessile, the blade entire. Flowers scentless or fragrant at dusk, pedicelled, in terminal mixed panicles with evident central axis, false racemes, false racemes secondarily converted to flat pinnate panicles, or a variety of loosely expanded or remotely glomerate systems with some too much dichotomy, rarely flowers associated with leaves instead of bracts. Calyx regular or irregular, 5-toothed or cleft, commonly much shorter than corolla, always persistent, usually somewhat enlarged on fruit. Corolla regular or slightly irregular, tubular, infundibular or salverform, the tubular portion often differentiated into a distinct tube ("tube proper") and distinct throat, the limb 5-cleft, shallowly 5-lobed or nearly entire, in bud contorted-plicate, rarely imbricate, at anthesis erect, spreading or recurving, unaffected by light intensity or loosely folding during the day and expanding at dusk. Stamens 5, free filaments equally or unequally inserted on corolla at some point below limb, commonly at base of corolla throat if throat is present, equal or unequal in length, usually included or nearly so, sometimes obsolescent; anthers with or without connective, dehiscing along longitudinal suture. Ovary bilocular, oblique in relation to surrounding whorls, base adnate to thick, sometimes nectiferous, annular hypogynous disk, placental cushions on the central dissepiments, ovules numerous, anatropous; style terminal; stigma slightly grooved. Capsule membranous- or slightly woody-walled, lower portion indehiscent, upper dehiscent by rather long septicidal and very short loculicidal cleavages, he former commonly cutting the partition in patterns which leave part attached to the wall, part to the placentae. Seeds minute, reniform, globose, elliptic, oblong or angular, one seed coat, surface honeycombed- to fluted-reticulate, infrequently obscurely wrinkled-reticulate or -pitted. Embryo straight, arcuate, hemicyclic or bent. Chromosome number chiefly 12 or 24 pairs. Natives of South America, North America, Australia and the South Pacific. (p. 331)

Also characteristic of the genus is the abundant production of a certain class of bicyclic alkaloids that include nicotine, nornicotine, anatabine, and anabasine. The extensive morphological diversity and geographic distribution of species led to the widespread use of a sub-genus sectional classification that was originally outlined by Goodspeed (1954) and has been modified by Knapp et al. (2004) to account for relationships only recently elucidated by molecular analyses.

19.2.2.4.2 Distribution, Habitat, and Abundance

In North America, there are seven extant native species of *Nicotiana*. Goodspeed (1954) postulated that three distinct diploid ($n = 12$) lineages of *Nicotiana* migrated from their South American point of origination into Central and North America as early as the Upper Pliocene, where they subsequently combined to form several endemic amphiploid ($n = 24$) species. However, recent genomic analyses of *Nicotiana* by Chase et al. (2003) and Clarkson et al. (2004) suggest that the third lineage was likely already an amphiploid during its migration and that it gave rise to all members of *Nicotiana* section *Repandae* (*N. nudicaulis* Watson, *N. repanda* Willd. ex Lehm, *N. stocktonii* Brandegee). The modern descendants of the two proposed diploid migrants are believed to be *N. attenuate* Torr. ex S. Watson and *N. obtusifolia* Martens & Galeotti, which are thought to have hybridized at least twice upon their arrival to North America. *N. clevelandii* A. Gray is the resultant amphiploid from an older hybridization while *N. quadrivalvis* arose from a more recent hybridization event (Clarkson et al. 2004).

Additionally, there have been four introductions of *Nicotiana* species into North America where the species are now considered naturalized. *N. acuminate* (Graham) Hook, *N. glauca* Graham, and *N. plumbaginifolia* Viv were all introduced from their native ranges in South America by unknown means. However, all are so thoroughly established and have been for well over a century that there was a prolonged debate over whether they were native and the implications that had on attempts to decipher the natural history of the genus. *N. glauca* and *N. plumbaginifolia* are now known as problematic invasive species on a global scale (Florentine et al. 2006; Gairola et al. 2016). *Nicotiana rustica* was also introduced as an agricultural species to Mexico, the eastern United States, and Canada, presumably through Native American trade, and while it can be considered a naturalized introduction, it has only rarely been reported in the wild. Occasionally other species, including *N. tabacum*, *N. longiflora* Cav, and *N. alata* Link & Otto, are seen growing as weedy escapes from some form of cultivation. The horticultural species, *N. x sanderae* W. Watson, can also be found growing ornamentally in North American flower beds.

While all of the North American species of *Nicotiana* prefer sandy and gravely disturbed soils, they exhibit individual preferences over a range of habitats (Fig. 19.3; Table 19.3). North American species clustered regionally by latitude and longitude, which corresponds to lower amounts of precipitation than for their relatives in South America (Kawatoko 1998). Within the regional cluster, *N. attenuata* Torr. ex S. Watson and *N. quadrivalvis* were further separated out from the rest of the group by their intolerance of higher temperatures. Goodspeed (1954) subdivided the native species further into four regional groups: Mexican desert is singularly populated by *N. obtusifolia* Martens & Galeotti which has strong preferences for arid landscapes and high temperatures; Great Basin includes *N. attenuata* which prefers montane habitats and is known as a postfire annual; Californian includes both *N. quadrivalvis* and *N. clevelandii*, but *N. clevelandii* is restricted to lower elevations where temperatures are greater; and Mexican semiarid is comprised of *N. nudicaulis*, *N. repanda*, and *N. stocktonii*.

19.2.2.4.3 Utilization

Formal tobacco breeding began in earnest very early in the twentieth century and by the 1930s the need for novel germplasm was recognized, leading the United States Department of Agriculture to conduct collecting expeditions into Central and South America in order to obtain diverse germplasm (Chaplin et al. 1982). This new

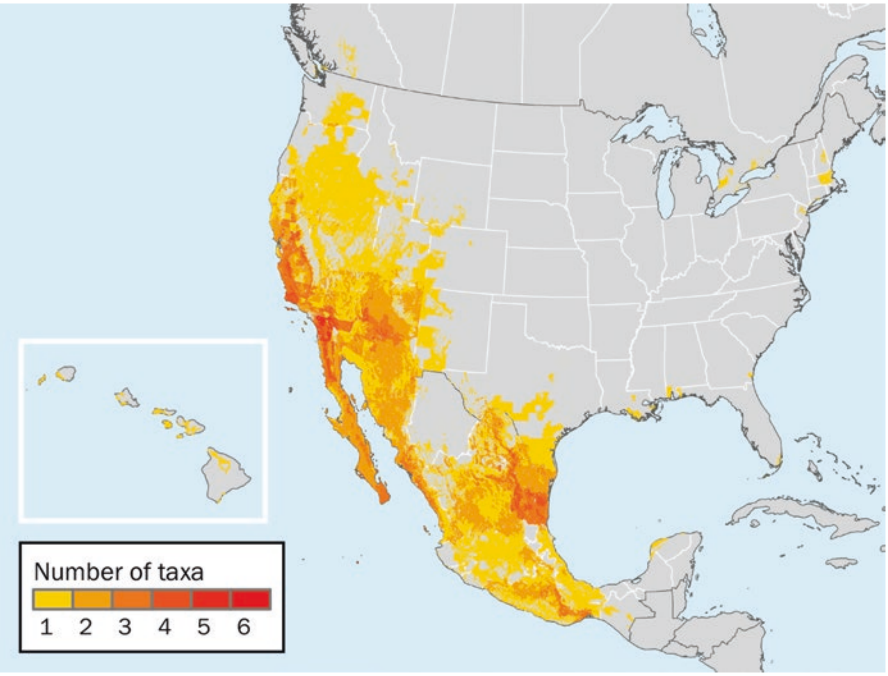

Fig. 19.3 Species richness map of modeled potential distributions of North American *Nicotiana* taxa, based on climatic and edaphic similarities with herbarium and genebank reference localities. Warmer colors indicate areas where greater numbers of taxa potentially occur in the same geographic localities. Full methods for generation of map and occurrence data providers are given in Appendix 1

primary pool of *N. tabacum* germplasm contained many plant architecture traits which would be used to increase yield capacity. Resistance to a number of pathogens was also found within these materials, but in many cases, the resistance was found to be inadequate in degree of protection or found to be unworkable due to complications in gene transfer (Burk and Heggestad 1966). Thus, in parallel with studies aimed at understanding speciation and polyploidy, tobacco breeders began utilizing CWRs as early as the 1940s for transferring disease resistance. The long, rich history of manipulating *Nicotiana* species includes utilizing techniques such as intra- and interspecific crossing (including bridges, chromosome doubling, somatic cell hybridization), intergeneric cellular hybridization and nuclear transfer, grafting, mutagenesis (chemical, ionizing radiation), and all known iterations of genetic transformation (reviewed in Lewis 2011).

While many of the North American species have disease resistance traits that would be beneficial additions to cultivated tobacco germplasm (Table 19.4), most interspecific crosses are very difficult, and efforts to transfer advantageous alien germplasm are often met with significant sterility barriers. Even successful transfers are often plagued with substantial yield losses or unacceptable phenotypes resulting

Table 19.3 North American tobacco CWRs

Group	Species	Range	Altitude (m)	Environment
Native	*N. attenuata* Torr. ex S. Watson	Baja, Mexico to S Canada; Great Basin	0–2600	Semi-desert; disturbed soils along roadsides
	N. clevelandii A. Gray	S Baja into S California and SE Arizona	0–500	Often seen growing under mesquite canopy; dry sandy soils along roads and coasts
	N. nudicaulis S. Watson	NE Mexico, primarily Nuevo Leon and Tamaulipas	300–2100	Dry, shaded rocky crevices
	N. obtusifolia M. Martins % Galeotti	Mexico, including Baja; SW United States	0–2300	Arid environments; gravel and rocky soils along roadside
	N. quadrivalvis Pursh	W United States, especially California; rare in Missouri	0–2000	Sandy soils, especially along creeks; full sun
	N. repanda Willd.	S Texas; Nuevo Leon and Tamaulipas, Mexico	0–600	Moist ground along streams
	N. Stocktonii Brandegee	Revillagigedo Archipelego (Socorro and Clarion Islands)	0–50	Valleys and rocky coasts; sandy gulches
Naturalized	*N. acuminata (Graham) Hook.*	Central California to Nevada; N Oregon and Washington	0–2000	Rocky soil, arid hillsides, disturbed soil along washes and roadsides
	N. glauca Graham	Mexico; SW and W United States; Hawaii	0–2300	Disturbed soils of roadsides and riverbanks
	N. plumbaginifolia Viv.	Cuba; Florida keys; Mexico	0–2100	Moist gravel or sand bars of streams, also scattered along roadsides; partial shade
	N. rustica L.	Rare in Mexico, New England, Appalachia, and Ontario	0–2100	

Data compiled from Goodspeed (1954), Kawatoka (1998), and herbarium records

from linkage drag. Due to these breeding hurdles, tobacco CWRs have not yet been evaluated for beneficial agronomic traits outside of disease resistance. However, in spite of these obstacles, successful introgressions have been made, such as the transfer of what is believed to be a single dominant black shank resistance gene, known as *Php*, from *N. plumbaginifolia* to *N. tabacum* that confers immunity to infection by race 0 of *Phytophthora nicotianae* Breda de Haan (Chaplin 1962). Genetic factors from *N. rustica*, which is also resistant to black shank, have likewise been transferred to tobacco, although the nature and utility of these factors are still being investigated. Unfortunately, we are likely past the golden era of tobacco breeding (1940s–1980s),

Table 19.4 Diseases of tobacco and sources of resistance in North American CWRs

Group	Species	An^{a}	BRR^{b}	BSh^{c}	BM^{d}	BSp^{e}	CN^{f}	FLS^{g}	FW^{h}	GW^{i}	PM^{j}	RKN^{k}	RV^{l}	TSWV^{m}	TEV^{n}	TMV^{o}	TS^{p}	WF^{q}
Native	*N. attenuata* Torrey ex S. Watson										x							x
	N. clevelandii A. Gray												x					
	N. nudicaulis S. Watson	x									x	x						x
	N. obtusifolia M. Martens & Galeotti	x			X						x							
	N. repanda Willd										x							x
	N. repanda Willd.	x		x			x	x			x	x	x			x		x
	N. stocktonii Grandegee	x										x						
Introduced-Naturalized	*N. acuminata* (Graham) Hook.										x		x			x		x
	N. glauca Graham	x	x								x		x		x		x	
	H. plumbaginifolia Viv.			x												x		x
Introduced-Ag/Hort	*N. x sanderae*	x									x					x		x
	N. tobacum L.		x	x	X				x	x	x	x				x		

[a] Anthracnose; causal organism *Colletotrichum destructivum*

[b] Black root rot; causal organism *Thielaviopsis basicola*

[c] Black shank; causal organism *Phytophthora nicotianae*

[d] Blue mold/Downy mildew; causal organism *Peronospora tabacina*

[e] Brown spot; causal organism *Alternaria alternata*

[f] Cyst nematodes; causal organisms *Globodera tabacum* subsp. solanacearum and *G. tabacum* subsp. Tabacum

[g] Frogeye leaf spot; causal organism *Cercospora nicotianae*
[h] Fusarium wilt; causal organism *Fusarium oxysporum*
[i] Granville wilt; causal organism *Ralstonia solanacearum*
[j] Powdery mildew; causal organism *Erysiphe cichoracearum*
[k] Rootknot nematodes; causal organisms *Meloidogyne* spp.
[l] Rattle virus
[m] Tomato spotted wilt virus
[n] Tobacco etch virus
[o] Tobacco mosaic virus
[p] Tobacco streak virus
[q] Wildfire; causal organism *Pseudomonas syringae* pv tabaci
Adapted from Burk and Heggestad (1966)

and the few programs that remain are left with cost-benefit analyses that tend not to favor breeding approaches involving interspecific hybridization. Progress is still being made however, as an introgression conferring black root rot resistance was recently introduced from *N. glauca* that appears to have less linkage drag than the traditional source from *N. forsteri* Roem. & Schult (Trojak-Goluch and Berbeć 2011).

Efforts to utilize *Nicotiana* CWRs as sources of disease resistance genes in conventional breeding are further hampered by insufficient data on the reactions of CWRs to pathogens. In Table 19.4 all incidences of reported pathogen resistance or tolerance among North American tobacco CWRs are recorded, but only a few sources have been examined in any detail. Often in early screenings, only one accession of each CWR was used as representative of the entire species. Screening a larger germplasm pool for each CWR is likely to yield more positive results, such as the recent discovery of blue mold resistance in a specific accession of *N. obtusifolia* (Heist et al. 2004). These classical screening studies were also often conducted with crude inoculation techniques that likely overwhelmed plants and skewed results. Thus, studies should be repeated in a manner that attempts to best mimic natural processes and what we now know about pathogen modes of infection.

In addition to its utility as a resource for breeding commercial tobacco, the genus *Nicotiana* has become a very powerful resource for investigating basic aspects of plant science. Historically, the genus as a whole has been a model for understanding the process of intraspecific hybridization (Smith 1968) and the evolution of polyploid species (McCarthy et al. 2016). *N. tabacum* and *N. benthamiana* Domin (an Australian species), which are known for their ease of genetic modification, are used to study an array of topics so diverse that it could fill an entire book. Excluding the aforementioned, *N. attenuata* may be the most well-studied *Nicotiana* species because it is widely used as a model to investigate ecological systems, including responses to herbivory (Kim et al. 2011) and plant-pollinator interactions (Kessler et al. 2012). *N. glauca* has also been used in the study of plant-pollinator interactions (Nattero and Cocucci 2007), often with specific interest in its invasive nature, as well as for the bioremediation of heavy metals from soils (Shingu et al. 2005).

