Chapter 14
Crop Wild Relatives of Sunflower in North America

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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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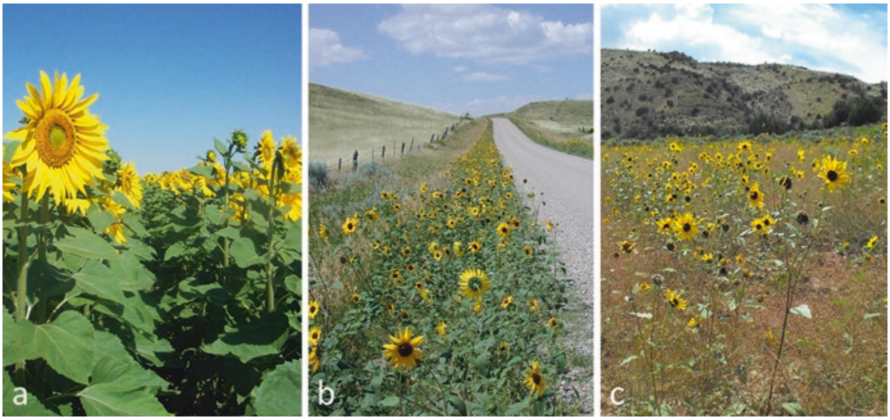

Fig. 14.1 *Helianthus annuus* L. (**a**) Cultivated sunflower field near Seville, Spain, Wild *H. annuus* in typical habitats, (**b**) disturbed roadside southwest of Chugwater, WY, (**c**) disturbed hillside field (possibly previous landslide) southwest of Big Water, UT

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

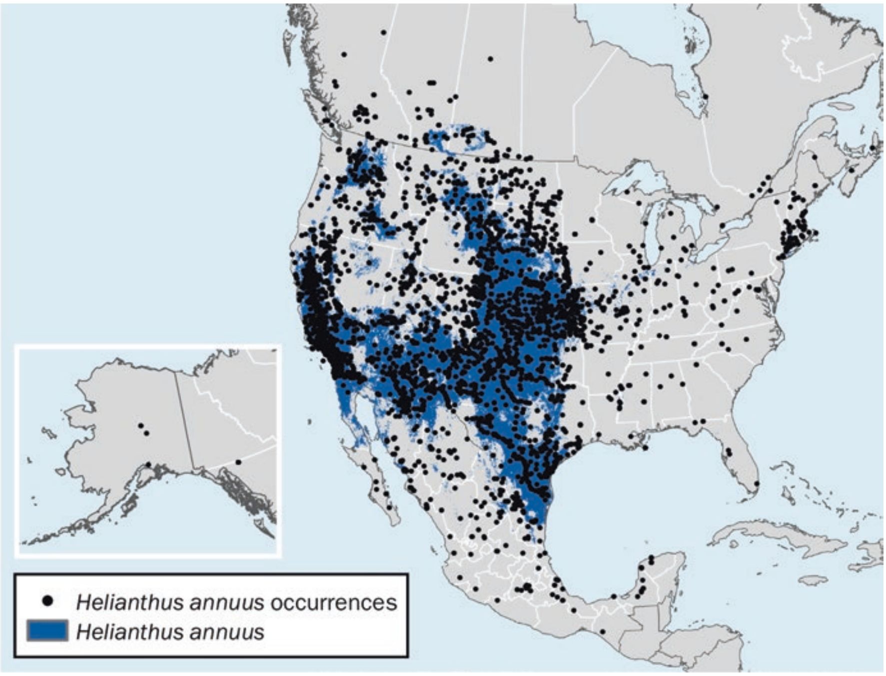

Fig. 14.2 The distribution of wild *H. annuus* L. across North America indicating occurrence points (black circles) and the geographic area of similar climate and soil (blue shading) defined by those occurrence points. The model used to generate the wild *H. annuus* distribution was limited to native 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.

