



# GLOBAL STRATEGY FOR THE CONSERVATION AND USE OF SUNFLOWER (*HELIANTHUS ANNUUS*) GENETIC RESOURCES

With support from



International Treaty  
on Plant Genetic Resources  
for Food and Agriculture



Federal Ministry  
of Food  
and Agriculture

# Global Strategy for the Conservation and Use of Sunflower (*Helianthus annuus*) Genetic Resources

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## COVER PHOTO

Sunflowers grow in field in Fargo, ND. USDA photo by Bruce Fritz

## ACKNOWLEDGEMENTS

The development of the Global Strategy for the Conservation and use of Sunflower Genetic Resources (GSCS) was funded by the German Federal Ministry of Food and Agriculture (BMEL) as part of the 3-year project led by the Crop Trust: "Breathing new life into the Global Crop Conservation Strategies: Providing an Evidence Base for the Global System of *Ex Situ* Conservation of Crop Diversity."

The Crop Trust also cooperated with the Secretariat of The International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA) in the development of this document.

Our deepest gratitude to the many genebank managers, curators, and administrators who took the time to respond to the Sunflower Strategy Questionnaire and/or helped disseminate the questionnaire to other major sunflower collections: Belul Gixhari, Daniel Álvarez, Katherine Whitehouse, Gergana Desheva, Juliano Gomes Pádua, Dallas Kessler, Petra Hlásná Čepková, Ulrike Lohwasser, Álvaro Monteros-Altamirano, Isaura Martín, Marie-Claude Boniface, John Dickie, Mangesh Dudhe, Fabiano Miceli, Matsikoane Sefotho, Hassan Ouabbou, Ohn Mar Aung, Randi Seljåsen, Maria Joița-Păcureanu, Silvia Străjeru, Vera Gavrilova, Sreten Terzić, Erik de Vahl, MAher Medini, Katerina Vedmedeva, Laura F. Marek, Mukombwe Graybill, Davidzo Seka. Thanks to those curators and breeders who participated in the Sunflower Strategy Virtual Consultation Series: Sally L. Norton, Daniela Valkova, Ulrike Lohwasser, Claudia Krebs, Ohn Mar Aung, Dan Sandru, Vera Gavrilova, Galina Khafizova, Sreten Terzić, Erik de Vahl, Maher Medini, Katerina Vedmedeva, Seka Davidzo, Aluana Goncalves de Abreu, Cláudio Guilherme Portela de Carvalho, Regina Maria Villas Bôas de Campos Leite, Axel Diederichsen, Dallas Kessler, Fabiano Miceli, Froylan Rincón, Maria Joița-Păcureanu, Vera Gavrilova, Galina Khafizova, Brent Hulke, Laura F Marek, Gerald Seiler, Federico Condón, Onismus Chipfunde. The strategy was also improved by discussions with, and feedback from: Dan G. Bock, Dylan H. Burge, Pauline Duriez, and Loren H. Rieseberg. The teams at the USDA (Brent Hulke, Laura Marek and Gerald Seiler) and the IFVC (Sreten Terzić),

## DISCLAIMER

This document, developed with the input of many experts, aims to provide a framework for the efficient conservation and effective use of globally important collections of sunflower genetic resources. The Global Crop Diversity Trust (the Crop Trust) provided support for this initiative and considers this document to be an important context for guiding the allocation of its resources. However, the Crop Trust does not take responsibility for the relevance, accuracy, or completeness of the information in this document and does not commit to funding any of the priorities identified. This strategy document, dated May 2023 is expected to continue to evolve and be updated as circumstances change and/or new information becomes available.

In case of any specific questions or comments, please direct them to Peter Giovannini, [peter.giovannini@croptrust.org](mailto:peter.giovannini@croptrust.org).

## DISCLAIMER ABOUT THE ESTIMATED NUMBERS OF ACCESSIONS PRESENTED IN THE STRATEGY

The numbers of accessions presented in the text and tables of this strategy are the best estimates the authors were able to make at the time of writing based on the data available and the methods used. Such estimates can differ depending on the sources of data and their completeness, the time of the analyses, and the assumptions made in carrying out the analyses.

## SUGGESTED CITATION

Drummond, EBM, Bramel, P., Lohwasser U., and P. Giovannini. 2023. Global Strategy for the Conservation and Use of Sunflower (*Helianthus annuus*) Genetic Resources. Global Crop Diversity Trust. Bonn, Germany. DOI: [10.5281/zenodo.8192536](https://doi.org/10.5281/zenodo.8192536)

## DOI

[10.5281/zenodo.8192536](https://doi.org/10.5281/zenodo.8192536)



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## Abbreviations and Acronyms

<b>CWR</b>	crop wild relative
<b>DNA</b>	deoxyribonucleic acid
<b>FAO</b>	Food and Agriculture Organization of the United Nations
<b>GBIF</b>	Global Biodiversity Information Facility
<b>GBS</b>	genotyping by sequencing
<b>GWAS</b>	genome-wide association study
<b>GS</b>	genomic selection
<b>ITPGRFA</b>	International Treaty on Plant Genetic Resources for Food and Agriculture
<b>MAS</b>	marker-assisted selection
<b>MTA</b>	material transfer agreement
<b>NGS</b>	next-generation sequencing
<b>PCR</b>	polymerase chain reaction
<b>PGRFA</b>	plant genetic resources for food and agriculture
<b>QTL</b>	quantitative-trait locus
<b>SMTA</b>	Standard Material Transfer Agreement
<b>SNP</b>	single-nucleotide polymorphism
<b>USDA</b>	United States Department of Agriculture



## EXECUTIVE SUMMARY

The genus *Helianthus* includes about 50 species native to North America (Schilling 2006, Heiser et al. 1969, Schilling & Heiser 1981). Native American people domesticated sunflower (*Helianthus annuus*) from wild *H. annuus*, which still exists today in parts of Canada, the United States, and Mexico.