19.2.2.5 Conservation Status of CWR and WUS

19.2.2.5.1 In Situ

Conservation of genetic resources is critical in order to allow for continued genetic improvement of a cultivated species and to provide flexibility for dealing with new production or industry needs. Many *Nicotiana* species are cosmopolitan due to their weedy nature, but special concern should be taken with those species which have narrow ranges, namely, the three members of *Nicotiana* section *Repandae*. While not listed as threatened, there is ample cause for concern regarding the status of *N. stocktonii* since it is only found on two islands within the Revillagigedo Archipelago, Mexico. The islands, which remain uninhabited except for a very small naval base, have been protected since 1994 as a biosphere reserve by the Mexican government, and the region has recently been inscribed as a UNESCO World Heritage site. A large portion of the range of *N. nudicaulis* is protected by the Parque Nacional Cumbres de Monterrey, which also protects much of the range of *N. repanda* along with the neighboring Reserva de la Biósfera El Cielo. Additional reserves and protected natural areas safeguard a large swath of Baja and the northern end of the Gulf of California, which is important for the conservation of *N. clevelandii*.

In the United States, *N. attenuata* (which is designated as "sensitive" in the state of Washington), *N. glauca*, and *N. obtusifolia* have long been known as poisonous weeds for livestock grazing in the southwestern regions of the country, and early USDA livestock researchers recommended that they be eradicated from grazing areas (Marsh et al. 1927). However, in the grazing lands now managed by the US Bureau of Land Management (BLM), *Nicotiana* species have a layer of protection, and seeds are actively saved for conservation and ecosystem restoration as a part of the Seeds of Success program. In fact, between BLM lands and other US preserves, much of the western and southwestern United States where *Nicotiana* species are known to occur is at least protected from development. Little is known, however, about the locations in which *N. rustica* grows in the eastern United States. Care should be taken to locate these regions and protect them as the plants found there are likely the direct descendants of those previously grown by Native Americans and thus have significant cultural and historical value.

19.2.2.5.2 Ex Situ

A global survey of *Nicotiana* genetic resources that is currently underway has revealed that almost all CWRs are poorly represented in ex situ germplasm collections, generally, with some preliminary data presented in Table 19.5 as it regards to North American *Nicotiana* CWRs (JM Nifong unpublished). The data show that, while large numbers of accessions from the primary germplasm pool of tobacco are often represented within collections, few, if any, CWRs are maintained. *N. rustica* was spread globally in conjunction with *N. tabacum*, and it is still grown for local consumption in some parts of the world. Like *N. tabacum*, it displays a large array of phenotypic diversity, and thus large numbers of this species are also maintained by germplasm collections, representing cultivars, breeding lines, and global sampling. With the exception of *N. attenuata*, which is bolstered by significant sampling done by the Seeds of Success program throughout much of its range, *Nicotiana* CWRs are poorly represented.

While global data may suggest that there are two dozen accessions of a particular species, this is an overestimate of the actual genetic diversity being maintained. Accessions have tended to be exchanged among collections, and thus several accessions can often be traced back to a common source collection event. As an extreme example, a single *Nicotiana repanda* Willd. ex Lehm. accession was collected by the University of California Botanical Garden (UCBG) and shared with

Table 19.5 North American tobacco CWRs present in ex situ germplasm collections

Institute	*N. attenuata*	*N. clevelandii*	*N. nudicaulis*	*N. obtusifolia*	*N. quadrivalvis*	*N. repanda*	*N. stocktonii*	*N. acuminata*[a]	*N. glauca*[a]	*N. plumbaginifolia*[a]	*N. rustica*[a]	*N. tabacum*[a]
IPK Gatersleben	0	1	2	5	4	2	0	6	3	3	112	355
Botanical Garden, Univ. of Nijmegen	8	2	4	4	4	8	2	3	11	3	48	53
CRA-Unitá di Ricerca per le Colture alternative al Tabacco	2	1	2	3	4	3	2	3	2	2	147	1424
Millennium Seed Bank	1	1	0	5	0	1	0	1	10	1	5	11
All other EURISCO members	3	6	2	1	5	2	3	2	2	3	196	4499
Imperial Tobacco, Bergerac	2	1	2	3	4	1	2	2	0	1	35	867
US Nicotiana Germplasm Collection	4	3	1	8	10	2	3	4	6	3	87	1928
Seeds of Success	28	0	0	3	1	1	0	1	0	0	0	0
All other collections in study	3	3	4	4	4	7	4	7	6	2	130	5780
Total	51	18	17	36	36	27	16	29	40	18	784	15,168

[a] These data include accessions not originating in North America

the Imperial Tobacco collection in Bergerac, France, and then duplicated at IPK Gatersleben in Germany, and the IPK accession was subsequently obtained by the Botanical Garden at the University of Nijmegen in the Netherlands. In addition, the IPK collection has another accession of *N. repanda* that has a designated UCBG origin that is likely the same as the one it ultimately received from Bergerac. Thus, four accessions of *N. repanda* can all be traced back to a probable singular collection event. In many long established germplasm collections, adequate source information is not available for older accessions, and it is believed that these types of duplications are common.

19.2.2.5.3 Ways to Improve Conservation

The long-term status of in situ preservation for North American *Nicotiana* CWRs looks promising as significant portions of their ranges are currently covered by designated protected natural areas of the US or Mexican governments. However, adequate survey data is lacking, and little is known about the structure of wild populations, which makes any assessment of the actual utility of the protected ranges in preserving the genetic diversity of these species difficult. *Nicotiana stocktonii* should mandate priority over other species when conducting future studies as it is probably the most vulnerable to loss due to its precarious existence on only two volcanic islands. Entire populations of *N. stocktonii* could easily be lost due to an eruption or passing hurricane, as the species prefers cliffs and washes where it could be swept away in a downpour. For the species that continue to be utilized by Native Americans for ceremonial purposes, partnerships could be made in a manner similar to those outlined by Nabhan (1985) for both the in situ and ex situ preservation of these genetic resources.

The overall low number of accessions of North American *Nicotiana* species maintained in global germplasm collections should be cause for concern. While direct exchange of materials among germplasm collections may seem like the go-to option for increasing the genetic diversity held at any given site, it is not believed that further *Nicotiana* CWR exchange among collections will be beneficial at this point due to the likelihood that existing accessions share a common source history. Further collecting expeditions would be valuable to secure important CWRs for future study, utilization, and conservation.

19.2.3 Black Cohosh (Actaea racemosa L.*)*

19.2.3.1 Summary

Black cohosh (*Actaea racemosa* L.) is a native North American medicinal plant traditionally harvested for its rhizomes and roots. Black cohosh-based products have been consistently listed as a top-selling dietary supplements from 2002 to 2017. Due to increasing commercial demand, there is a need to develop sustainable propagation protocols suitable for large-scale production purposes to replace current methods of wild harvesting from native populations.

19.2.3.2 Introduction

Actaea racemosa, formerly *Cimicifuga racemosa* (L.) Nuttal, is a member of the Ranunculaceae family which comprise 2450 species distributed in 62 genera (Weakley 2015). Native only to the eastern forests of North America, *A. racemosa* populations range from Ottawa, Canada, to Georgia, USA. The genus *Actaea* is characterized by perfect, actinomorphic flowers with shedding sepals, small staminodes, and many stamen which form elongated racemes or panicles (Compton and Culham 1998a). *A. racemosa* is a long-lived herbaceous perennial, derived from multi-annulated rhizomes up to 30 cm long and 15 cm wide with few to many roots. A typical mature rhizome from a native population averages approximately 15 cm in length and 2–3 cm in width with roots 8–23 cm long and 1–5 mm in diameter (Ramsey 1965). Rhizomes typically have few to many curved stems bearing foliage and/or fruit along with few to many buds which remain dormant throughout the growing season. Originally classified in the *Actaea* genus (1753) by Linnaeus, *A. racemosa* was later transferred, with reservation, into the *Cimicifuga* genus by Nuttal in 1818 as *Cimicifuga racemosa* (L.) Nutt (Compton and Culham 1998a). Reclassified through morphological analysis and DNA sequence variation analysis, *C. racemosa* L. was reinstated into the expanded *Actaea* genus as *Actaea racemosa* L. (Hasegawa 1993; Kyung-Eui et al. 1997; Compton and Culham 1998b). Many countries still refer to it as *Cimicifuga racemosa* as opposed to *Actaea racemosa.*

19.2.3.2.1 Origin

Actaea racemosa L. is an endemic North American plant whose medicinal use by Native Americans predates European settlement and continues today. Eastern Native American tribes, including the Cherokee, Delaware, Iroquois, Micmac, and Penobscot, predominantly used the herb for pain management and to combat inflammation (Upton 2002). Historical literature also recorded indigenous peoples use of *A. racemosa* for menstrual pain with cramping, sore throats (as a gargle), and rheumatism (Pengelly and Bennett 2012). *A. racemosa* was also used in emergency medicine treating snake bites, “for which purpose it [was] bruised and applied to the wound; and at the same time a little of the juice was to be taken internally” (Pengelly and Bennett 2012). In 1830, the species was included in the Pharmacopoeia of the United States, after many settlers began incorporating the species in medical practices. At the time, it was referred to as “black snakeroot.” *A. racemosa* became even more popular in 1844 when a physician, John King, recommended it to treat rheumatism. Other physicians were known to use it to treat endometritis, sterility, menorrhagia, dysmenorrhea, and amenorrhea, as well as to increase milk production in breastfeeding women (Anon 2003).

The rhizomes of *A. racemosa* have been harvested and used as medicine, including the Lydia Pinkham famous patented "Vegetable Compound" medicine, of the early 1900s (Upton 2002), which reached $3 million in sales in 1925 (Lewis 2011). In Germany, *A. racemosa* has been prescribed by physicians since 1940 to treat premenstrual, dysmenorrheal, and menopausal neurovegetative symptoms. Today only menopausal neurovegetative symptoms (such as hot flashes and profuse sweating) are accepted as indications for use. According to the Commission E Monograph, only the dried rhizome is used for the relief of menopausal symptoms (Committee on Herbal Medicinal Products 2010). To date, approximately 56 human clinical trials have been conducted investigating the safety and/or efficacy of *A. racemosa* for premenstrual and menopausal symptoms (PUBMED search 2/24/2017). Unadulterated, it is recognized to have no toxicity, although it is not recommended for pregnant, breastfeeding mothers or individuals with estrogen-driven tumors.

Due to the growing concerns over the potential risks of breast cancer, heart disease, and stroke from the use of conventional hormone replacement therapy (HRT) treatments currently on the market, many health professionals are now looking to natural substances to treat menopausal symptoms. This positive view coupled with continued promising clinical trial results of *A. racemosa* as a HRT continues to drive demand for the plant. As a result, *A. racemosa*-based products have consistently been listed as one of the top 10 selling herbal dietary supplements for more than a decade (Smith 1968).

19.2.3.2.2 Current Harvest and Challenges to Cultivation

Most commercial *A. racemosa* material used for medicinal purposes is wild harvested exclusively from eastern North American hardwood forests where it grows as a native understory, shade-tolerant, hardy perennial. Ninety-five percent of this harvest is thought to be exported to Europe. Owing to increasing harvest pressures, *A. racemosa* is listed among the top species of concern on both The Nature Conservancy and The United Plant Saver's lists of medicinal species at risk due to wild-collection. Additionally, in 1999, *A. racemosa* was recommended for inclusion in Appendix II of CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) (CITES 2000).

Potential challenges to cultivation include various pathogens which have been recorded. *A. racemosa* is susceptible to leaf spot, root rot, and damping off (*Rhizoctonia solani* J.G. Kühn 1858), especially under crowded conditions. Leaf spot fungi include *Ascochyta actaeae* Bres (CT, NC, NY), *Ascochyta* sp. Lib (Canada), *Ectostroma afflatum* (Schwein) (VA), and *Phyllosticta* sp. (ID, MT, NC). Nematode infestations include *Ditylenchus destructor* Thorne, *Meloidogyne* sp. Göldi (rootknot) (NJ); root and stem rot, *Leptosphaeria clavigera* (Cooke & Ellis) Sacc. (GA), *Ophiobolus nigro-clypeata* Riess (GA), *Pythium* (MO), *Rhizoctonia solani* J. G. Kühn (damping off of seedlings); rust, *Puccinia recondite* Dietel & Holw. (NC, TN, Canada); *Puccinia rubigo-vera* (D. C.) (OH, MD, PA, VA, West

Germany); *Puccinia rubigo-vera* var. *agropyrina* (Erikss.) (MD, NC, OH, VA); and smut, *Urocystis carcinodes* (Berk. & M.A. Curtis) (NC, NY, OH, PA, TN, VA, Germany). 22 accessions of *A. racemosa* have been propagared for 10 years and never experienced a serious pathogen issue (McCoy 2013).

The largest suppliers of wild-harvested rhizome materials are based in the southeastern portion of North America where the highest-quality plant material is reported to originate (Upton 2002). As the rhizome is collected, there is concern over the sustainability of current wild-harvesting practices as future demands increase. Overharvesting is thought to currently be the number one true threat to the survival of the species in the wild. Both rhizomes and roots are harvested for commercial medicinal purposes and standardized to various concentrations of three triterpene glycosides – actein, 27-deoxyactein, and cimiracemoside (Upton 2002). Because *A. racemosa* occurs in moist cove habitats, there is concern that erratic climate patterns could potentially adversely alter future populations. Current efforts are underway to identify populations with potential drought resistance.

19.2.3.2.3 Current Production

From 2000 to 2010, 2.7 million dry pounds of *A. racemosa* entered the world market. This equates to 40.4–54 million *A. racemosa* plants harvested for the medicinal herb trade over 10 years (Davis and Persons 2014). A 2010 American Herbal Products Association report compiled of surveys from raw materials suppliers in North America noted that the harvest (as aggregate tonnage) of dried plant, both root and rhizome, grew over 379% from 2600 cultivated in 1999–9862 in 2010. Wild-harvested tonnage experienced a similar growth of 216% with 145,367 pounds of root and rhizome being harvested in 1999 to 314,695 pounds in 2010 (Dentali and Zimmerman 2012). The American Botanical Council, 2015 herb market report describes consumer spending on herbal dietary supplements in the United States as having reached an all-time high in 2015. Consumers spent approximately $480 million more on herbal products in 2015 than in the previous year – an increase that marks the 12th consecutive year of growth for these products. *A. racemosa* products were sixth in total sales from multi-outlet channel stores and were reported to have reached $43 million in the United States alone (Source- SPINSscan Natural/IRI) (Smith 1968). As a result, wild harvesting has increased significantly and will threaten future populations throughout its limited range.

19.2.3.3 Crop Wild Relatives

There are 28 closely related species to *A. racemosa* with eight found in North America, two in Europe, and 18 in Asia (Compton and Culham 1998a; Weakley 2015). It should be noted that there are numerous reports of toxicity and misidentification between the various species and only *A. racemosa* is used for commercial medicinal products. The North American species, *A. racemosa*, provides the majority of plant material for commercial and medicinal use, though some Asian species are also used for their medicinal properties. It is believed that the closely related *Actaea podocarpa* DC (formerly *Cimicifuga americana*), *Actaea pachypoda* Elliott, *Actaea rubifolia* (Kearney) Kartesz, *Actaea rubra* (Ait.) Willd, *Actaea elata* (Nutt.) Prantl, and *Actaea cordifolia* DC are erroneously harvested as *A. racemosa*, though their populations are much smaller and are at higher risk of extirpation (Lyke 2001; McCoy 2004a, b). An additional variety, *Actaea racemosa* var. *dissecta* (Gray) J. Compton, which has not been verified in its natural range for the past 40 years, was recently discovered in North Carolina for the first time (McCoy 2004a, b). All of these *Actaea* species share similar foliage and habitat characteristics, and thus could be easily misidentified for *A. racemosa* when not in reproductive stage (Weakley 2015; McCoy2004a, b). In a typical population, a large proportion of individuals are in the vegetative stage of their life cycle which makes identification to species level difficult due to similar ternate foliage and branching morphology (McCoy 2004a, b; Kaye and Kirkland 1999; Cook 1993). The species are however easily distinguished by their floral morphology and staggered flowering dates. *A. pachypoda* typically blooms from April to May and August to October, and *A. racemosa* blooms from May to July and *A. podocarpa* from July to September (Radford et al. 1968; McCoy 2004a, b). There are no data available comparing chemical compositions among the newly revised *Actaea* genus. Also, with the recent reclassification of *Actaea* to include the former *Cimicifuga* and *Souliea* genera, it is necessary to revise and publish updated taxonomic keys which distinguish the species (Compton and Culham 1998a; Hasegawa 1993).