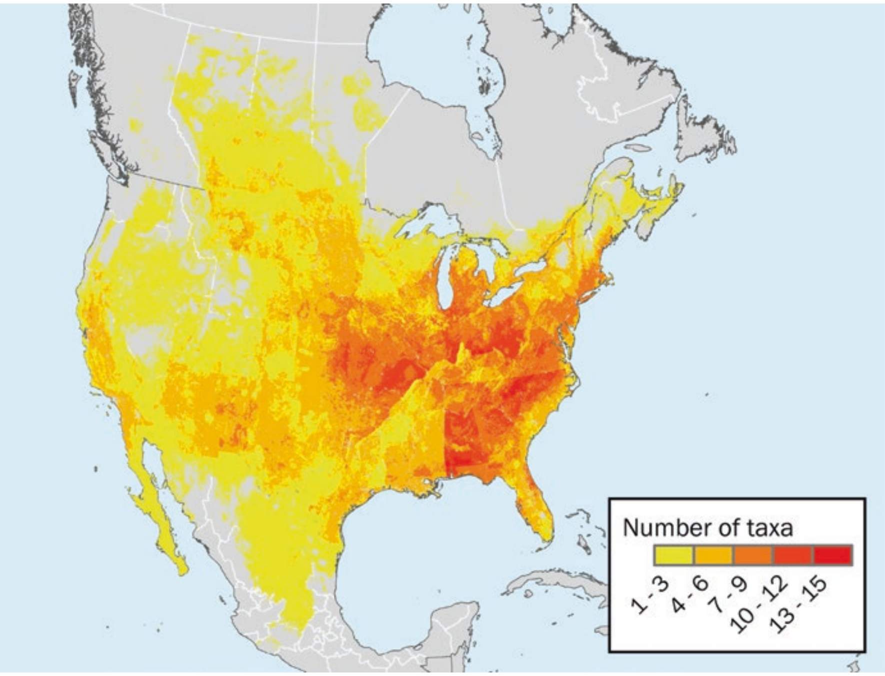

Fig. 14.3 Heat map indicating the spread of all taxa of wild sunflowers across North America. Colors indicate the number of different species/taxa not specific species. Full methods for map generation and occurrence data are given in Appendix 1

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

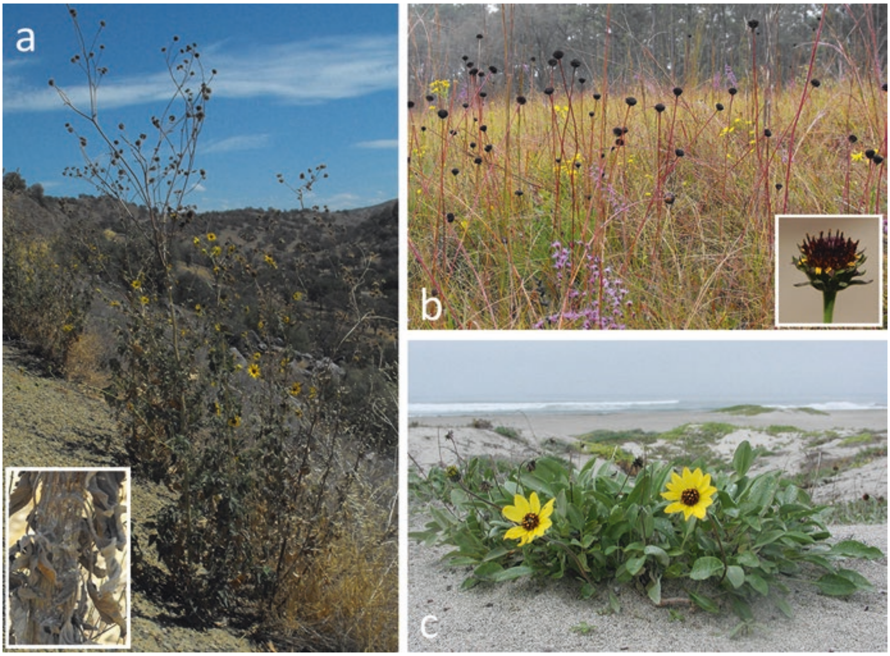

Fig. 14.4 (**a**) *H. winteri* J. C. Stebbins, type locality east of Fresno, CA; insert, older, woody stem with exuded resin drops, (**b**) *H. radula* (Pursh) Torr. & A. Gray longleaf pine habitat, Ft. Stewart, GA; insert, this species typically lacks ray flowers although some plants in some populations 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