The average annual world production of sunflower seeds between 2016–2021 was estimated at around 52 million metric tons, covering over 27 million hectares in 73 countries. More than half of the world production is concentrated in Ukraine and Russia.

The process of developing this Global Strategy for the Conservation and Use of Sunflower Genetic Resources included: conducting a literature review, retrieving and analyzing accession-level information from open databases, and conducting a survey and virtual consultations with sunflower collection curators.

The survey questionnaire was circulated to 28 institutes holding “large” collections and 32 institutes holding “small” collections. A total of 17 large collections returned questionnaires. Ten of the “small” collections returned a full survey.

Overall, the survey respondents conserved about 77% of the estimated total number of accessions globally.

Accession information provided by other curators and retrieved from the literature was used for two large collections that did not respond to the questionnaire.

In the compiled data, 40,501 accessions were identified from 107 institutes. Nineteen institutions conserve about 90% of the total *Helianthus* accessions held globally and 89% of the accessions of *Helianthus* wild species held globally. The USDA collection has the largest and most diverse collection of these other *Helianthus* species.

Two described species are not currently conserved *ex situ*: *Helianthus inexpectatus* D. J. Keil & Elvin, and *Helianthus x intermedius* R. W. Long. Also, the annual *Helianthus* species are generally not well conserved, with seven of the 12 species having poor representation in the global system.

The current global system of conservation and use of sunflower diversity is generally insecure, with a number of poorly resourced operations, limited availability of seed to all users, limited online sharing of accession-level information, and limited engagement of conservers and users globally, nationally, and locally. Some of these weaknesses are due to the fluctuating priority given to sunflower by international donors, national governments, public and private

researchers, local authorities, farmers, urban markets, and consumers. Any decline in priority is a risk not only to *ex situ* conservation but also to the continued conservation of diversity in farmers' fields. If and when the priority of the crop rises again, there may not be the diversity available to take advantage of the opportunity of the increased demand.

However, the current global system for the conservation of sunflower genetic resources does have some advantages that can be built upon. There are at least 12 genebanks with experience and expertise that other conservers can turn to for help and guidance, in their efforts to meet international standards. These genebanks, especially that of USDA, can also serve as conveners in global efforts to increase the security of conservation, adopt new technology and methods, enhance capacity and expertise on sunflower and collectively address some of the major constraints to a more effective and sustainable global system. These genebanks can also take on leadership in advocacy and communication on the importance of conservation and use of sunflower diversity. Another strength of the current system is the considerable national and local capacity for conservation in North America, where the largest national collection is located, which increases the opportunities for expanding the secure conservation of landraces and most of the wild species

Recommendations and priority actions were identified that aim to provide a framework for the efficient conservation and effective use of globally important collections of sunflower genetic resources. These are:

**Establish a global international advisory group (IAG) for the engagement of key collection holders and main users of sunflower genetic resources, and to lead the implementation of agreed priority activities.** It is suggested that the IAG should work closely with the USDA Crop Germplasm Committee for sunflower to implement the recommendations in this strategy.

**Establish a partnership among North American countries and address collection gaps for cultivated landraces and CWR:** Future field research and extensive collections are needed to fully document the *Helianthus* species in Mexico, including: their abundance and distribution; genetic diversity and population structure; and morphological variation. Similarly, little recent collecting activity has gone into surveying the northern end of the range for *H. annuus* in Canada. The other priority gaps in *ex situ* conservation are the wild species that have a small number of accessions conserved in genebanks, have a small distribution or/and an alarming (or unknown) *in situ* conservation status. A comprehensive collecting, multiplication and safety duplication plan should be developed and put in place for these CWR.

**Safety backup of cultivated and CWR accessions:**

It is recommended that all CWR accessions that are not safety duplicated should be sent to the USDA for regeneration and safety backup. Additionally, if possible, a safety duplicate should also be deposited at Svalbard Global Seed Vault.

**Rationalize the global sunflower collection and increase the accessibility of genetic diversity from CWR, landraces, and open-pollinated varieties: more can be done to facilitate the rationalization and use of the diversity that is conserved in *ex situ* collections through:** (a) increasing accession-level data that is accessible on international PGRFA portals and its completeness, and using digital object identifiers (DOIs), (b) phenotyping and genotyping together with screening for abiotic/biotic stress resistance to get detailed information about the genebank accessions, (c) increased data availability and (d) the development of a minimum descriptor list to stimulate the generation of more data.