Widely distributed across deciduous forests of eastern North America, *A. racemosa* reaches peak abundance in mesic cove forests of the southern Appalachians (Fleming et al. 2010; (NatureServe 2017). In rich cove habitats where *A. racemosa* is commonly found, it shares its distinctively characteristic two to three alternately compound leaf form with many other cove genera including *Astilbe* (Saxifragaceae), *Aruncus* (Rosaceae), *Caulophyllum* (Leonticaceae), *Aralia* (Araliaceae), *Angelica*, and *Ligusticum* (Apiaceae) (Weakley 2015; McCoy 2004a, b). All of these species, in addition to the associated members of the *Actaea* genus, are potential adulterants in products containing *A. racemosa*, if wild harvesters are not familiar with the local flora:

> Adulteration of black cohosh, mainly with herbal ingredients from Chinese *Actaea* species, remains a problem in the dietary supplement industry. In the absence of easily recognizable morphological features, e.g., when cut or powdered roots and rhizomes, or root and rhizome extracts are purchased, authentication of black cohosh material is difficult

noted Stefan Gafner, PhD, chief science officer of the American Botanical Council and technical director of the Botanical Adulterants Program. Researchers from the NY Botanical Garden developed a DNA fingerprinting technique to identify *A. racemosa* in products using amplified fragment length polymorphisms (AFLP) (Zerega et al. 2002). In their study, 262 AFLP markers were generated with one proving to be unique to *A. racemosa* when compared to the three closely related species, *A. pachypoda*, *A. cordifolia*, *and A. podocarpa*. More recently 36 analytical methods have been identified, including high-performance liquid chromatography

(HPLC), nuclear magnetic resonance (NMR), flow injection mass spectrometry (MS), DNA-based tests, high-performance thin-layer chromatography (HPTLC), and macroscopic and microscopic analyses (Upton 2002; Harnly et al. 2016).

19.2.3.4 Habitat

Kaye and Kirkland (1999) state that some *Actaea* species are “light-flexible” herbs rather than “shade restricted” and thus are “shade-tolerant” as opposed to “shade-dependent.” Light-flexible herbs are defined as “herbs which tolerate full sun and shade, but are restricted to neither” (Kaye and Kirkland 1999; Kaye 2000). Light-flexible herbs tolerate a wide range of conditions and respond favorably to increased light due to canopy gaps. Increased flowering, seed production, seedling recruitment, and survival result from these increases. Traditionally, *A. racemosa* requires 70% shade for propagation; but it has now been accepted that it can tolerate more light than previously thought. In a preliminary study by the Yellow Creek Botanical Institute (Graham County, NC), *A. racemosa* rhizome sections were planted in full sun in 2001 for observation. Plants in full sun were stunted during the first year of growth, but emerged vigorously and produced flowers and seed in year two, and were vigorous and disease free in year three (Suggs 2003). *A. racemosa* is reported to thrive under a wide variety of soil types, including loam, sand, shale, and clay (Cech 1999). It has been further speculated that the native range of *A. racemosa*, which is limited to the eastern portion of North America (Fig. 19.4), is due to seed distribution method via a dry dehiscent

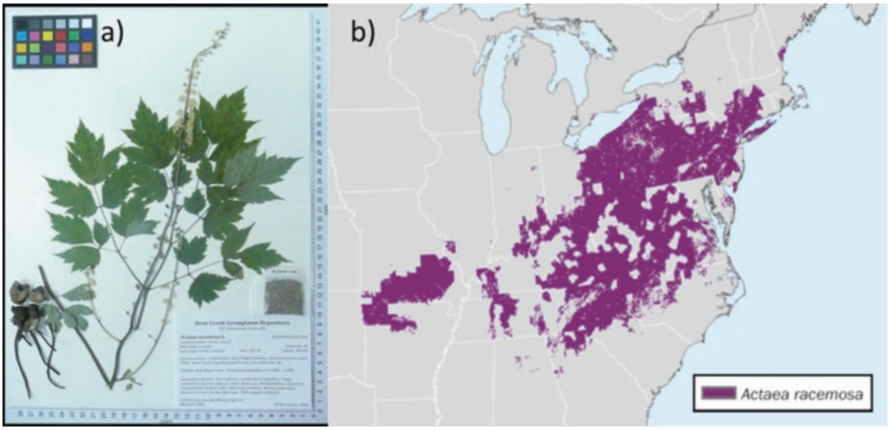

Fig. 19.4 (**a**) *Actaea racemosa L.* voucher specimen. USDA, NRCS. 2004. The PLANTS Database, Version 3.5 (http://plants.usda.gov). National Plant Data Center, Baton Rouge, LA 70874-4490 USA. (**b**) Modeled potential distribution of *Actaea racemosa L.* based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are given in Appendix 1

follicle which limits the distribution of seeds to the immediate area surrounding the parent plant (Compton and Culham 1998a). Closely related *Actaea* species with fleshy fruits such as *A. pachypoda* and *A. rubra* have much larger native ranges due to seed dispersal by birds, although their populations are much smaller in size. These various facts imply that *A. racemosa* may possibly be propagated without shade given adequate moisture and weed control.

19.2.3.5 Conservation

Wild harvesting *A. racemosa* began long before Europeans settled the region in the early 1700s (Chamberlain et al. 2002; Sanders and McGraw 2005). With increased knowledge of the plant's therapeutic properties, market demand and harvest pressures have dramatically impacted this medicinal plant. It has been estimated that millions of kilograms of plant material have been extracted from Appalachian forests, with little effort to manage the plant species as a natural resource (Chamberlain et al. 2002). Growing concern for the conservation and sustainability of *A. racemosa* in the wild over the last 20 years has led to increased efforts to understand the ecological impacts of harvesting on natural populations (Small et al. 2011).

The American Herbal Products Association (AHPA-2007) has estimated that between 1997 and 2005, more than 1 million kg of *A. racemosa* roots and rhizomes were wild harvested from the Appalachian forests. Because plant reproduction and population expansion occur primarily through regrowth of buds from belowground rhizomes (Predny et al. 2006), wild harvesting presents a problem for long-term survival because the vast majority of black cohosh sold commercially is collected from native populations (Predny et al. 2006; McCoy 2004a, b; Davis and Greenfield 2003; Chamberlain et al. 2002). As *A. racemosa* sales maintain their top 10 status as a popular natural product, these conservation challenges will have to be addressed. To better understand wild-harvest impacts, researchers with the US Forest Service Southern Research Station investigated the likelihood of postharvest recovery by studying the effects of 2–4 years of experimental harvest on natural *A. racemosa* populations in the George Washington and Jefferson National Forest in southwest Virginia. It was found that after 2–3 years of intense harvest (66% plant removal), significant reductions in foliage area, stem production, and mean and maximum plant height occurred. After 3 successive years of experimental harvest, treatments were terminated to assess population regrowth. Populations experiencing intensive harvest showed no evidence of recovery after 1 year. Results suggest that *A. racemosa* is highly responsive to harvest intensity and that low to moderate harvest intensities and/or longer recovery periods will be necessary for prolonged and sustainable harvests of wild populations (Small et al. 2011).

Despite the current status of *A. racemosa* being "apparently secure" (N4) in the United States (NatureServe 2017), global projections of increased use suggest a 10–30% decline in *A. racemosa* populations over the next decade unless sources of cultivated plant material are established (NatureServe 2017). Of 15 major medicinal herb buyers contacted, 80% named black cohosh as one of the top three herbs most difficult to find at that time. Thus, demand for cultivated black cohosh will increase as wild-harvested populations become fewer in number and unable to keep up with demand. As growers in Germany and Canada have found, this could be a significant opportunity for forest farmers wanting to participate in the industry. As the supply of black cohosh continues to diminish, prices are expected to rise steadily (Davis and Persons 2014). Commercial production will grow as naturally occurring populations will not satisfy the expected increase in demand of 30–40% annually over the next 3–5 years. Lack of significant cultivation protocols creates an opportunity for private forest landowners or cultivators to fill the gap in supply as wild populations continue to decline (Davis and Persons 2014).

19.2.3.6 Suggested Methods to Improve Conservation

As a result of the increasing commercial demand for *A. racemosa*, there is a need to develop propagation protocols suitable for large-scale production purposes to replace current methods of harvesting from wild populations. Propagation studies have been completed, with the following objectives:

1. Determine optimal rhizome propagule division size for successful regeneration.
2. Analyze triterpene glycoside concentrations.
3. Quantify survival rates after 3 years of production.
4. Evaluate net yield results.

Experimental sites included a shade cloth structure in an agricultural research field, a shaded forest interior, and a shaded, disturbed forest edge. Plant emergence, growth, and survival were assessed at each site over a 3-year period. Optimal rhizome division size for propagation was a 10–30 g section originating from terminal rhizome portions. Rhizome survival averaged 97% among all treatments tested by year 3 at three sites. No differences in mean triterpene glycoside concentrations were detected between rhizome size classes or sites tested. Mean cimiracemoside concentrations ranged from 0.80 to 1.39 $mg.g^{-1}$ d/w tissue, 0.47 to 0.92 $mg.g^{-}1$ for deoxyactein, and 10.41 to 13.69 $mg.g^{-1}$ for actein (Fig. 19.5). No differences in triterpene levels were detected between flowering and nonflowering plants, nor were yields reduced. Net yields from a shade cloth production site were 9 and 17 times higher than for disturbed forest edge and forest interior site, respectively. The results of this study indicate that *A. racemosa* is a strong candidate for commercial propagation under adequate site selection (McCoy et al. 2006).

Joe-Ann McCoy, PhD, Director of the NC Arboretum Germplasm Repository located in Asheville, NC, currently maintains the USDA Agricultural Research Service National Plant Germplasm System (NPGS) collection of *A. racemosa* consisting of 22 populations representing its native range and maintained in controlled-pollination regeneration field cages. All populations have been propagated for over 10 years by the curator with control-pollinated seed stored in three seedbanks for long-term conservation. The NPGS collection is a valuable

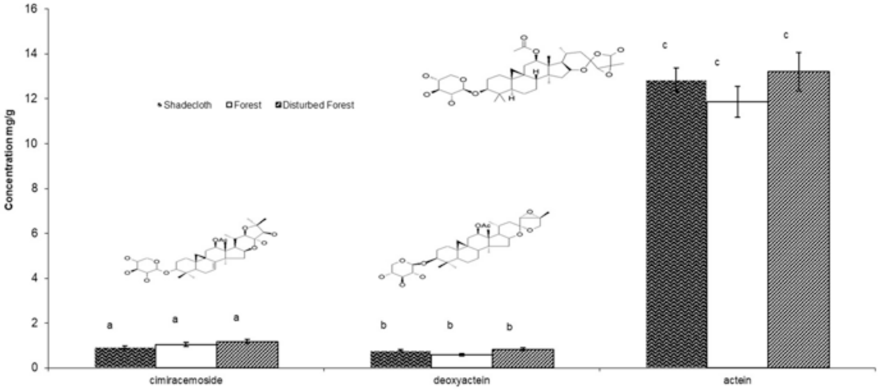

Fig. 19.5 Mean individual concentrations (mg/g dry weight) of cimiracemoside, deoxyactein, and actein from black cohosh rhizomes at three sites. Bars represent standard error. Bars with the same letter are not significantly different ($\alpha = 0.05$)

resource for researchers and GMP compliant companies looking for taxonomically verified botanical reference materials for research. As majority of plant material is wild harvested, there is concern over the sustainability of current wild harvesting practices. These concerns, along with increasing demand, support the need to develop high-quality *A. racemosa* cultivars in order to create a sustainable supply of material to meet consumer demand and preserve native populations. The collection is currently being utilized for various research projects including phytochemical analysis of various compounds between populations, endophyte isolation, phylogenetic mapping, bioassays, in vitro studies, seed studies, propagation, cultivar, and demographic studies (Eisenstein et al. 2013; Pate et al. 2012; Clement et al. 2012).

19.2.4 Hops (Humulus L.*)*

19.2.4.1 Summary

The versatile hop plant, *Humulus* L., is a climbing vine with a perennial root. The genus includes three species, *H. japonicus* Siebold & Zucc., *H. lupulus* L., and *H. yunnanensis* Hu. The European hop (*H. lupulus*) is the species of primary economic importance from which all hop cultivars have been selected. This species has five botanical varieties distributed in Europe, Asia, and North America. Hop cones yield lupulin glands containing α and β acids and other compounds, which provide the bitterings, flavoring, and bacteriostatic properties needed for brewing beer. Hops has also been used for medicinal and pharmaceutical products, salad greens, ornamental decorations, fibers, and fodder. In 2014, 132,631 MT of hops, worth about $565 million US, were produced in 33 countries. The largest producers are Germany, Ethiopia, the United States, China, and Czechia. Major production challenges include fungal and viral pathogens, insect pests, and climate. Breeders and researchers seek disease resistance, dwarfing, low chilling, and improved and varied acid and flavor components from crop wild relatives. Conservation of hop plants in public and private genebanks includes growing containerized living plants under protected cultivation structures, tissue culture as backup plants, and seed and pollen stored in freezers. Broader collections of crop wild relatives are being developed through plant collection and ex situ preservation to increase diversity of global *Humulus* species available for research.

19.2.4.2 Introduction

The hop plant, *Humulus* L., is an herbaceous, dioecious or monoecious, climbing, dextrose-twining bine with a perennial root that is part of the hemp family (Cannabaceae). This plant grows wild to a length of >6 m in the temperate Northern Hemisphere (Small 1978) and tends to grow in riparian environments that are well-drained terraces along streams and rivers, in open areas, along hedge rows, and in deciduous woodlands of Eurasia (including Japan), northeastern and mid-western North America, and in moist locations in the island montane regions of southeastern United States. The genus likely originated in China, where all three species of the genus occur. Distinct populations of plants dispersed to the rest of Asia, Europe, and North America (Murakami et al. 2006), and likely speciated through geographic isolation.

Over the centuries, hop plants have been used for a variety of purposes including medicinal and pharmaceutical products, salad greens, ornamental decorations, pillow stuffing, textile fibers, and fodder (Hampton et al. 2001). The mature female flowers (also called cones, infructescenses, strobili, or commonly known as “hops”) are the primary economic product of the plant and are used in the production of beer. Hops contain resins found in lupulin glands containing α and β acids and essential oils, which are widely used as flavoring and aromatic agents in fermented liquors (Small and Catling 1995). The five common α acids are humulone, cohumulone, adhumulone, posthumulone, and prehumulone. The three main β acids are lupulone, colupulone, and adlupulone. Hop resins have bacteriostatic properties that are valuable for beverage preservation.