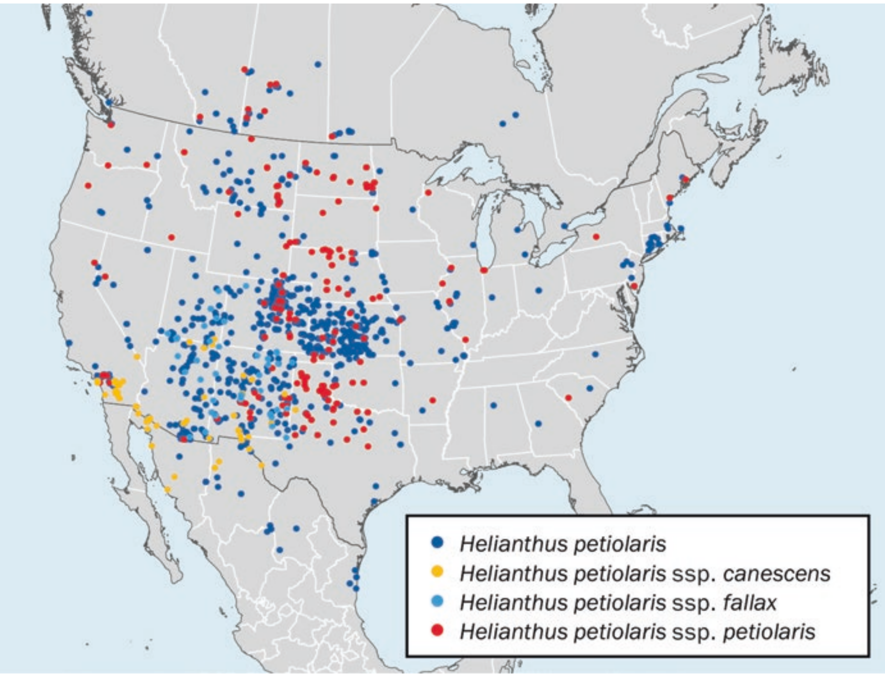

Fig. 14.5 The distribution of *H. petiolaris* Nutt. across North America indicating occurrence points for each of the three subspecies as well as occurrences for which a subspecies was not defined. Full methods for map generation and occurrence data are given in Appendix 1

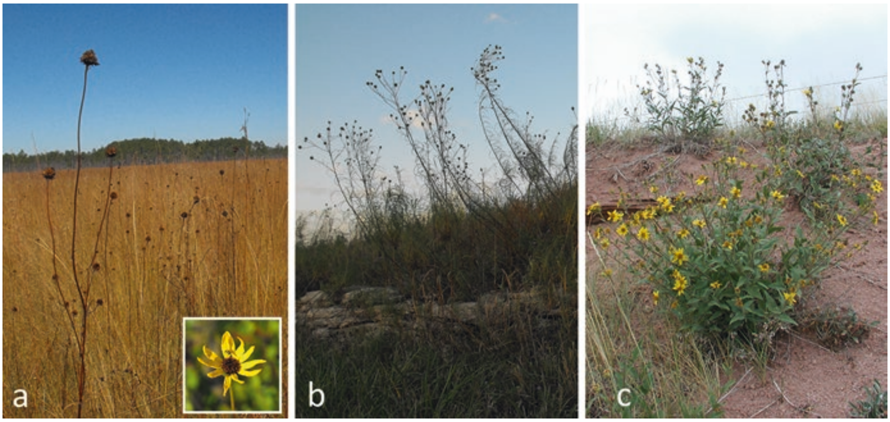

Fig. 14.6 (**a**) *H. heterophyllus* Nutt. expansive population past flowering north of Apalachicola, FL; insert: *H. heterophyllus* flower in MS west of Perkinston, (**b**) *H. salicifolius* A. Dietr., limestone ledge south of Garnett, KS, (**c**) *H. pumilus* Nutt., roadside northwest of Tie Siding, WY

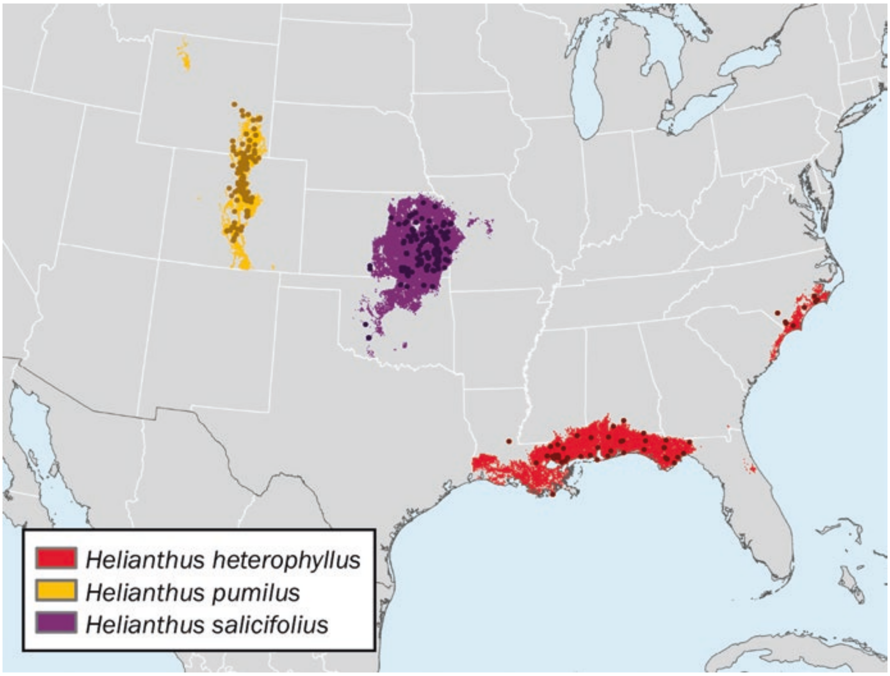

Fig. 14.7 The distribution of three perennial sunflower species (images from sampled populations of these species in Fig. 14.6) indicating occurrence points and the geographic area of similar climate and soil defined by those occurrence points; *H. heterophyllus* (dark red circles and red shading), *H. 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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