**Hold a meeting to discuss the future needs for conservation and use with key representatives of the users.**

The blazing Sunflower, black and bold,  
Burns yet to win the sunset's gold,





Sunflowers in Argentina.  
Photo: Luis Salazar/Crop Trust

# 1 INTRODUCTION TO THE STRATEGY

The development of this Global Strategy for the Conservation of Sunflower Genetic Resources (GSCS) was funded by the Government of Germany (BMEL) as part of the three-year project led by the Crop Trust: “Breathing new life into the Global Crop Conservation Strategies: Providing an Evidence Base for the Global System of *Ex situ* Conservation of Crop Diversity.” The Crop Trust also cooperated with the Secretariat of the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA) in the development of this document. This project aims both to update some of the 26 global crop conservation strategies existing pre-2019 and to develop additional conservation strategies for new crops and/or crop groups. In October 2019, a project initiation meeting sought the advice of crop experts worldwide to select these new crops and/or crop groups; sunflower (*Helianthus* spp.) was one of the crops selected. This strategy provides an assessment of the status of conservation and use of sunflower genetic resources and concludes by outlining recommendations and priority actions to strengthen the global system for the conservation of this crop genetic resources.

The following steps were undertaken in the development of this conservation strategy:

1. The *Standard Model Outline for Crop Strategies*, created for the Crop Trust in 2019, was used to guide the content, format, and structure of the draft GSCS document.
2. A literature review was conducted to compile background information on the sunflower oilseed and confectionary crop (*Helianthus annuus* L.), including its economic importance, domestication and origins, dispersal, and current patterns of use. The literature was also used to identify major sunflower collections worldwide, as well as to detail each collection and its activities, purpose, and patterns of use. To examine sunflower genetic resources more broadly, information (taxonomy, phylogenetic relationships, centres of diversity, use in breeding, etc.) was also compiled for the wild relatives (*Helianthus* spp.) which form the crop’s gene pools.
3. International, regional, and national collections of sunflower (*Helianthus* spp.) germplasm were identified by searching global plant genetic resource (PGR) databases, including Genesys and WIEWS



(FAO), which also incorporate information from EURISCO (ECPGR) and GRIN-Global (USDA). Further collections were identified from the literature and from consultation with sunflower experts. A database was compiled to document the names and addresses of each collection purportedly holding more than ten sunflower accessions. Manual web searches were used to identify the curator of each collection and their contact information; if these data were not publicly available, assistance was sought from a genebank administrator, regional PGR network coordinator, etc.

4. A questionnaire was developed to survey the sunflower collections identified for the purpose of gathering up-to-date information on each, including the numbers and types of sunflower accessions held, the conditions under which they are stored, their accessibility to users, safety duplication status, and the long-term security of the collection. The questionnaire is provided in Appendix 1. The questionnaire was uploaded to the SurveyMonkey online platform, and a link to this platform provided as well as a Word version of the questionnaire. Invitations were sent to participate to all previously identified curators and collections (Appendix 2). The survey was initiated in June 2021 and closed at the end of 2021.
5. The questionnaire results were compiled, and additional data gathered from the literature to describe two major collections that did not participate in the survey. The analysis of these data, as well as information collated from global PGR databases (on accessions numbers by institute and species), form the basis of Chapter 3 of the GSCS draft (“*Ex Situ* Collection Conservation Status”). This Chapter was shared with all curators who participated in the global survey, as well as the curators of major collections yet to respond. Feedback was gathered from all interested parties to inform the conclusions and recommendations presented in the GSCS draft document.
6. Owing to travel restrictions imposed by the global COVID-19 pandemic, a series of virtual consultations was hosted for sunflower collection curators (November 2021) to discuss the survey analysis and conservation priorities. These discussions also informed the action plan developed in the first GSCS draft document.
7. The consolidated draft of the GSCS was sent to all survey respondents for comments, corrections, recommendations, and additions.
8. Incorporation of inputs from all stakeholders and submission of the final draft to the Crop Trust for review and eventual publication on their website.