19.2.4.3 Origin and Brief History of Use

In the seventh century, monks in Carolingian monasteries began adding hops to preserve and flavor their beer. Hop cultivation probably began in Eastern Europe before the eighth century. From there hop cultivation spread to the rest of Europe (Neve 1991). However, cultivation for beer production began largely in the thirteenth century (Barth et al. 1994). Cultivation began in England in the early 1500s when production practices were adopted from Flemish growers (Burgess 1964).

As Europeans began colonizing the New World, they brought the knowledge and tradition of hop cultivation and beer brewing with them. English settlers introduced hops into the Southern Hemisphere in South Africa, New Zealand, and Australia in the 1800s. Early European settlers to North America picked native hops growing wild. Dutch settlers chose to import preferred dried hops from the old country. English settlers imported cuttings from England, and in 1629, the Massachusetts Company that began growing hops commercially in North America and New England became the first American hop-growing area (Barth et al. 1994). Production eventually migrated to New York, which had better soil and was closer to population centers.

By 1880, New York was producing 21 million pounds of hops annually. During the beginning of the twentieth century, downy mildew disease and hop aphids along with the advent of prohibition disrupted the New York hop growing and brewing industries. The main hop producing region shifted to the Pacific Northwest (Oregon, Washington, California, and Idaho), where hops were grown for export. The Pacific Northwest states continue to lead hop production in the United States.

19.2.5 Modern-Day Use and Agricultural Importance

In 2014, 132,631 MT of hops, worth about $565 million US, were produced in 33 countries (FAOSTAT 2017). Germany has the largest production of any country; Ethiopia, the United States, China (mainland), and Czechia were the next largest country producers. Brewing is by far the largest economically important use of hops; however, the nature of this use has been undergoing change over the past several decades. In the 1980s and 1990s, large national brewing companies dictated the research strategies for hop development. The breeding objectives were conservative and included maintaining stable α/β acid ratios in hops and increased disease and pest resistance. Recently microbrewing by small privately owned companies has increased greatly. There has been a resurgence of the need for diverse flavors and essential oils in hops for brewing, largely due to the microbrewing industry. Each microbrewery seeks individuality through new flavors and varied aroma profiles of their products. In 2014, the craft brewing industry contributed $55.7 billion to the US economy, providing more than 424,000 jobs (Brewers Association 2017). The demand for the availability of diverse hops from wild material and germplasm collections has had a parallel increase.

19.2.5.1 Challenges in Cultivation: Diseases, Pests, and Edaphic and Climatic Limitations

19.2.5.1.1 Fungal Diseases

Several fungal disease causing organisms have been distributed throughout the Northern Hemisphere. These diseases have not yet been reported in South Africa or New Zealand. Powdery mildew, caused by *Podosphaera macularis*, is a major pathogen. This organism may persist either as bud infections or as chasmothecia (sexually produced overwintering structures). Bud infections are the only confirmed overwintering inoculum source in the Pacific Northwest (Ocamb and Gent 2017). Once a field is infected, the disease usually recurs the following season. Spore movement within the field is the greatest threat for disease spread.

Powdery mildew grows between 54 °F and 85 °F and can tolerate more extreme temperatures especially during high humidity. In addition to leaves, flowers and cones may be infected. If a variety is susceptible, cones can be infected throughout most of their development. Growth stops in the infected area. Infected cones are stunted, malformed, and mature rapidly, leading to shattering and uneven crop maturity. Cultural control is recommended to reduce overwintering and buildup of early-season disease inoculum. Spores can move between fields, so management timing is important.

Another important disease is downy mildew, caused by *Pseudoperonospora humuli (Miyabe & Takah.) G.W. Wilson*, a fungus-like microorganism specific to hop. The disease is promoted by wet or foggy weather. The fungus persists from year to year in infected hop crowns or plant debris in the soil (Gent and Ocamb 2017). In early spring, spikelike infected bines rise among normal shoots. Tips of the normal branches may become infected and transformed into spikes. Leaves of all ages are attacked, resulting in brown angular spots. Flower clusters become infected, shrivel, turn brown, dry up, and may fall. Cones also are affected, becoming brown. Severe infection in some susceptible cultivars may produce a rot of the perennial crowns. Cultural control is recommended. Planting disease resistant or tolerant hop cultivars and diligently removing old bines are recommended.

A third significant fungal disease is black root rot, which is caused by *Phytophthora citricola Sawada*, a fungus-like microorganism that survives in soil by long-lived oospores. It also may survive in infected plant parts but not in dead tissue. The disease requires abnormally wet soils and is most often observed in areas of fields with soil or irrigation conditions that cause water to pool. The disease, normally restricted to certain areas of a field due to past irrigation and soil conditions, may become more distributed within a given field with increased use of drip irrigation. The symptoms include bine decline and wilt. The plant tissues become blackened and soft-rotted. Cultural control to avoid pooling water is recommended.

19.2.5.1.2 Virus Diseases

Hops can have many viruses (Eastwell and Ocamb 2017), including *Hop latent virus* (HpLV), *American hop latent virus* (AHLV), *Hop mosaic virus* (HpMV), and *Apple mosaic virus* (ApMV), all of which have been found in Pacific Northwest. The first two viruses (HpLV and AHLV) produce no symptoms and are not known to cause crop loss. HpMV, a *Carlavirus*, has not been a problem traditionally even when detected in a planting. ApMV, an *Ilarvirus* previously known in hop as *Prunus necrotic ringspot virus*, can cause up to 30% loss in cone production and also decrease α acid levels, but ApMV effects are cultivar dependent. HpLV, AHLV, and HpMV are transmitted by plant-to-plant contact and by the Damson-hop aphid (*Phorodon humuli*); HpMV is also transmitted by the green peach aphid, *Myzus persicae*. ApMV moves by plant-to-plant contact. The cultural control method of selecting certified pathogen negative planting material is recommended. Exclusion is an important means of virus control.

19.2.5.1.3 Insect Pests

The hop aphid (*Phorodon humuli* (Schrank)) is a frequent pest in Pacific Northwest. The aphid survives the winter as an egg on woody hosts of the genus *Prunus* (cherry, peach, or plum). Winged aphids move to the top of plant late in the spring. Aphid populations may build very rapidly and if left uncontrolled may result in defoliation. Sometimes mother aphids carry embryos that are carrying their own embryos. This reproduction strategy results in quick population growth. Scouting and natural predators can minimize aphid populations. The economic threshold for the Pacific Northwest of the United States is eight to ten aphids per leaf.

Other insect pests include the two-spotted spider mite (*Tetranychus urticae* C. L. Koch). Adults are small, eight-legged, spiderlike animals. They are pale green to yellowish to reddish, often with a dark spot on each side of the body. They suck plant juices from leaves and hop cones. Control options vary depending on the intensity of the infestation. The least invasive measures that may control mites include removing and destroying infested leaves or spraying the leaves with water to knock off the mites. Pepper or garlic sprays can be applied to plants as a deterrent to the mites. Flower borders such as African marigold and nasturtiums and garlic plants which promote beneficial insect predators may deter the mite where numbers are low in the early stages. Organic insecticides such as pyrethrum, insecticidal soap, nicotine, or diatomaceous earth can be used for control. When mite infestations have gone unchecked and are at high numbers, using commercial insecticides such as diazinon or malathion sprays may be the only option.

19.2.5.1.4 Edaphic and Climatic Limitations

Hops tend to grow best between the 35° and 55° latitude both in the Northern and Southern Hemispheres (Barth et al. 1994). The day length during the growing phase is significant to flowering and yield. The furthest north that hops are cultivated is the Chuvash region of Russia; Tasmania and Australia are the furthest south. To grow hops below 35° latitude in either hemisphere requires day length extension using artificial illumination. Despite these requirements, a number of countries at lower latitudes, such as Mexico, Colombia, Chile, Argentina, Brazil, Egypt, Kenya, Myanmar, and India, are experimenting in hop growing for production. Soil also is important to produce quality hops. A well-drained loam or sandy soil is favored for the best hop growth. Soils that are compacted or tend to become waterlogged are not suitable for hop cultivation due to disease issues.

19.2.5.2 Nutritional and Functional Use

Hops provide a complex flavor for beer, contributing as many as 800 chemical components. The major classes of compounds include the α acids, the β acids, essential oils, and esters (Stevens 1967). Essential oils contribute the major flavor and aroma to the beer. Although there are three main compounds (caryophyllene, humulene, and myrcene), 22 are significant in many brewed products. The esters, such as ethyl hexanoate, which produces a red apple anise aroma, are formed from the reaction of alcohol and the organic acids. They provide fruity flavors to beer. These are controlled by yeast, brewing time, and temperature. The five common α acids are humulone, cohumulone, adhumulone, posthumulone, and prehumulone. The α acids degrade during boiling to form iso-α acids which provide soft bittering qualities in beer. The three main β acids are lupulone, colupulone, and adlupulone. During fermentation, β acids add a harsh bittering quality. They also have bacteriostatic properties. The ratio of α acids/β acids, which is cultivar dependent, is important to brewers for their final product. Hop resins also have bacteriostatic properties that are valuable for beverage preservation. The associated tannins aid in clarification of the brews after boiling and give the flavor to beer (Snyder 1997; USDA 2017).

19.2.5.3 Crop Wild Relatives and Wild Utilized Species

Humulus encompasses three species: *H. japonicus* Siebold and Zucc., from Asia originally, but now introduced throughout the world; *H. lupulus* L., with the type species from Europe from which cultivated hops are derived; and *H. yunnanensis* Hu from Yunnan, China. The first species is an annual, while the other two are perennial (GRIN-Global 2017).

Humulus japonicus is a dioecious species native to Asia where it spreads as an aggressive weed. It has been introduced to the east coast of the United States where it has an exotic invasive weed status in several eastern states (Natureserve 2017). *H. japonicus* cytotypes have complex chromosome numbers. The base chromosome number for this species is $x = 8$. Female plants have $2n = 2x = 14 + 2$ (XX) = 16, and male plants have $2n = 2x = 14 + 3(XY_1Y_2) = 17$ chromosomes (Alexandrov et al. 2012). This species has not been used for breeding hop cultivars because crosses between *H. lupulus* and *H. japonicus*, or with *Cannabis* (a relative in the same family), produce inviable embryos (Tournois 1914; Winge 1914).

The *H. lupulus* cytotypes have a base chromosome number of $x = 10$ and a diploid formula of $2n = 2x = 20$. Tetraploids, $2n = 4x = 40$, are occasionally found in the wild or can be produced artificially by doubling the diploid set in the laboratory using colchicine. Tetraploids can be crossed with diploids to produce triploids, $2n = 3x = 30$. Triploid female cultivars, which are more vigorous plants, produce seedless hops which improves yield. Triploid males stimulate cone growth of normal diploid female cultivars while producing limited seed set.

Small (1978, 1980, 1981) divided *H. lupulus* into five botanical varieties: one Japanese, one European, and three North American. These varieties can be hybridized to produce fertile offspring. The Japanese, *H. lupulus* var. *cordifolius* (Miguel) Maximowicz, can be found on the islands of Hokkaido and Honshu. This taxon has been bred into a few Japanese hop cultivars. The European, *H. lupulus* var. *lupulus* L., grows throughout Northern Europe and provides the main germplasm from which most hop cultivars have been regionally selected or bred. The American varieties are *H. lupulus* var. *nemomexicanus* Nelson and Cockerell, which is endemic to the North American Cordillera; *H. lupulus* var. *pubescens* E. Small from the midwestern United States and Canadian provinces; and *H. lupulus* var. *lupuloides* E. Small of central and eastern North America. The European *H. lupulus* var. *lupulus* was introduced to North American from Europe for brewing by the colonists.

Humulus yunnanensis is not well described in western literature, and chromosome counts are not recorded. It is dioecious, and its leaves are less lobed and its cones longer than those of *H. japonicus*, though narrower than *H. lupulus*.

19.2.5.3.1 Distribution, Habitat, and Abundance

The North American distribution of the *Humulus lupulus* botanical varieties (Small 1978) are presented in Fig. 19.6. The American varieties within *H. lupulus* introgress where they are sympatric in the wild and can be hybridized in the laboratory for breeding purposes. The European hop, *H. lupulus* var. *lupulus*, was naturalized in North America after colonial introductions in the east coast from Ontario and Quebec, Canada, to New Hampshire, Vermont, New York, Pennsylvania, New Jersey, and Maryland. This introduced distribution is sympatric with that of *H. lupulus* L. var. *lupuloides* E. Small (Fig. 19.7), though it ranges further westward to the Dakotas, Nebraska, Montana, Manitoba, Saskatchewan, and Alberta.

H. lupulus var. *pubescens* E. Small ranges in the middle of the United States from Ohio through Indiana, Illinois, Arkansas, Missouri, Nebraska, and Kansas; *H. lupulus* var. *neomexicanus* A. Nelson & Cockerell (Fig. 19.8) is allopatric in the Cordillera of the southwestern states. Pleistocene pollen deposits confirmed that this species is autochthonous to the New World (Cushing 1963). These *Humulus* taxa are frequently found and are not listed as endangered or threatened in either the IUCN Red List or the US National Resources Conservation List.

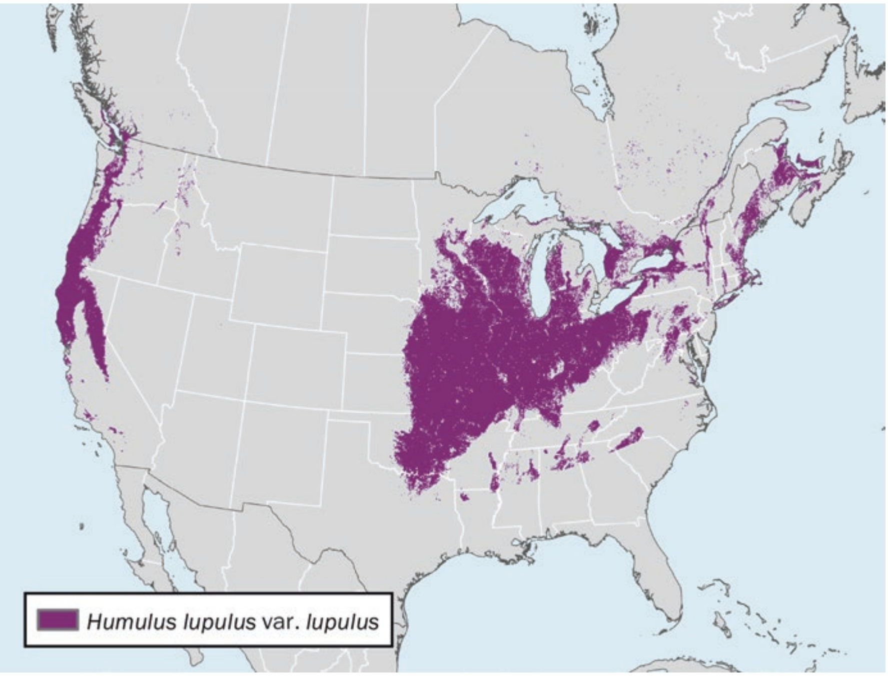

Fig. 19.6 Modeled potential distribution of *H. lupulus* L. var. *lupulus* (European hops) introduced into North America based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps are given in Appendix 1

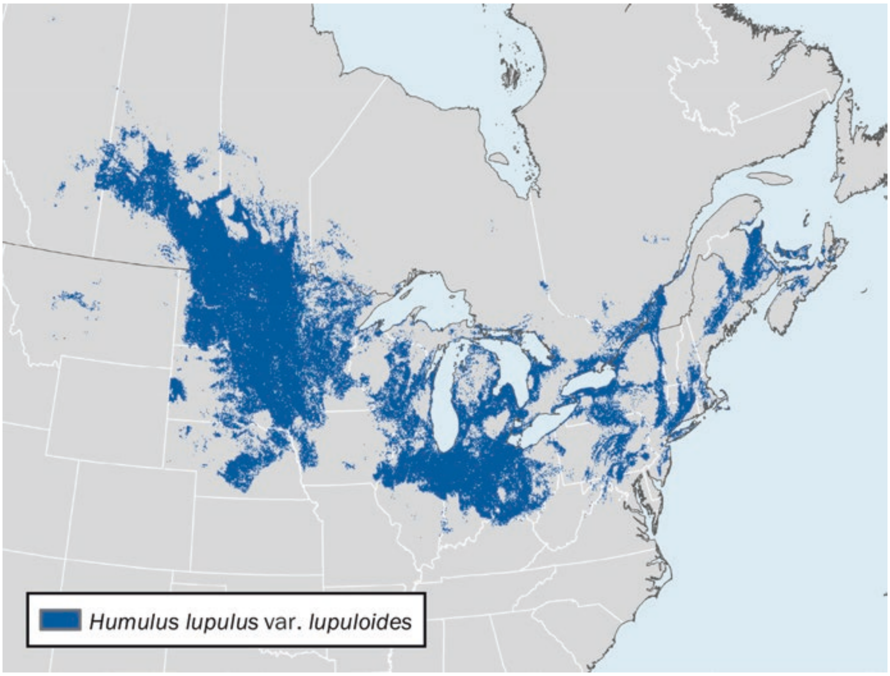

Fig. 19.7 Modeled potential distribution of *H. lupulus* L. var. *lupuloides* E. Small, native to the United States, based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps are given in Appendix 1

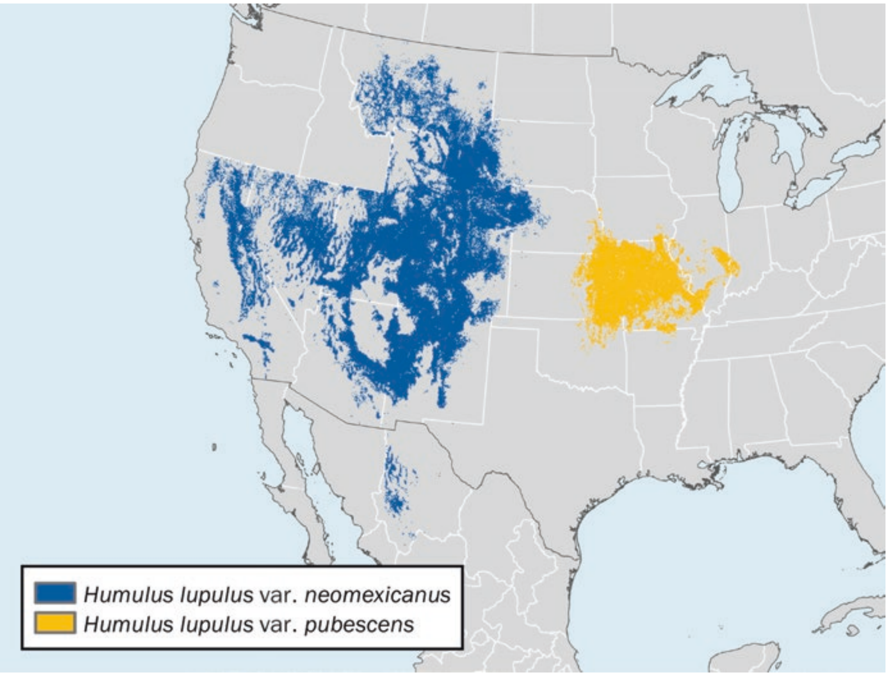

Fig. 19.8 Modeled potential distribution of *H. lupulus* var. *neomexicanus* A. Nelson & Cockerell native to the United States and *H. lupulus* var. *pubescens* E. Small native to the United States based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps are given in Appendix 1

19.2.5.3.2 Utilization: North American Breeding Contributions

Commercial hops are selected landraces from, or hybrid crosses of, the species *Humulus lupulus*. Most named cultivars were originally derived from European hops, *H. lupulus* var. *lupulus*. The desirable traits of this taxon include a relatively low content of soft resins, an α/β acid ratio that approaches one, low cohumulone, moderately low essential oil content, and relatively low myrcene in the essential oil fraction. Domesticated land races such as the German "Hallertauer," "Hersbrucker," "Saazer," and "Tettnanger" are regional selections that have become standards of the industry.

The first report of using North American native species as a parent for breeding hops was made by Professor E.S. Salmon (1934), who hybridized a wild female hop collected in 1916 from Morden, Manitoba, Canada, with a traditional English hop cultivar to increase the soft resin content in seedlings. From this cross, Salmon released "Brewers Gold," "Northern Brewer," and "Bullion." "Brewers Gold" was subsequently included in the pedigrees of many new cultivar releases from breeding programs throughout the world. Zimmerman et al. (1975) released "Comet," a cross including *H. lupulus* var. *neomexicanus* from Utah. For the past several decades, American wild hops were not preferred as breeding parents because of undesirable traits such as a low quantity of soft resins, less than 10% of cone weight (Haunold et al. 1993). Plants with α acids above 5% were rare, and the α/β acid ratio tended to be less than 50%. Native American hops tended to have high cohumulone and colupulone complexed with a pungent, unpleasant aroma (Haunold et al. 1993). However, American hops could also provide positive traits: dwarfing tendency, production precocity, early season flowering, high yield potential, disease and pest resistance, frost resistance, drought resistance, and novel chemistry. In 1986, the value of the contribution of native American hops to commercial brewing was estimated at $20 million annually (Prescott-Allen and Prescott-Allen 1986). Microbrewing, privatization, and individualization of hop breeding programs have caused many breeders and brewers to experiment with higher β-acid hops and a broad spectrum of essential oils previously thought unacceptable.

19.2.5.3.3 Conservation Status of CWR and WUS

No in situ conservation agreements have been made in the United States for the indigenous botanical varieties of *Humulus lupulus* to date. The US National *Humulus* Germplasm Collection is housed at the USDA ARS National Clonal Germplasm Repository in Corvallis, Oregon. This living collection is comprised of 330 accessions. In addition, 194 seedlots represent wild collected taxa. As a backup, ~110 in vitro cultured plantlets are stored at NCGR and at a remote backup site of the USDA ARS at Ft. Collins, Colorado. The tissue cultures are stored at 4 °C using semipermeable plastic bags. Plants can remain in the bags for up to 3 years without re-culturing. The primary collection is composed of European cultivars and American cultivars (particularly those released from Pacific Northwestern breeding programs), along with species representatives of crop wild relatives from around the world. Gaps in the collection include the Asian species, *H. yunnanensis*, and better representation of the wild botanical varieties of the Japanese, American, and European *H. lupulus*. Broader representation of CWR are being sought through plant collection and ex situ preservation to increase diversity of global *Humulus* species available for research.

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Part V
The Way Forward

Chapter 20
Conservation and Use of the North American Plant Cornucopia: The Way Forward

Colin K. Khoury, Stephanie L. Greene, Karen A. Williams, Michael B. Kantar, and Laura F. Marek

Abstract The pages of this extensive book document the potential of a great many North American plants to enhance the productivity, sustainability, and nutritional quality of crops or to be further developed into important cultivated species in their own right. But this potential can only be realized if the plants are adequately conserved to ensure their survival and availability for research, invested in to promote their development, and marketed so as to be attractive to producers and consumers. We outline some of the key steps needed to boost the conservation and use of our regional cornucopia. *In situ* and *ex situ* conservation of North America's useful plants are being accomplished by a variety of institutions with different mandates,

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C. K. Khoury (✉)
USDA, Agricultural Research Service, Center for Agricultural Resources Research, National Laboratory for Genetic Resources Preservation, Fort Collins, CO, USA

International Center for Tropical Agriculture (CIAT), Cali, Colombia
e-mail: colin.khoury@ars.usda.gov; c.khoury@cgiar.org

S. L. Greene
USDA, Agricultural Research Service, Center for Agricultural Resources Research, National Laboratory for Genetic Resources Preservation, Fort Collins, CO, USA
e-mail: stephanie.greene@ars.usda.gov

K. A. Williams
USDA, Agricultural Research Service, Beltsville Agricultural Research Center, National Germplasm Resources Laboratory, Beltsville, MD, USA
e-mail: karen.williams@ars.usda.gov

M. B. Kantar
Tropical Plant and Soil Science, University of Hawaii at Manoa, Honolulu, HI, USA
e-mail: mbkantar@hawaii.edu

L. F. Marek
Department of Agronomy/North Central Regional Plant Introduction Station, Iowa State University, Ames, IA, USA
e-mail: lmarek@iastate.edu

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but habitat destruction and other threats to wild populations continue to negatively impact many species. Information sharing, coordinating efforts, filling research gaps for wild plants, and increasing support for conservation will be necessary to more comprehensively safeguard these plants and to make them available for use. Technologies enabling more efficient exploration of the diversity within these species are rapidly advancing and offer the potential to contribute to quick advances in improvement of cultivars, but considerable further research and partnerships are needed to generate and share the results widely. Marketing of new crops can take advantage of the increasing public interest in diverse and nutritious foods, learning from successful collaborations between producers, researchers, and consumers. As a whole, North America already possesses a strong foundation from which the conservation and use of its flora can be enhanced. This includes many protected areas, strong conservation institutions, innovative research, and the willingness to collaborate across fields, institutions, and borders. There are still many silos that need to be broken down and reorganized through innovative partnerships to better conserve and benefit from the North American cornucopia. But given the incredible diversity of interesting and useful plants in the region, the remarkable efforts for many decades by many organizations to care for these plants and share them with humanity, and the increasing public interest in more diverse, healthy, and resilient food and agricultural systems, there is reason for hope.

Keywords Crop wild relatives · Ex situ conservation · Food security · In situ conservation · Wild utilized species

20.1 Introduction

The plants that make up North America's native cornucopia span the full spectrum with regard to recognition of their historic, current, and potential future uses. Maize, or corn (*Zea mays* L.), benefiting from at least 9000 years of keen interest by people (Larson et al. 2014), ranks among the most important plants in the world (Khoury et al. 2014; FAO 2017; Cruz-Cárdenas et al. 2018). Common bean (*Phaseolus vulgaris* L.), chili pepper (*Capsicum annuum* L.), American cotton (*Gossypium hirsutum* L.), sunflower (*Helianthus annuus* L.), pepo squashes (*Cucurbita pepo* L.), avocado (*Persea americana* Mill.), papaya (*Carica papaya* L.), and a handful of other indigenous species also play profoundly important dietary, economic, and cultural roles worldwide (Khoury et al. 2016; Avendaño-Arrazate et al. 2018; Barchenger and Bosland 2018; Doyle et al. 2018; Jenderek and Frelichowski 2018; Kates 2018; Marek 2018). These are North America's most celebrated plant gifts to humanity.

On the other end of the spectrum is a long list of "underutilized" species that, given the equally long set of compounding challenges to the persistence of wild plant populations (Brummitt et al. 2015), may disappear before most of humanity has the opportunity even to be introduced to them. These include many plants that were consciously managed, selected upon, or incipiently domesticated long ago but have fallen to the wayside as casualties of colonialism, agricultural industrialization, globalization, changing cropping preferences, and demographic change (Khoury et al. 2014). Very few of these species benefit from active conservation and breeding programs. Will American potato bean (*Apios americana* Medik), once an important food source both for Native Americans and European settlers from the Atlantic coast to the Missouri River basin (Beardsley 1939), be given the opportunity to reach its potential as a high-protein tuber crop for temperate regions? And what of its beautiful and threatened cousin, traveler's delight (*Apios priceana* B. L. Rob.), which was also once a food source and has now been reduced to a dozen remaining populations due to the destruction of its habitat (USFWS 2015)? The list of such fascinating, essentially wild, species with unique potential is long; the outlook for the future is not very bright.

Between these extremes lie a wide range of North American food plants with some relevance within and beyond the region, but relatively minor investment currently with regard to their conservation, breeding, and marketing. Examples include pecan (*Carya illinoinensis* [Wangenh] K. Kochs), cranberry (*Vaccinium macrocarpo*n Aiton), and blueberry (*Vaccinium* section *Cyanococcus*, especially *Vaccinium corymbosum* L.), blackberry (*Rubus fruticosus* L., sensu lato and hybrids), wildrice (*Zizania palustri*s L.), cushaw squash (*Cucurbita argyrosperma* C Huber subsp. *argyrosperma*), chayote (*Sechium edule* [Jacq.] Sw.), chia (*Salvia hispanica* L.), tomatillo (*Physalis philadelphica* Lam.), guava (*Psidium guajava* L.), cherimoya (*Annona cherimola* Mill), paw paw (*Asimina triloba* [L.] Dunal), and sapotes (*Pouteria sapota* [Jacq.] H. E. Moore & Stearn, *Casimiroa edulis* Llave & Lex., and *Diospyros nigra* [J.F.Gmel.] Perrier) (Avendaño-Arrazate et al. 2018; Hummer et al. 2018; Kates 2018; Porter 2018; Preece and Aradhya 2018; Volk 2018). Some of these plants, such as jicama (*Pachyrhizus erosus* [L.] Urb.) and sunchoke (*Helianthus tuberosus* L.), are tasty and filling yet of very low-energy density and thus may fill an increasingly important dietary niche in a world of caloric overabundance (The Global Burden of Disease 2015 Obesity Collaborators 2017). Many of these species are rich in vitamins, minerals, and phytonutrients. Also among these "somewhat-utilized" North American plants are numerous nonfood species of economic and cultural importance, including medicinals such as American ginseng (*Panax quinquefolius* L.), coneflower (*Echinacea* Moench), and black cohosh (*Actaea racemosa* L.) (McCoy et al. 2018); industrial use plants such as jojoba (*Simmondsia chinensis* [Link] C. K. Schneid.), guayule (*Parthenium argentatum* A. Gray), bladderpod (*Physaria fendleri* [A. Gray] O'Kane & Al-Shehbaz), and meadowfoam (*Limnanthes* R.Br.) (Jenderek et al. 2018); fiber plants such as false yucca (*Hesperaloe* Engelm.) and agave (*Agave* L.) (Jenderek and Frelichowski 2018); and many ornamental species, such as those within *Phlox* L., *Coreopsis* L., and *Rudbeckia* L (Jourdan 2018). Virtually all of these plants have both "improved" and wild types distributed in North America. Many are fairly productive without significant inputs and are resistant to pests and diseases. Their contributions to diet, economy, and culture, particularly in other world regions, would very likely expand if crop development and product marketing were given greater investment.

Finally, there are the wild and weedy North American plants that have already, or may in the future, play important roles as genetic resources in increasing the productivity, nutritional quality, and sustainability of agricultural crops cultivated around the world. North America is the home of many progenitors and close relatives of domesticated plants, including those of the important crops listed above that were domesticated hundreds to thousands of years ago in the region, as well as those whose major crop taxa originated elsewhere (e.g., of apples [*Malus* Mill.], cacao [*Theobroma* L.], currants [*Ribes* L.], grapes [*Vitis* L.], hops [*Humulus* L], lettuce [*Lactuca* L.], onions [*Allium* L.], quinoa [*Chenopodium* L.], strawberries [*Fragaria* L.], and walnut [*Juglans* L.]) (Brenner et al. 2018; Heinitz et al. 2018; Hummer et al. 2018; Lebeda et al. 2018; McCoy et al. 2018; Preece and Aradhya 2018; Volk 2018). There are also thriving populations of introduced relatives of important staples (e.g., of wheat [*Aegilops* L.], oats [*Avena* L.], and sugar beets [*Beta* L.]), which have diversified within the region sufficiently to have become interesting to plant breeders as sources of agronomically valuable traits (Khoury et al. 2013).