Sunflowers seeds. Photo: Luis Salazar/Crop Trust

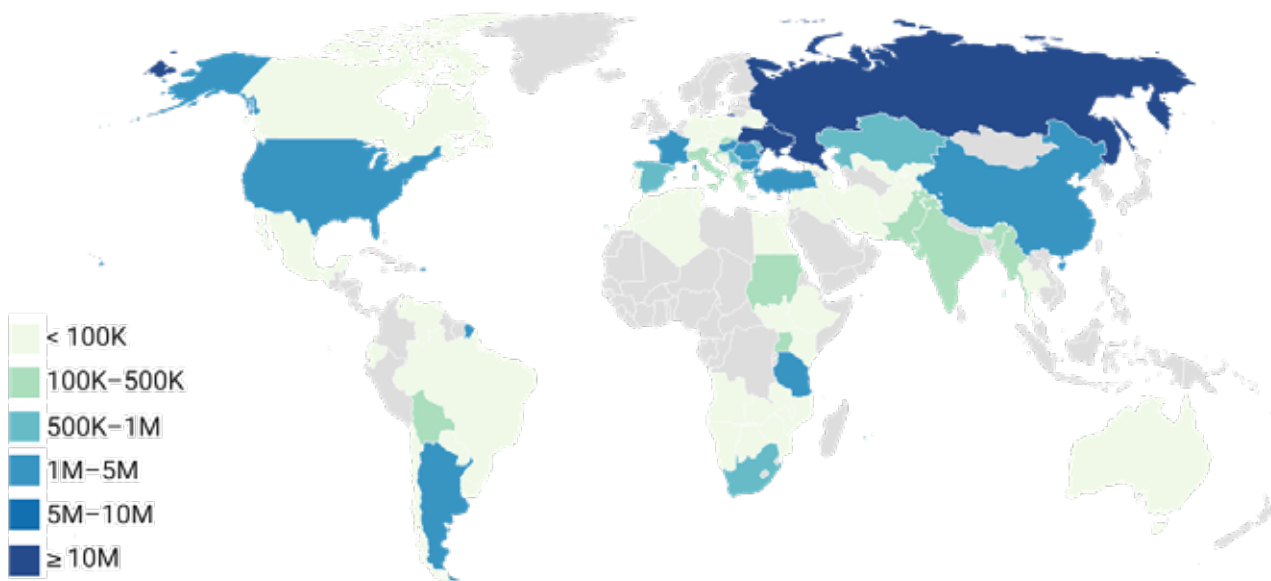
## 2 BACKGROUND REVIEW

The common annual sunflower, *Helianthus annuus* L., from the Greek word “helios” for sun and “anthus” for flower, has pleased and fascinated humankind for thousands of years with its vibrant yellow flowers and the sun-tracking habit of the primary capitula (flower head, or inflorescence). As a crop, it has a relatively recent origin (some 4,000 years before present) in central-eastern North America, where it was domesticated by First Nations peoples. Cultivated sunflower is instantly recognizable from its single stem, large broad leaves and conspicuously large flower head con-

taining large seeds, although variation is seen across the cultivated varieties. It is significantly differentiated from its wild progenitor (extant today across North America as wild *Helianthus annuus*) which has thinner stems, a high degree of branching, and as many as hundreds of significantly smaller flowers per plant.

Originally grown and domesticated by Native Americans for the oil and protein in their seeds, sunflower was later developed as a forage, an oilseed crop and for confectionary purposes. Today, it is also used in

Average production/year (2016-2021)



Map: Peter Giovannini • Source: FAOSTAT • Created with Datawrapper

Figure 2.1 Average production quantities (tonnes) of sunflower seeds by country. K = 1000; M = 1 Million. 2021 (FAOSTAT, 2023). [Online interactive version.](#)

animal feed, as birdseed, and as an ornamental for home gardens and the cut-flower industry. Sunflower derives most of its economic value globally as one of the top oilseed crops, behind soybean and rapeseed, and is strategically critical as a model species for adapting to climate change.

The average annual world production of sunflower between 2016–2021 was estimated at around 52 million metric tons (FAOSTAT 2023), covering over 27 million hectares in 73 countries. More than half of the

world production is concentrated in Ukraine (>14M t) and Russia (>13M t). Another 20% of world production comes from Argentina (>3M t), Romania (2M t), China (>2M t) and Turkey (>2M t) (Figure 2.1). Bulgaria, Hungary, France, USA and Tanzania follow with an average production of between 1 and 2 M tonnes. Between 2016 and 2021, the average global average yield per year of sunflower seeds was about 1.9 metric tonnes per hectare (FAOSTAT 2023). Global total harvested area, production, and yield of sunflower seed from 1961 to 2021 are shown in Figure 2.2.

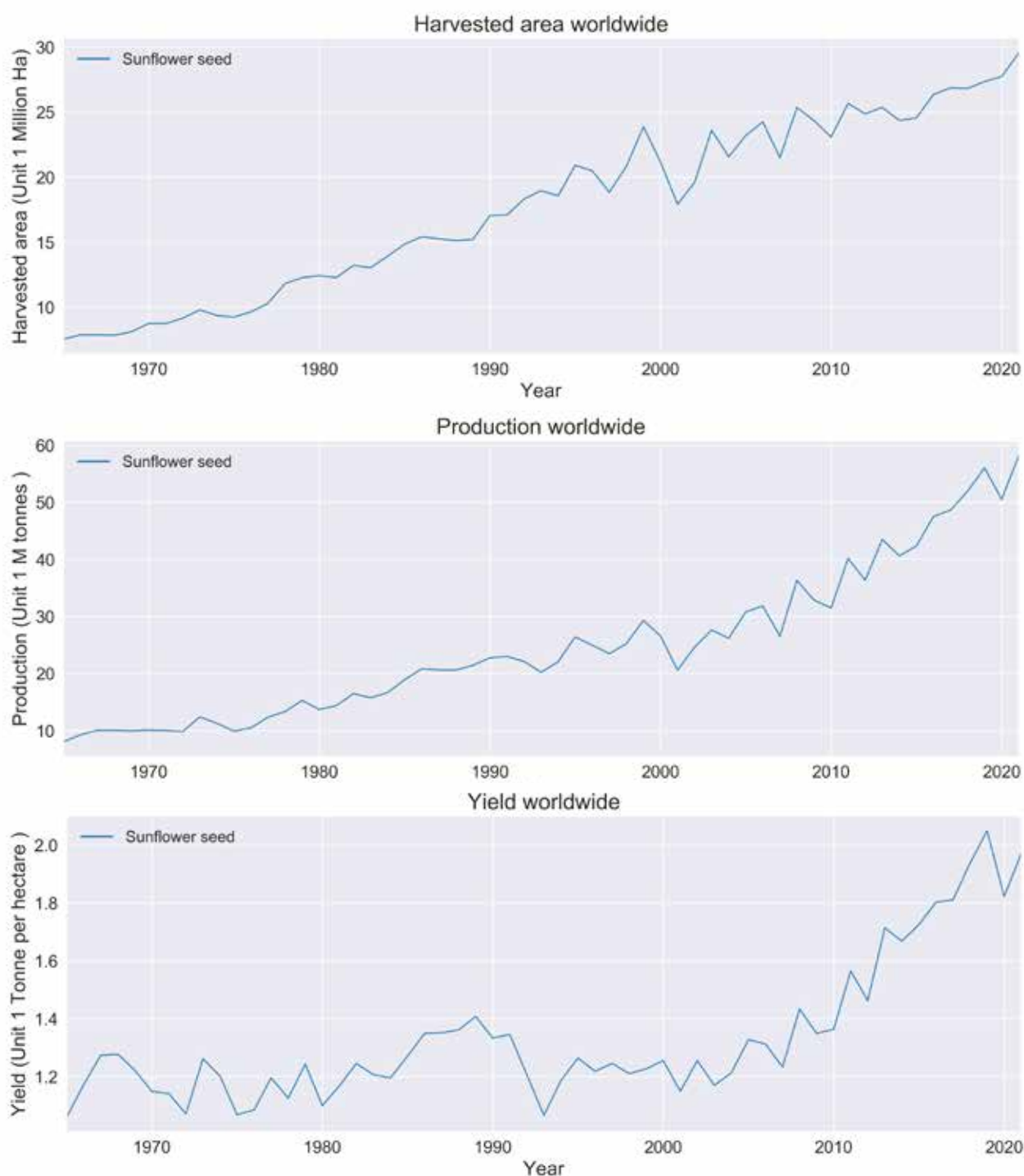


Figure 2.2 Global total harvested area, total production and yield of sunflower seed from 1961 to 2021 (FAOSTAT, 2023).

Cultivated sunflower derives the most economic value from oil extraction and some additional value from meal. The oil extracted from sunflower achenes (the combination of the inner kernel or seed, and the husk, or hull or outer pericarp) accounts for over 80% of the total value of the crop (Fick & Miller 1997). Hull percentage and oil content in the kernel differ among genotypes. For high oil cultivars and hybrids, the average hull percentage has been improved to 20% and kernel oil content to over 600 g/kg (Miller & Fick 1997).

Sunflower oil is categorized as a premium oil due to its chemical profile (Dorrell & Vick 1997). The primary use of sunflower oil is for cooking and salads, and as a major ingredient in some shortening products and margarine. As an edible oil, sunflower oil is very attractive for health-conscious consumers due to its high linoleic acid concentration; it is considered a polyunsaturated oil with a 90% ratio of oleic and linoleic fatty acids to saturated fat (Mensink et al. 1994; Willett 1994). Cultivated varieties have also been developed that have negligible trans fatty acid content and do not require hydrogenation, as well as high-oleic types that have no trans fatty acids and only moderate levels of saturated fatty acids.

Sunflower kernels are used in the baking industry and in other foods. Sunflower meal can be used in feeds for ruminants, swine, and poultry. Sunflower achenes are also used for feeding pet birds.

Selecting for high protein content in sunflower seeds usually results in a lower oil concentration, because oil and protein content are negatively correlated. However, careful breeding work has maintained oil concentrations while doubling the protein content to over 400 g/kg (Ivanov & Stoyanova 1978). Sunflower flour and concentrated protein derivatives show promise and growing use in bakery products, infant formula, and meat extenders.

Tocopherols (vitamin E) are powerful natural fat-soluble antioxidants that inhibit lipid oxidation. The presence of tocopherols in sunflower oil is a characteristic of growing interest from the commercial sector, and consequently the development of high-tocopherol varieties represents a current breeding goal. However, a high tocopherol content can lower oil stability for frying, so, alternatively, substitutions of tocopherol derivatives with greater antioxidant action may be made.

## 2.1 Taxonomy and Relationships within *Helianthus*

Cultivated sunflower (*H. annuus*) belongs to the genus *Helianthus*, in the Asteraceae family (also known as the Compositae), which is the largest of the flowering

plant families, with 25,000+ known species in over 1,700 genera (Mandel et al. 2019). The Asteraceae family has long been recognized as a clearly-defined, monophyletic group owing to many synapomorphies, such as the capitulum. Morphological and molecular evidence to date place the Asteraceae as sister to the small Calyceraceae family, which is endemic to southern South America (Lundberg 2009; Lundberg & Bremer 2003; Winkworth et al. 2008). Asteraceae species are distinguished from those of other plant families by their compound inflorescences (or capitula, singular capitulum), among other traits; the capitulum is comprised of many individual rays and/or disk florets arranged within a receptacle, giving the impression of a single “composite” flower.