As a whole, there are many thousands of crop wild relative species distributed across North America (this book; USDA, ARS, National Plant Germplasm System 2017b), with at least a couple hundred being of particular interest due to their relatively close genetic relationship with major crops, making introgression of useful traits quite feasible (Khoury et al. 2013). Of these, the native sunflowers as a group have probably been of greatest use in crop breeding thus far, particularly for pest and disease resistance (Dempewolf et al. 2017; Seiler et al. 2017; Marek 2018). Other celebrated examples include North American wild grapes' contribution to resistance to phylloxera (*Phylloxera vitifoliae* Fitch) in European rootstocks (late 1800s–present) (Khoury et al. 2013; Heinitz et al. 2018) and the use of native wild hops (*Humulus lupulus* L. var. *lupuloides* E. Small) in the breeding of important European cultivars (Townsend and Henning 2009; McCoy et al. 2018). Breeding efforts that have made important contributions to crop improvement through the use of North American wild genetic resources have been located not only in the region but also in Europe, Asia, Australia, and elsewhere (e.g., sunflower breeding, reviewed in Marek 2018).

Yet despite these successes, and even while crop wild relatives have gained increasing visibility within the texts of international agreements on agriculture, development, and conservation (e.g., Sustainable Development Goal Target 2.5 (United Nations Sustainable Development Platform 2016); Aichi Biodiversity Target 13 (Convention on Biological Diversity 2016); and the International Treaty on Plant Genetic Resources for Food and Agriculture [Plant Treaty], Article 5 (FAO 2002)), the great majority of North American wild and weedy genetic resources certainly fall on the underappreciated end of the spectrum with regard to recognition of their potential value. Introgression of useful traits from wild relatives and the elimination of linkage drag of non-useful traits are, in comparison to the status quo use of improved domesticated germplasm, challenging and lengthy processes. Such useful traits are often masked in the wild types (Tanksley and McCouch 1997), making predictions of their value difficult. And many taxa are common and weedy in form and thus catch the eyes and capture the hearts only of the most enthusiastic of botanists and land managers. These are some of the historic reasons why crop wild relatives have not, in general, been given major priority within the strategies of the crop improvement, genetic resources conservation, and land management communities. This needs to change, as the use of wild relatives in crop breeding is gaining momentum (Guarino and Lobell 2011; McCouch et al. 2013; Dempewolf et al. 2017) to help address serious agricultural production challenges (Lobell et al. 2008; Cordell et al. 2009) and because threats to their natural populations are compounding (Castañeda-Álvarez et al. 2016).

The pages of this extensive book document a great many North American plants that could contribute much more to human culture than they currently do. But only, of course, if they are adequately conserved to ensure their survival and availability for research, invested in to promote their development, and marketed so as to be attractive to producers and consumers. Below we outline some of the key steps that we have identified as needed to boost the conservation and the use of our regional cornucopia.

20.2 Conservation

20.2.1 In Situ

Federal, state, and other official threatened and endangered species lists provide a primary medium by which conservation investment can be both acquired and defended and should be advocated for and enforced wherever possible. A worrying number of North American crop wild relatives are already listed as threatened or endangered (e.g., 62 wild relative taxa native to the USA are listed endangered under the Endangered Species Act, 10 taxa as threatened, and 11 as candidates for listing; and NatureServe assessed 8 US wild relative taxa as known or presumed extinct in the wild, 115 as globally critically imperiled, 111 as imperiled, and 337 as vulnerable) (Khoury et al. 2013). Many of these conservation assessments were completed a decade or more ago and are in need of re-evaluation, given the compounding threats to wild plants from habitat destruction and degradation, invasive species, overharvesting, and climate change (Brummitt et al. 2015). Furthermore, a considerable proportion of North American wild relatives have not yet been fully assessed for threats to their natural populations, even while the available literature gives much cause for concern (e.g., dire warnings for the last remaining populations of the wild progenitor of maize (Wilkes 2007)).

Fortunately, independent of the long and complicated processes required to successfully place plants on official threatened species lists, *in situ* conservation of North American crop wild relatives and other wild utilized plant species is occurring in federal, state, provincial, Native American, First Nations, Indigenous peoples, nongovernmental, and privately managed protected areas. Aside from a handful of designated conservation programs for iconic wild relatives (i.e., US Forest Service wild chili [*Capsicum annuum* var. *glabriusculum* (Dunal) Heiser & Pickersgill] preservation activities in Southern Arizona, USA (USDA Forest Service 2016); and the management of a wild relative of maize (*Zea diploperennis* H. H. Iltis et al.), various wild beans, and other crop wild relatives in the Sierra de Manantlan Biosphere Reserve in Jalisco/Colima, Mexico), such conservation is essentially "passive" (i.e., without active management plans for individual species or populations and without regularly scheduled monitoring). Because of this, information on the status of populations of most of these plants in most protected areas is not available, and it cannot be assumed that these populations are thriving.

Major steps forward in the active *in situ* conservation of crop wild relatives and wild utilized species in North America could be taken by improving the documentation of the status of populations persisting in existing protected areas, sharing this information on one or a few common platforms, and enhancing the monitoring of populations identified through the process as being unique and valuable. While such efforts would require additional investment in staffing and information technologies, the resources needed would almost certainly be a fraction of those required to fulfill obligations enforced for officially listed threatened and endangered species and would be more politically achievable across the different organizations, landowners, and countries. Such initiatives would also provide more flexibility for land managers to achieve conservation goals in their own manner and aligned with their own sets of priorities and would thus probably represent more sustainable arrangements for long-term regional collaborations on conservation of useful wild plants.

20.2.2 Ex Situ

Information on *ex situ* collections for North American crop wild relatives and wild utilized plants is generally available and relatively easy to access for public genebanks and to a more limited degree for botanic gardens. Data on university, private, nonprofit, local seedbank, and other *ex situ* collections are not nearly as accessible. Previous assessments of the representation of crop wild relatives in *ex situ* conservation systems have provided an indication that there are serious gaps for North American taxa (e.g., Castañeda-Álvarez et al. 2016). However, these findings are incomplete in their coverage of institutions performing *ex situ* conservation, largely due to lack of access to the pertinent data on existing collections. This is unfortunate, as some of these nongovernmental collections may be playing significant conservation roles, particularly for useful wild food plants, and deserve fuller recognition.

Parallel to the priorities for *in situ* conservation, comprehensive information on *ex situ* collections for North American wild plants, shared on one or a few centralized online resources and including as many collections as possible both within and beyond the region, represents a critically important priority to enable a full assessment of the state of conservation of such taxa and to identify the regional gaps in their representation *ex situ*. Such coordinated information resources also provide a primary medium by which useful information on these plants can be shared with plant breeders and other researchers and furthermore can bolster the justification of investment in conservation from a rational, regionally coordinated perspective.

Data management programs under development or being utilized by genebanks (e.g., GRIN-Global (USDA, ARS, National Plant Germplasm System 2017a) and Genesys (Data Providers and the Crop Trust 2017)) and by botanic gardens (e.g., BG-BASE (BG-BASE Inc. 2017), IrisBG (Botanical Software Ltd. 2017), and BGCI PlantSearch (Botanic Gardens Conservation International 2017)) in the region have many years of investment and could be used to combine and share such information but require modification to be able to receive inputs from institutions which have managed their data using different technologies. In some institutions, collections and associated provenance data have been purposely obscured from the public for fear of theft of specimens in botanic and public gardens or because the information could lead to overharvesting of specimens from the wild. Thus information sharing also needs to be accomplished with attention paid to potential risks to species, especially those with few remaining populations persisting *in situ*.

A detailed regional analysis of the representation of North American crop wild relatives and wild utilized species in *ex situ* conservation is needed to identify those taxonomic groups and geographic regions least well protected and to provide focus for efforts to overcome the funding and political challenges to improving their conservation. National inventories of useful wild plants have already been completed (Khoury et al. 2013; Contreras-Toledo et al. 2018), and these in combination with updated high-quality taxonomic (USDA, ARS, National Plant Germplasm System 2017b) and floristic (e.g., Flora of North America Association 2008) information and an increasing availability of occurrence (e.g., GBIF 2017) and ecogeographic data (e.g., Fick and Hijmans 2017; Hengl et al. 2017) and modeling tools (e.g., Phillips et al. 2017) make the completion of a high-quality regional analysis possible. Inputs by field botanists and conservation practitioners ground-truthing species occurrences will be critical to ensuring that the analyses reflect real distributions, especially for species whose ranges have changed dramatically in recent decades (e.g., rock grape [*Vitis rupestris* Scheele] (Heinitz et al. 2018) and various wild cotton species [*Gossypium* L.] (Jenderek and Frelichowski 2018)).

Such an analysis could additionally be adapted for use in assessments of the state of wild plants conserved *in situ* in existing protected areas, forming in combination a truly comprehensive conservation analysis for the North American plant cornucopia. Following from these assessments, coordinated collecting for *ex situ* conservation of gaps in collections, and the creation of or enhancement of existing management plans for wild populations in protected areas, can be prioritized and initiated.

The information compiled in this book on existing *ex situ* collections of seeds, buds, other propagules, and whole plants conserved in the national public genebanks, botanic gardens, universities, and other institutions reveal a diverse array of banked resources that are often the result of decades or indeed lifetimes of efforts of dedicated botanists, curators, and plant breeders. The collections of relatives of major commodity crops, such as those of sunflowers and North American wild potatoes (*Solanum* L.) are comparatively the most well represented and documented, both taxonomically and geographically. The wild relatives of minor crops and the many underutilized North American wild species are much more sparsely represented.

Furthermore, even the most comprehensive collections still have recognized gaps with regard to representation *ex situ* of the full array of taxonomic, geographic, and genetic variation in extant wild populations. One of the reasons for these persisting holes in major collections is that many species groups are distributed in more than one country, thus requiring coordination between nations. Part of the challenge results from the very complicated policies regarding biodiversity and the sharing of genetic resources, which are being negotiated primarily via the Convention on Biological Diversity (CBD) (Convention on Biological Diversity 2017), the Plant Treaty (FAO 2002), and the Nagoya Protocol of the CBD (Buck and Hamilton 2011). These agreements provide international frameworks for collaboration across borders, but at the current time, each of the countries in North America differs in membership status (de la Torre et al. 2018; Diederichsen and Shellenberg 2018; Williams and Greene 2018). Moreover, considerable further efforts are needed to implement these policies in North America in standardized and clear ways such that they are understandable to collectors, conservationists, researchers, and political authorities.

For such reasons, large publicly accessible genebank collections for wild relatives of crops such as sunflower (e.g., threatened species such as Algodones sunflower [*Helianthus niveus* (Benth.) Brandegee subsp. *tephrodes* (A. Gray) Heiser] and paradoxical sunflower [*Helianthus paradoxus* Heiser]) are incomplete in the sense of lacking representation *ex situ* of the entire diversity of populations identified by experts as important from multiple countries (Marek 2018). As access to genebank collections maintaining plant genetic resources at high standards is useful to researchers in all of the North American countries, as with elsewhere around the world (Hoisington et al. 1999; Gepts 2006; Khoury et al. 2016), the region should actively work to improve the ways that wild plants can be conserved and exchanged internationally.

Various challenges to the success of *ex situ* conservation efforts for North American wild plants are apparent. The initial processing activities required to maintain a high degree of viability during storage, the placement of the species in conditions that enable their survival over long periods, and the periodic regeneration/multiplication of accessions are all generally more challenging and more expensive for wild plants than for crops. Research at the species and even at the population/accession level is often needed to develop appropriate protocols (Hellier 2018; Walters et al. 2018), particularly for challenging taxa such as the wildrices (*Zizania* L.) (Porter 2018). Some plant species, especially the perennials, can be maintained as specimens in botanic gardens or in conservation fields to avoid some of these challenges, but available space and management costs constrain the ability to curate a broad range of infraspecific diversity with these methods.

While these research and curatorial challenges are all surmountable from scientific and technical perspectives, they persist due to insufficient resources devoted to wild plant conservation *ex situ*. Investment in public national and other repositories has, in general, declined in recent decades, especially when understood in light of increasing costs, particularly for distribution of materials (Fu 2017). Funders increasingly want evidence of social impact. Unfortunately, beyond documentation of the number of distributions made, the impact of using plants distributed from genebanks is not currently readily determinable, as breeding by the private sector is generally proprietary information and as utilization even by the public sector is rarely easily accessible. An information system under development by the Plant Treaty (FAO 2002) may help to provide more thorough documentation of the use of some of North America's native wild relatives in the future, but the data is unlikely to be comprehensive, and the lag time between requesting of materials from genebanks and release of crop varieties is often many years or even decades, giving this feedback cycle dubious power to bolster arguments for improved maintenance of *ex situ* collections.

The need for greater support for public genebanks and other *ex situ* facilities committed to the conservation and distribution of useful plant diversity has been highlighted for decades (Hoisington et al. 1999; Esquinas-Alcázar 2005). Keeping distributions free to plant breeders and other researchers is a laudable value and an important means of recognizing that crop wild relatives and wild utilized species are public goods that should remain openly available for the benefit of humanity (Gepts 2006). How to improve the support of these institutions remains a perennial challenge (Fu 2017). Advocacy by the larger conservation community and by public and private users of the conserved genetic resources could be strengthened through coordinated efforts (Gepts 2006; Guarino and Lobell 2011). Furthermore, given the relatively low level of awareness in the public of the importance of genetic resource conservation to agriculture, efforts to increase this awareness could be helpful (Moreau and Novy 2018).

20.3 Improvement and Marketing

20.3.1 Documentation, Characterization, and Evaluation

Crop wild relative and wild utilized plant accessions conserved *ex situ* in the North American public genebanks and other genetic resource collections range in the degree of existing and available documentation, characterization, and evaluation data. In general, most have basic documentation with regard to taxonomy and origin (i.e., passport data) but have little available characterization and only in exceptional cases evaluation data. "Offline" datasets curated by academic researchers and by the private sector may provide further valuable information on these accessions but are not currently widely accessible.

Useful data on such species is being generated more efficiently via ecogeographic modeling, high-throughput characterization and evaluation, and genomics, generally by way of crop genepool or trait-specific projects. These efforts lack a coordinated mechanism to pool and make such data easily accessible, constraining greater use and also more sophisticated conservation of this diversity (Gur and Zamir 2004; Dempewolf et al. 2017). Incentivizing organizations and individuals not only to generate but also to share data should be prioritized so that this information can be put to use by plant breeders and genetic resource conservationists (Volk and Richards 2011; McCouch et al. 2013).

Building on the existing national efforts to inventory wild relatives and wild utilized species and taking advantage of available documentation, characterization, and evaluation data, national and regional lists of species with significant potential for development as genetic resources or as new crops should be completed and advocated for within organizational research priorities. These efforts are important foundational steps toward producing new crops and new varieties adapted to target climates and soils and filling target market niches.

20.3.2 Pre-breeding and Breeding

Incorporating useful traits from wild relatives into crop cultivars can be facilitated by pre-breeding, the process of crossing exotic genetic resources with modern breeding materials in order to generate offspring that contain novel useful diversity which can be incorporated more easily into advanced plant breeding programs (Prohens et al. 2017). Pre-breeding has historically been performed mostly by public organizations, but these efforts have declined in recent decades due to funding limitations (Morris et al. 2006). Renewed support is thus very much needed for public programs and for public-private partnerships that tackle the initial challenges of introducing traits of interest from wild relatives into domesticated materials and making these materials available to the public (Guarino and Lobell 2011).