The Asteraceae has a global distribution (Funk et al. 2005), with species occupying almost every habitat imaginable, from deserts to swamps, open grasslands to climax forests, and polar tundra to tropical seashores. Asteraceae species are also spectacularly morphologically diverse, particularly in their floral traits (Anderberg et al. 2007); most species take the form of annual and perennial herbs, yet shrubs, trees, and vines are not unknown in the family. Despite this diversity, as compared to other plant families (e.g., the Fabaceae or Poaceae), the Asteraceae contains relatively few food crops or medicinal species, with lettuce (*Lactuca sativa* L.) and sunflower the only two major crops in the family (Dempewolf et al. 2008). Yet Asteraceae species provide food and habitat for a wealth of animal species, including agronomically-beneficial pollinators; ~75% of all food crops benefit from pollinator services (Klein et al. 2007; Lautenbach et al. 2012; Ricketts et al. 2008). Many Asteraceae species are also valued as ornamentals (e.g., asters, chrysanthemums, cosmos, dahlias, gerberas, and marigolds). Finally, though most species have restricted ranges, the Asteraceae also contains its share of problematic weeds (Hodgins et al. 2015), with over 100 species listed as “noxious” in the United States alone (USDA, NRCS 2017).

Characterizing the relationships within the Asteraceae has proven challenging (Funk et al. 2005), and for many years the lack of a well-resolved phylogeny hampered research on the origins of the family, its subfamilies ( $n = 13$ ), and tribes ( $n = \sim 45$ ) (Panero et al. 2014). However, with the benefit of next-generation sequencing technologies, recent work (Mandel et al. 2019; Zhang et al. 2021) has resolved a well-supported backbone phylogeny using genomic and transcriptomic data. The work of Mandel et al. (2019) supports a late Cretaceous origin for the Asteraceae (~83 MYA) in southern South America, followed by a series of rapid radiations during the mid-Eocene, during which most present-day lineages originated. Interestingly, a series of ancient whole-genome duplications (or

“paleopolyploidization events”) within the family may have contributed to the diversification and present-day ecological success of the Asteraceae (Barker et al. 2008, Barker et al. 2016, Huang et al. 2016).

Within the Asteraceae, the sunflowers belong to the largest, and most recently derived, of the 13 currently recognized subfamilies: the Asteroideae, a monophyletic group of some 17,000+ species which began to radiate ~37 MYA (Mandel et al. 2019). Within the Asteroideae, *Helianthus* is part of the large Heliantheae Alliance, which comprises 13 tribes and 5,600+ species, most of which have phytomelanic<sup>1</sup> fruits (Anderberg et al. 2007, Panero et al. 2007, Pandey et al. 2014). After colonizing North America (from either Africa or Asia), the Heliantheae Alliance diversified rapidly beginning ~25 MYA (Panero & Crozier 2016). Two factors are thought to have facilitated the radiation of this clade: a whole-genome duplication event at the crown node of the alliance (Barker et al. 2008, Barker et al. 2016) and a recurring pattern of long-distance dispersal into new habitats (Mandel et al. 2019). Within the Heliantheae Alliance, the Heliantheae (the sunflower tribe) is sister to the Coreopsideae (cosmos, dahlias, etc.), and together these two tribes are sister to the Neurolaeneae (Mandel et al. 2019, Zhang et al. 2021).

The generic composition of the tribe Heliantheae, generic delimitations within the tribe, and the relationships among these genera remain poorly resolved to date (see e.g., Robinson 1981, Panero et al. 1999). However, the sunflowers fall within a somewhat better-characterized subtribe, the Helianthineae, a group of some 350 species and 21 genera, according to a recent reclassification (Schilling & Panero 2011). While generic relationships within the Helianthineae were also long obscure (not resolvable with morphological data), the more recent application of molecular phylogenetics has proven useful (see Schilling 2001, Schilling & Panero 2002, Schilling & Panero 2011); however, efforts thus far have relied on limited data (ITS and ETS regions, as well as plastid DNA restriction sites), and, given the challenges associated with frequent hybridization within the subtribe, more complete genomic data will likely be needed to fully address outstanding uncertainties. Nonetheless, within the Helianthineae, *Phoebanthus* has been (robustly) identified as the sister genus to *Helianthus*, and the two genera are estimated to have diverged between 2.47 and 5.41 MYA (Mason 2018). Other closely related genera include *Aldama*, *Pappobolus* (a South American clade once considered part of *Helianthus*), *Simsia*, and *Tithonia*, among others; these diverse taxa, which occur from Mexico through southern South America, form a sister clade to *Helianthus-Phoebanthus*.