The decline in investment in public breeding programs within governmental and in academic institutions has also affected the breadth of crops of primary development focus, generally narrowing this focus further on important commodity crops and in turn abandoning the riskier longer-term projects directed toward turning promising wild utilized species into productive crops (Fuglie and Walker 2001; Morris et al. 2006; Pardey et al. 2016). Given that the suite of crop plants underlying the global food system has become increasingly homogeneous (Khoury et al. 2014), making greater space in agricultural research investment for the plants with the greatest potential to make agricultural production and the human diet more diverse is prudent. Such efforts can be supported by stimulating diversification research, engendering research arrangements that enable the open distribution of promising new varieties while providing appropriate acknowledgement to individuals and organizations, providing production support via agricultural extension and training, and further developing seed systems facilitating the multiplication and distribution of seed and other propagules to growers (Naylor et al. 2004; Khoury and Jarvis 2014; Rotz and Fraser 2015).

In recent decades, major advances have been made in the sophistication of tools used to identify functionally useful diversity in plants and to introgress traits from these sources into improved varieties. Many of these tools could enable rapid domestication advances in wild utilized species, for example, by helping to overcome biological constraints such as flowering time or daylength sensitivity, agronomically challenging growth habits, or the uneven maturation of fruits or seeds (Naylor et al. 2004; Runck et al. 2014; DeHaan et al. 2016). Some of these tools can provide valuable additions to conventional plant breeding programs. Others, such as the introgression tools that help move genes between exotic sources and the emerging techniques enabling the "editing" of genes based on a thorough knowledge of the genome of species or of related plants (Zhang et al. 2014), are subjects of strong public opinion and complicated policy (Jordan et al. 2017). Their potential to contribute to the diversification of food systems is dependent on the ways breeding targets are chosen and the benefits of the research are shared, as well as the manner by which research is performed and communicated to the public (Naylor et al. 2004; Jordan et al. 2017).

20.3.3 Marketing

The relatively recent expansion in global harvested area and increase in consumption worldwide of crops such as quinoa (*Chenopodium quinoa* Willd.) and chia provides evidence that agricultural production and food supplies can be diversified through research, within a climate of growing consumer interest in healthier and more varied food alternatives. Local food, regionally adapted food, and organic food movements are long-term trends which provide opportunities for growers to be profitable with new, niche, or value-added crops. Both private and also public organizations promoting new foods are becoming more sophisticated in their ability to influence markets, both by way of traditional advertising and via social media, collaborations with recognizable advocates (such as celebrity chefs), and innovative packaging of such foods to fit modern lifestyles which value convenience (Beans 2017). Further efforts to diversify food systems with North American plants should learn from these successes. Increasing public demand for foods and other agricultural products of North American origin will be critical to any significant progress in increasing the use of this diversity, as the region currently primarily produces and consumes plants of foreign origin (Khoury et al. 2016).

20.4 Final Remarks

North America is remarkably well positioned to more comprehensively conserve its native plant cornucopia and to use these plants to diversify the food that is eaten and the crops that are used for fiber, industrial purposes, medicine, ornamentals, and other purposes, both within the region and around the world.

Canada, Mexico, and the USA have existing legislation that provides protection for threatened plants and a significant number of public and other managed lands that are functioning to safeguard species *in situ*. National genebank systems have the appropriate infrastructure and working information systems and a long record of regional collaboration (e.g., via the North American Network on Plant Genetic Resources [NORGEN] (PROCINORTE 2015)). Annual distributions to plant breeders and other researchers around the world by the USA and Canadian genebanks count among the largest worldwide, and all of the national genebanks in the region serve important within-country distribution functions. Many hundreds of botanic and public gardens are distributed throughout the region, providing not only conservation functions but also important opportunities for the public to interact with these plants (Moreau and Novy 2018). A range of local, nonprofit, and community-based initiatives also play conservation roles. National and international policy on the conservation and sharing of wild plants is actively being negotiated. Crop wild relative and wild utilized plant inventories have been completed for most of the region. Collaborations across organizations, countries, and fields, from agricultural research to botanic gardens to land management agencies, are being created and strengthened (e.g., USDA Forest Service and USDA Agricultural Research Service 2014).

There are still many conceptual, organizational, and political silos that need to be broken down and reorganized through innovative partnerships to take the major steps forward needed to better conserve and benefit from North American crop wild relatives and wild utilized plants. But given the incredible diversity of interesting and useful plants in the region, the remarkable efforts for many decades by many organizations to care for these plants and share them with humanity, and the increasing public interest in more diverse, healthy, and resilient food and agricultural systems, there is reason for hope.

Thomas Jefferson, one of the founding fathers of the USA, an avid gardener, and a passionate advocate for food crop diversity, said in 1800 that “The greatest service which can be rendered to any country is to add a useful plant to its culture.” Given the very real and pressing need to make food systems around the world more nutritious and more sustainable, an expanded version of Jefferson’s words continues to be relevant. We hope that this book contributes to increasing the interest in, and bolstering the efforts devoted to, adding well-conserved useful North American plants to global culture.

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Appendix 1
Map Methods and Occurrence Data Sources

Colin K. Khoury and Chrystian C. Sosa

The distribution maps in this book were created using occurrence (i.e., plant location/presence) information gathered from digitized herbarium records and genebank collections (i.e., passport/provenance) data, largely accessed via the Global Crop Wild Relatives Occurrence Database (CIAT 2017), Global Biodiversity Information Facility (GBIF 2017), and chapter author datasets. A full list of occurrence data providers follows this text. For taxa with few occurrence points (i.e., map coordinates) but with narrative information on location of occurrence, geo-referencing was performed via the GeoLocate web application (Tulane University 2017).

Coordinates were mapped and evaluated by chapter authors, with clearly incorrect data points deleted and additional data sought and added to the extent possible to reflect the known distributions of taxa. In some cases, available occurrence data did not sufficiently reflect the known distributions of taxa well enough for authors to be confident in their inclusion in the book; therefore, maps were not completed for these taxa.

Potential species distribution maps for taxa were modeled using the maximum entropy (Maxent) algorithm (Phillips et al. 2006), with unique occurrence locations and ecogeographic variables used as inputs. Ecogeographic variables included altitude and 19 "current" bioclimatic variables from the WorldClim database (Hijmans et al. 2005) and seven major edaphic drivers of plant species distributions with consistent data coverage throughout North America, obtained from ISRIC-World Soil Information (Hengl et al. 2014) (Table 1).

C. K. Khoury (✉)
USDA, Agricultural Research Service, Center for Agricultural Resources Research,
National Laboratory for Genetic Resources Preservation, Fort Collins, CO, USA

International Center for Tropical Agriculture (CIAT), Cali, Colombia
e-mail: colin.khoury@ars.usda.gov; c.khoury@cgiar.org

C. C. Sosa
International Center for Tropical Agriculture (CIAT), Cali, Colombia
Genetics and Biotechnology Laboratory, Plant and AgriBioscience Research Centre (PABC),
Ryan Institute, National University of Ireland Galway, Galway, Ireland
e-mail: c.sosaarango1@nuigalway.ie

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Table 1 Ecogeographic variables used for potential species distribution modeling

Variable number	Variable name	Units
0	Altitude	m
1	Annual mean temperature	°C
2	Mean diurnal temperature range	°C
3	Isothermality	N/A
4	Temperature seasonality (standard deviation)	°C
5	Maximum temperature of warmest month	°C
6	Minimum temperature of coldest month	°C
7	Temperature annual range	°C
8	Mean temperature of wettest quarter	°C
9	Mean temperature of driest quarter	°C
10	Mean temperature of warmest quarter	°C
11	Mean temperature of coldest quarter	°C
12	Annual precipitation	mm
13	Precipitation of wettest month	mm
14	Precipitation of driest month	mm
15	Precipitation seasonality (coefficient of variation)	%
16	Precipitation of wettest quarter	mm
17	Precipitation of driest quarter	mm
18	Precipitation of warmest quarter	mm
19	Precipitation of coldest quarter	mm
20	Bulk density	kg/m^3
21	Cation exchange capacity	cmol/kg
22	Percent clay	%
23	Organic carbon	g/kg
24	pH in H_2O	pH
25	Percent silt	%
26	Percent sand	%

For taxa with sufficient occurrence data (≥5 unique occurrences), a species-specific subset of the most important ecogeographic drivers of distributions was used in order to avoid overfitting (i.e., we removed highly correlated variables). To create the subsets, we used a nonlinear iterative partial least squares (NIPALS) algorithm to perform a principal component analysis (PCA), then identified those variables with the greatest contribution (>0.7 or <-0.7) to the first two principal components per taxon, and finally used a variance inflation factor (VIF) to select and use only those variables with a low degree of collinearity (Khoury et al. 2015). For taxa with fewer than five unique occurrences, all ecogeographic variables were employed.

Modeling was performed at a resolution of 2.5 arc-minutes (~5 km^2 cell size at the equator), employing 10,000 pseudo-absence background points within North America (that did not overlap with cells having presence locations) for model training, and clipped by measuring the shortest distance between the receiver operating characteristic curve (ROC curve) and the top-left corner of the plot (Liu et al. 2005). The final model was chosen among three variations: the mean and median of model replicate probabilities ($k = 10$) and the sum of thresholded areas of all model replicates, with the final choice determined by the area under the curve (AUC) (Khoury et al. 2015), true skill statistic (TSS) (Allouche et al. 2006; Georgopoulou et al. 2016), sensitivity, and specificity values.

To mitigate the challenges of underfitting due to a lack of signal between occurrence points and ecogeographic variables, particularly for species with few and/or dispersed presence locations, we constrained each final model using a native range boundary defined at the US county level as given in USDA PLANTS (USDA NRCS 2017) for taxa with such information and when such information was determined by the authors and modeling team to be sufficiently comprehensive, and at the state level as given in USDA GRIN Taxonomy for Plants (USDA, ARS National Plant Germplasm System 2017) for those species not listed in USDA PLANTS or when USDA PLANTS data was not sufficiently comprehensive. For those taxa not appearing in either database, we constrained the final model with a convex hull around presence points. As a final step, models were adjusted to exclude urban areas, water bodies, bare areas, and permanent snow and ice regions (ESA GlobCover 2005). Resulting models were again evaluated by chapter authors, who made the final decision on their inclusion in the book.

The ecogeographic data preparation and species distribution modeling were performed in R (R Core Team 2013), packages maptools (Bivand and Lewin-Koh 2014), rgdal (Bivand et al. 2014), SDMTools (van der Wal et al. 2014), raster (Hijmans 2014), sp (Pebesma and Bivand 2005; Bivand et al. 2013), dismo (Hijmans et al. 2013), plsdepot (Sanchez 2012), and usdm (Naimi 2015). Resulting spatial files were mapped in ArcMap (ESRI 2011) and in R packages ggmap (Kahle and Wickham 2013; Kahle and Wickham 2016) and ggplot2 (Wickham and Chang 2016).

For access to the occurrence data used in this book, as well as potential distribution models for individual taxa, please contact the editors.

List of Occurrence Data Providers

AAU (Aarhus University); ACAD (Philadelphia Herbarium at the Academy of Natural Sciences); Acadia (Acadia University); AGG (Australian Grains Genebank); Agriculture and Agri-Food Canada (Canadian Biodiversity Information Facility); ALA (University of Alaska Fairbanks Herbarium); Ales Lebeda; ALTA-VP (University of Alberta Vascular Plant Herbarium); Anymals.org (Museum für Naturkunde Berlin); ARIZ (University of Arizona Herbarium); ASC Deaver Herbarium (Northern Arizona University); ASU (Arizona State University Global Institute for Sustainability); AVH (Australian Virtual Herbarium); AVRDC (World Vegetable Center); AWC (Arizona Western College Herbarium); BAYRT (via BIEN); BC (Royal BC Museum); BCMEX (University of Baja California Herbarium); BDI (Putnam Museum herbarium); BGBM (Botanic Garden and

Botanical Museum Berlin-Dahlem); Biodiversity Institute of Ontario; Bioimages; Bioversity International; BISON (United States Geological Survey); BLM (Bureau of Land Management); BM (British Museum of Natural History); BNHM-UCB (Berkeley Natural History Museum); BOUM (Muséum d'Histoire Naturelle de Bourges); BPBM (Bernice Pauahi Bishop Museum); BRIT (Botanical Research Institute of Texas); BRY (Brigham Young University Herbarium); BU (Brock University); BUT (Butler University Friesner Herbarium); California State University Chico; CAN (National Herbarium of Canada); CANB (National Herbarium of New South Wales); CAS (California Academy of Sciences); CATIE (Centro Agronómico Tropical de Investigación y Enseñanza); CCH (Consortium of California Herbaria); CDA (California Department of Food and Agriculture Herbarium); CEN (EMBRAPA Recursos Geneticos e Biotecnologia – CENARGEN Herbario); CEPLAC (Comissão Executiva do Plano da Lavoura Cacaueira); CERETI (via BIEN); CHAP (Universidad Autonoma Chapingo Herbario); CHIC (University of Illinois Herbarium); CHR (Landcare Research); CHSC (the Chico State Herbarium); CIAT (International Center for Tropical Agriculture a global database for the distributions of crop wild relatives); CIB (Universidad Veracruzana Herbario); CIBNOR (Centro de Investigaciones Biológicas del Noroeste Herbario); CIB-UAEH (Centro de Investigaciones Biológicas Universidad Autónoma del Estado de Hidalgo); CIB-UV (Centro de Investigaciones Biológicas Universidad Veracruzana); CIBYC-UAEM (Centro de Investigación en Biodiversidad y Conservación Universidad Autónoma del Estado de Morelos); CICB-UAT (Centro de Investigación en Ciencias Biológicas de la Universidad Autónoma de Tlaxcala); CICY (Centro de Investigacion Cientifica de Yucatan A.C. Herbario); CIHS-UAC (Universidad Autónoma de Campeche); CIIDIR-DURANGO/CIIDIR-IPN-DGO (Instituto Politecnico Nacional Herbario Durango); CIIDIR-IPN (Instituto Politecnico Nacional Herbario); CIMI (Centro Interdisciplinario de Investigacion para el Desarrollo Integral Regional Michoacan Herbario); CIMMYT (International Center for the Improvement of Maize and Wheat); CIP (International Potato Center); Claire Heinitz; CLARK-A (Clark Atlanta University); CLEMS (Clemson University Herbarium); CM (Carnegie Museums); CMN (Canadian Museum of Nature); CNH (Consortium of Northeastern Herbaria); CNS-UT (College of Natural Sciences University of Texas at Austin); COA (Botanical Garden of Córdoba); COAH (Instituto Amazonico de Investigaciones Cientificas SINCHI Herbario Amazonico Colombiano); COL (Universidad Nacional de Colombia); COLO (University of Colorado Museum Herbarium); CONABIO (La Comisión Nacional para el Conocimiento y Uso de la Biodiversidad); CONN (University of Connecticut Herbarium); Consortium of California Herbaria; Coppens; COTECOCA (Comisión Técnico Consultiva de Coeficientes de Agostadero); CP (Faculty of Life Sciences University of Copenhagen Herbarium Botany Group); CP-CT (via BIEN); CPNWH (Consortium of Pacific Northwest Herbaria); CRIA (Centro de Referência em Informação Ambiental); CS (Colorado State University Herbarium); CUVC (Universidad del Valle Herbario Luis Sigifredo Espinal-Tascon); CZE National PGR Inventory; DACB-UJAT (División Académica de Ciencias Basicas Universidad Juárez Autónoma de Tabasco); DAV (University of California Davis); DBG (Denver