1 Dark-colored

## 2.2 The Genus *Helianthus*

The genus *Helianthus* includes circa 50 species native to North America (Schilling 2006, Heiser et al. 1969, Schilling & Heiser 1981). The number of species remains approximate, as the identification of sunflower species has long been problematic (Seiler 2010). This taxonomic complexity results from several factors (Rieseberg & Seiler 1997): (1) rampant natural hybridization and introgression within the genus (leading to morphological inter-gradation among affected species); (2) the occurrence of polyploidy within the perennial species; and (3) extensive within-species phenotypic and genetic variation in many wide-ranging species (leading to difficulties with species identification and classification). Phenotypic variation across species' ranges may be heritable or non-heritable, adding to the complexity. Over the past two centuries, these challenges have led botanists to propose multiple infrageneric classification schemes for *Helianthus*, including from 10 up to 200+ species (summarized in Seiler 2010). Today, our most comprehensive knowledge of the genus comes from the work of Charles B. Heiser, whose seminal publication “The North American Sunflowers (*Helianthus*)” (Heiser et al. 1969), compiled extensive morphological work and crossing studies. Heiser recognized 14 annual species and 36 perennial species from North America, as well as an additional 17 South American species; the latter were subsequently moved to the genus *Helianthopsis* (Robinson 1979) and then *Pappobolus* (Panero 1992). More recently, molecular data are being applied to better resolve species boundaries and relationships (e.g., Bock et al. 2014, Owens et al. 2016, Zhang et al. 2019), as described below.

As a basis for describing our current understanding of *Helianthus* systematics, GRIN-Taxonomy is utilized here as a standard reference (GRIN-Global 2021). Within GRIN-Taxonomy, 53 *Helianthus* species are currently recognized (15 annuals and 38 perennials), with a larger number of subspecies (see Table 2.1 and Table 2.2). The GRIN-Taxonomy entry for *Helianthus* also lists an additional four hybrid species: *H. × doronicoides* Lam., *H. × intermedius* R. W. Long, *H. × laetiflorus* Pers., and *H. × multiflorus* L. Note that these are included in a much longer list of putative natural hybrids compiled by Heiser et al. (1969). Although Heiser recognized that hybrids were not uncommon in the landscape, their relative scarcity (in terms of abundance) and general occurrence in disturbed areas (in contrast to “natural” habitats), led Heiser to exclude hybrids from his key to named *Helianthus* species. However, *H. × laetiflorus* and *H. × multiflorus* represent two exceptions: these were included in Heiser's key, given that both are well-studied and widely

grown as ornamentals. Additionally, *H. × multiflorus* is a completely sterile triploid, reproductively isolated from its parental species (*H. annuus* × *H. decapetalus* L.). Since the publication of Heiser's work, several of the named species he described have been revealed to be of ancient hybrid origin, highlighting the prevalence of hybridization as a creative force within the genus. For example, *H. anomalus* S. F. Blake, *H. deserticola* Heiser, and *H. paradoxus* Heiser are now known to be stabilized diploid hybrid derivatives of *H. annuus* × *H. petiolaris* (Rieseberg 1991); these species occupy extreme environments, with hybridization facilitating these ecological transitions (from the parental species) (Rieseberg et al. 2003).

As a practical tool, many authors have sought to define sections within *Helianthus* (including Heiser: see Heiser 1965, Heiser et al. 1969 and discussion therein on earlier efforts), but there has been a general lack of agreement on any categories proposed between genus and species, and indeed even on the utility of such a classification. Nonetheless, the most generally accepted scheme, detailed by Schilling & Heiser (1981) and refined by Rieseberg & Seiler

(1997) and Seiler (2010), is presented here (Table 2.1 and Table 2.2), as it will be useful for understanding emerging phylogenetic hypotheses for the genus presented later. As originally conceived by Schilling and Heiser (1981) and refined by Rieseberg and Seiler (1997), the scheme divides 50 *Helianthus* species into four sections (*Helianthus*, *Agrestes*, *Ciliares*, and *Atrorubens*) and six series based on crossability and morphology. Here, we additionally follow Seiler (2010) in suggesting that the annual *H. porteri* (A. Gray) Pruski be placed in its own section (*Porteri*), rather than within the perennial section *Atrorubens*, as this better agrees with current understanding of intrageneric relationships (Stephens et al. 2015). While useful, note that the placement of some species in the scheme, particularly within the perennials, remains arbitrary to some extent. Future work should aim to further refine the infrageneric classification scheme on the basis of emerging insights from molecular phylogenetics.

The species composition of the annual *Helianthus* sections is presented in Table 2.1 and of the perennial *Helianthus* sections in Table 2.2. These tables also include information on the ploidy of each listed