Botanic Gardens); DES (Desert Botanical Garden Herbarium); DICTUS-USON (Departamento de Investigaciones Científicas y Tecnológicas de la Universidad de Sonora); DS (California Academy of Sciences Dudley Herbarium); DSC (Delta State University Herbarium); DSUND (Dickinson State University Herbarium); E (Royal Botanic Garden Edinburgh); EB-BUAP (Escuela de Biología Benemérita Universidad Autónoma de Puebla); ECOSUR (El Colegio de la Frontera Sur); ECPGR (European Cooperative Programme for Plant Genetic Resources); EIU (Eastern Illinois University Stover-Ebinger Herbarium); EKY (Eastern Kentucky University Herbarium); EMBL-EBI (European Bioinformatics Institute); EMC (Eastern Michigan University Herbarium); ENCB (Instituto Politecnico Nacional Herbario Mexico); ENLC (Eastern Nevada Landscape Coalition); ENMU (Eastern New Mexico University Herbarium); EST (via BIEN); EURISCO (European Search Catalogue for Plant Genetic Resources); F (Field Museum); FB-UMSNH (La Universidad Michoacana de San Nicolás de Hidalgo); FCB-UAEM (Facultad de Ciencias Biológicas Universidad Autónoma del Estado de Morelos); FCF-UANL (Facultad de Ciencias Forestales Universidad Autónoma de Nuevo León); FCN-UAQ (Facultad de Ciencias Naturales Universidad Autónoma de Querétaro); Universidad Nacional de la Plata; FC-UABC (Facultad de Ciencias Universidad Autónoma de Baja California); FC-UNAM (Universidad Nacional Autónoma de México); Fernando de la Torre; FESI-UNAM (Universidad Nacional Autónoma de México); FFPRI (National Institute of Genetics ROIS); FITECMA-UMSNH (Universidad Michoacana de San Nicolás de Hidalgo); FLAS (Florida Museum of Natural History); Flora Nacional Cumbres Monterrey; FML (Fundacion Miguel Lillo); FMVZ-UADY (Campus de Ciencias Biológicas y Agropecuarias Universidad Autónoma de Yucatán); FR (Senckenberg); FRT (via BIEN); FSU (Florida State University Herbarium); FTG (Fairchild Tropical Botanic Garden); G (Conservatoire et Jardin botaniques de la Ville de Genève); GA (University of Georgia Herbarium); GB (University of Gothenburg Herbarium); GBIF (Global Biodiversity Information Facility); GCNP (Grand Canyon National Park Herbarium); GDA (Universidad de Granada Herbario); GEO (Tag der Artenvielfalt); GMDRC (Granite Mountains Desert Research Center Herbarium); GOET (Georg-August-Universität Göttingen Albrecht-von-Haller-Institut für Pflanzenwissenschaften Abteilung Systematische Botanik); Gouvernement du Quebec; Greater Good; GUA (DIVEA, DEP, FEEMA Herbario Alberto Castellanos Rio de Janeiro Brazil); GZU (University of Graz Institute of Plant Sciences); H (Finnish Museum of Natural History); H.A. Stephens Herbarium; HAL (Martin-Luther-Universitet Herbarium); HAM (Royal Botanical Gardens Herbarium Canada); HUH (Harvard University Herbaria); HAST (Biodiversity Research Center Academia Sinica Herbarium Taiwan); HBC (Herbarium Bradeanum Herbario Brazil); HBG (Biozentrum Klein-Flottbek Herbarium Germany); HCIB (Centro de Investigaciones Biologicas del Noroeste S. C. Herbario Mexico; Herbarium GeoBHinton; HIBG (High Plains Herbarium at Chadron State College); HNT (Huntington Botanical Gardens Herbarium); HPC (Howard Payne University Herbarium); HSC (Humboldt State University Vascular Plant Herbarium); HU (University of Zhejiang Herbarium); IAC (Instituto Agronômico); IB-CUCBA-UDG (Centro Universitario de Ciencias Biológicas y

Agropecuaria Universidad de Guadalajara); IBT (Instituto de Botânica); IBUG (Universidad de Guadalajara Herbario); IBUNAM (Arboles de la Península de Yucatán/ Flora del Distrito de Tehuantepec/Oaxaca y Familia Asteraceae en México); ICBG (Agentes Bioactivos de Plantas Desérticas de Latinoamérica); IE (Comisión nacional para el conocimiento y uso de la biodiversidad); IEA-UAT (Instituto de Ecologia Aplicada Universidad Autónoma de Tamaulipas); IEB (Instituto de Ecologica A.C. Herbario del Centro Regional del Bajio); IE-DF/UNAM (Arboles y Arbustos Nativos para la Restauración Ecológica y Reforestación de México); IEX (via BIEN); IF (Instituto Florestal); IHNE (Instituto de Historia Natural y Ecología Chiapas Mexico); IIZD-UASLP (Instituto de Investigación de Zonas Desérticas Universidad Autónoma de San Luis Potosí); ILLS (Illinois Natural History Survey Herbarium); IMC y P (via BIEN); IMECBIO-UDG (Departamento de Ecología y Recursos Naturales Universidad de Guadalajara); iNaturalist; INECOL (Instituto de Ecología A.C.); INHS (Illinois Natural History Survey); INIFAP/ INIFAP-CECOY/INIFAP-SARH/INIFAP-UPN (Instituto Nacional de Investigaciones Forestales y Agropecuarias Mexico); INIREB (Instituto Nacional de Investigaciones En Recursos Bióticos Mexico); INPA (Instituto Nacional de Pesquisas da Amazônia); IPA (Instituto Agronômico de Pernambuco); IPN (Instituto Politécnico Nacional); IRENAT-CP (Instituo de Rescursos Naturales Mexico); IRN-CP (via BIEN); IRVC (Irvine Herbarium); JABOT (Jardim Botânico do Rio de Janeiro); James Frelichowski; Jardin Botanique de Montréal; JBRJ (Rio de Janeiro Botanical Garden Herbarium Collection); JEMEZ (Jemez Mountain Herbarium); JEO (via BIEN); JOTR (Joshua Tree National Park Herbarium); JROH (Oakmead Herbarium and Collections of Jasper Ridge Biological Preserve); K (Royal Botanic Gardens Kew); K MSB (Royal Botanic Gardens Kew Millennium Seed Bank Partnership); KANU (University of Kansas R. L. McGregor Herbarium); Karen Williams; KHD (Kathryn Kalmbach Herbarium); Kim Hummer; KNK (Northern Kentucky University Herbarium); KNWR (Arctos); KSP (Pittsburg State University Theodore M. Sperry Herbarium); KSTC (Emporia State University); KU (University of Kansas Biodiversity Institute); LA (University of California Herbarium Los Angeles); Laura Marek; LD (Lund Botanical Museum); LEGON-GC (Ghana Biodiversity Information Facility (GhaBIF)); LISC (Instituto de Investigação Científica Tropical Portugal); LISU (National Museum of Natural History and Science University of Lisbon); LL (University of Texas at Austin Lundell Herbarium); LSU (Louisiana State University Herbarium); M (Botanische Staatssammlung Munchen Herbarium); MA (CSIC-Real Jardín Botánico); MABA (New Mexico Natural History Institute Herbarium); MACN (Museo Argentino de Ciencias Naturales); MADUG; MANCH (University of Manchester Herbarium); MARY (University of Maryland Norton-Brown Herbarium); MB (Philipps University Marburg Herbarium Marburgense); McDonald & Austin 1990; Melanie Harrison; MESA (Walter Almond Kelley Herbarium); Mexico Burge; MexSEINet; MEXU (Universidad Nacional Autonoma de Mexico Herbario Nacional); MICH (University of Michigan Herbarium); Midwest Herbaria; MIREN_ETH (Mountain Invasion Research Network); MISS (University of Mississippi Pullen Herbarium); MISSA (Mississippi Entomological Museum); MISU (Minot State University

Herbarium); MMNS (Mississippi Museum of Natural Science Herbarium); MNA (Museum of Northern Arizona); MNCH (University of Oregon Museum of Natural and Cultural History); MNCR (Museo Nacional de Costa Rica); MNHN (Museum national d'Histoire naturelle); MO (Missouri Botanical Garden); MOR (Morton Arboretum Herbarium); MPM (Milwaukee Public Museum); MSC (Michigan State University Herbarium); MT (Universite de Montreal Herbier Marie-Victorin); MTTHORT (via BIEN); MUR (Murray State University Herbarium); MWI (R.M. Myers Herbarium); NA (United States National Arboretum USDA/ARS Herbarium); Naturalis (Naturalis Biodiversity Center); Naturgucker (naturgucker.de); NCSC (North Carolina State University Herbarium); NCU (University of North Carolina Herbarium); ND (University of Notre Dame Greene/Nieuwland Herbarium); NHM UK (Natural History Museum UK); NHN Leiden (National Herbarium of the Netherlands); NMC (New Mexico State University Herbarium); NMCR (New Mexico State University Range Science Herbarium); NMSU (Northwest Missouri State University Herbarium); NordGen (Nordic Genetic Resource Center); NPS (Inventory and Monitoring Program – NPSpecies Park Species Lists); NSW (the Royal Botanic Gardens and Domain Trust); NTSRV (NatureServe); NYBG (New York Botanic Garden); O (Natural History Museum University of Oslo); OAC (University of Guelph OAC Herbarium); OBI (Cal Poly State University Herbarium); OHN (Biological Museum, Oskarshamn Herbarium); OKLA (Oklahoma State University Herbarium); OSA (National Museum of Nature and Science Japan); OSC (Oregon State University); OTS (Organization for Tropical Studies Herbarium); Pablo Jourdan; PARADA; PBDB (Paleobiology Database); PH (Academy of Natural Sciences Herbarium Philadelphia); Plants of Taiwan; PMT (via BIEN); POM (Pomona College Herbarium); Programa de repatriacion de datos de ejemplares mexicanos; QFA (Universite Laval Herbier Louis-Marie); QMEX (Universidad Autonoma de Queretaro Centro Universitario Herbario); R. L. McGregor Herbarium Vascular Plants Collection; Reilley; RENO (University of Nevada Herbarium); RM (University of Wyoming Rocky Mountain Herbarium); RMBL (Rocky Mountain Biological Laboratory); RMCA-Metafro-Infosys (via BIEN); ROM (Royal Ontario Museum (ROM)); Rosalinda Gonzalez Santos; RSA/RSABG (Rancho Santa Ana Botanic Garden Herbarium); SALA (Dep. of Plant Biology Botany Faculty of Pharmacy Univ. Salamanca); SANBI (South African National Biodiversity Institute); SANT (Herbario SANT Universidade de Santiago de Compostela); SBBG (Santa Barbara Botanic Garden Herbarium); SCFS (Sagehen Herbarium); SCIR (Santa Cruz Island Reserve Herbarium); SD/SDNHM (San Diego Natural History Museum Herbarium); SDSU (San Diego State University); SEINET (Regional Networks of North American Herbaria); SERBO AC (via BIEN); SEV (Department of Plant Biology and Ecology University of Seville); SFV (California State University Northridge); SI (Museo Botanico Herbarium Argentina); SINGER (System-Wide Information Network on Genetic Resources); SJNM (San Juan College Herbarium); SJSU (Carl W. Sharsmith Herbarium San Jose State University); SMNK (State Museum of Natural History Karlsruhe); SNM (Western New Mexico University Dale A. Zimmerman Herbarium); SNSNMC (Société des Sciences Naturelles et Mathématiques de

Cherbourg); Sonoran Atlas; Stebbins 2013; STU (Staatliches Museum fur Naturkunde Herbarium); SUU (Southern Utah University's Herbarium); Swain 2012; TAIF (Taiwan Forestry Research Institute); TAMU (Texas A&M University Herbarium); TEX (University of Texas at Austin Herbarium); TLAX (Universidad Autónoma de Tlaxcala); TLMF (Tiroler Landesmuseum Ferdinandeum); TRH (Norwegian University of Science and Technology Herbarium); TROM (UiT The Arctic University of Norway); Tropicos; TROY (Troy University Herbarium); TTRS (Tall Timbers Research Station Herbarium); U (National Herbarium of the Netherlands Herbarium Utrecht); UA (University of Alabama Biodiversity and Systematics); UAAAN (Universidad Autonoma Agraria Antonio Narro); UABC (Universidad Autonoma de Baja California); UACh (Universidad Autónoma de Chihuahua); UAG (University of Guadalajara); UAM (University of Alaska Museum of the North); UAM (University of Arkansas at Monticello Herbarium); UAN (Universidad Autónoma de Nayarit); UANL (Universidad Autónoma de Nuevo León); UAQ (Universidad Autónoma de Querétaro); UAS (Universidad Autonoma de Sinaloa Herbario Jesus Gonzalez Ortega); UBC (University of British Columbia Herbarium – Vascular Plant Collection); UC/JEPS (University of California Jepson Herbarium); UCB (University and Jepson Herbaria); UCBG (University of Botswana Herbarium); UCD (University of California Davis); UCMC (University of Colorado Museum of Natural History); UCMP (University of California Museum of Paleontology); UConn (University of Connecticut); UCR (University of California Riverside); UCS (Universidade de Caxias do Sul); UCSB (University of California Santa Barbara; UCSC (University of California Santa Cruz); UEFS (Universidade Estadual de Feira de Santana); UFMG (Universidade Federal de Minas Gerais); UFPR (Universidade Federal do Paraná); UFRGS (Universidade Federal do Rio Grande do Sul); UFSC (Universidade Federal de Santa Catarina); Uglasiirsity; UM (Herbarium of Université de Montpellier 2 Institut de Botanique); UMN (University of Minnesota Herbarium); UNA (University of Alabama Herbarium); UNAM (National Autonomous University of Mexico); UNESP/FCA (Universidade Estadual Paulista); UNICACH (Universidad de Ciencias y Artes de Chiapas); UNICAMP (Universidade Estadual de Campinas – Instituto de Biologia); Universidad de Antioquia; Universite de Montreal Biodiversity Centre; Université Laval; University of Alberta Museums; University of Arizona; University of Lethbridge; University of Manitoba; UNM (Museum of Southwestern Biology); UPS (Uppsala University Herbarium); US (National Museum of Natural History Smithsonian Institution); USCH (University of South Carolina Herbarium); USDA NPGS GRIN (USDA National Plant Germplasm System Genetic Resources Information Network); USDA PLANTS Database; USF (USF Water Institute); USFS (United States Forest Service); USMS (University of Southern Mississippi Herbarium); USNM (Smithsonian); USON (Universidad de Sonora Herbario); USP (Universidade de São Paulo); USU (Utah State University); USUUB (Utah State University Uintah Basin Herbarium); UT (University of Utah Garrett Herbarium); UTC (Utah State University Intermountain Herbarium); UTEP (University of Texas at El Paso Biodiversity Collections); UVSC (Utah Valley University Herbarium); UWBM (University of Washington Burke Museum);

UWSA (University of Wisconsin); UWSP (University of Wisconsin Stevens Point); VAL (University of Valencia); VegBank – Vegetation Plot Database; VIT (Natural History Museum of Alava (Museo de Ciencias Naturales de Álava)); VSC (Valdosta State University Herbarium); W (Natural History Museum Vienna Herbarium); WAG (Wageningen University National Herbarium Nederland Wageningen University branch); WASH; WCUH (Western Carolina University Herbarium); Wildlife Sightings; WILLI (Herbarium of the College of William & Mary); Wilson et al. 2017; WIS (University of Wisconsin Herbarium); WOODS; WTU (University of Washington Herbarium); WU (Universitat Wien Herbarium); WVU (West Virginia University); YM-YOSE (Yosemite National Park Herbarium); YPM (Yale University Peabody Museum); Z (Herbaria of the University and ETH Zürich (Z + ZT)); ZSS (Sukkulenten-Sammlung Zurich Herbarium).

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Common Name Index

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