**Table 2.1** The annual sunflower species (all diploid: n = 17). Following Seiler 2010.

Section	Species	Common Name
<i>Agrestes</i>	<i>H. agrestis</i> Pollard	Rural, Southeastern
<i>Helianthus</i>	<i>H. annuus</i> L.	Common Annual
	<i>H. anomalus</i> S.F. Blake	Anomalous
	<i>H. argophyllus</i> Torr. & A. Gray	Silverleaf
	<i>H. bolanderi</i> A. Gray	Bolander's, Serpentine
	<i>H. debilis</i> Nutt.	
	ssp. <i>cucumerifolius</i> (Torr. & A. Gray) Heiser	Cucumber-Leaf
	ssp. <i>debilis</i>	Beach
	ssp. <i>silvestris</i> Heiser	Forest
	ssp. <i>tardiflorus</i> Heiser	Slow-Flowering
	ssp. <i>vestitus</i> (E. Watson) Heiser	Clothed
	<i>H. deserticola</i> Heiser	Desert
	<i>H. exilis</i> A. Gray	Serpentine
	<i>H. neglectus</i> Heiser	Neglected
	<i>H. niveus</i> (Benth.) Brandege	
	ssp. <i>canescens</i> (A. Gray) Heiser	Gray
	ssp. <i>niveus</i>	Snowy
	ssp. <i>tephrodes</i> (A. Gray) Heiser	Ash-Coloured, Dune
<i>H. paradoxus</i> Heiser	Pecos, Puzzle, Paradox	
<i>H. petiolaris</i> Nutt.		
ssp. <i>fallax</i> Heiser	Deceptive	
ssp. <i>petiolaris</i>	Prairie	
<i>H. praecox</i> Engelm. & A. Gray		
ssp. <i>hirtus</i> (Heiser) Heiser	Texas	
ssp. <i>praecox</i>	Texas	
ssp. <i>runyonii</i> (Heiser) Heiser	Runyon's	
<i>Porteri</i>	<i>H. porteri</i> (A. Gray) Pruski	Confederate Daisy, Porter's

**Table 2.2** The perennial sunflower species, after Seiler 2010.

Section	Series	Species	Common Name	Chromosome Number (n)		
Atrorubens	Angustifolii	<i>H. angustifolius</i> L.	Narrowleaf, Swamp	17		
		<i>H. carnosus</i> Small	Fleshy	17		
		<i>H. floridanus</i> A. Gray ex Chapm.	Florida	17		
		<i>H. heterophyllus</i> Nutt.	Variable-Leaf	17		
		<i>H. longifolius</i> Pursh	Long-Leaf	17		
		<i>H. radula</i> (Pursh) Torr. & A. Gray	Scraper, Rayless	17		
		<i>H. simulans</i> E. Watson	Muck, Imitative	17		
		Atrorubens	Atrorubentes	<i>H. atrorubens</i> L.	Purple-Disk	17
<i>H. occidentalis</i> Riddell						
ssp. <i>occidentalis</i>	Fewleaf, Western			17		
ssp. <i>plantagineus</i> (Torr. & A. Gray) Heiser	Fewleaf, Western			17		
<i>H. pauciflorus</i> Nutt.						
ssp. <i>pauciflorus</i>	Stiff			51		
ssp. <i>subrhomboideus</i> (Rydb.) O. Spring & E.E. Schill.	Stiff			51		
<i>H. silphoides</i> Nutt.	Odorous			17		
<i>H. verticillatus</i> Small	Whorled			17		
Atrorubens	Corona-Solis			<i>H. californicus</i> DC.	California	51
		<i>H. decapetalus</i> L.	Ten-Petal	17, 34		
		<i>H. divaricatus</i> L.	Divergent	17		
		<i>H. eggertii</i> Small	Eggert's	51		
		<i>H. giganteus</i> L.	Giant	17		
		<i>H. grosseserratus</i> M. Martens	Sawtooth	17		
		<i>H. hirsutus</i> Raf.	Hairy	34		
		<i>H. maximiliani</i> Schrad.	Maximilian	17		
		<i>H. mollis</i> Lam.	Softy, Ashy	17		
		<i>H. nuttallii</i> Torr. & A. Gray				
		ssp. <i>nuttallii</i>	Nuttall's	17		
		ssp. <i>parishii</i> (A. Gray) Heiser	Los Angeles, Parish's	17		
		ssp. <i>rydbergii</i> (Britton) R. W. Long	Rydberg's	17		
		<i>H. resinus</i> Small	Resinous	51		
		<i>H. salicifolius</i> A. Dietr.	Willowleaf	17		
		<i>H. schweinitzii</i> Torr. & A. Gray	Schweinitz's	51		
		<i>H. strumosus</i> L.	Swollen, Woodland	34, 51		
		<i>H. tuberosus</i> L.	Jerusalem Artichoke	51		
		Atrorubens	Microcephali	<i>H. glaucophyllus</i> D.M. Sm.	Whiteleaf	17
				<i>H. laevigatus</i> Torr. & A. Gray	Smooth	34
<i>H. microcephalus</i> Torr. & A. Gray	Small-Headed			17		
<i>H. smithii</i> Heiser	Smith's			17, 34		
Ciliares	Ciliares	<i>H. arizonensis</i> R.C. Jacks.	Arizona	17		
		<i>H. ciliaris</i> DC.	Texas Blueweed	34, 51		
		<i>H. laciniatus</i> A. Gray	Alkali	17		
Ciliares	Pumili	<i>H. cusickii</i> A. Gray	Cusick's	17		
		<i>H. gracilentus</i> A. Gray	Slender	17		
		<i>H. pumilus</i> Nutt.	Dwarfish	17		

species; note that the base chromosome number for *Helianthus* is  $n = 17$ . A brief overview of each section and series is provided here:

- *Agrestes* (annual): contains the single, self-compatible species *H. agrestis* Pollard, which is not closely related to the other annual species (and does not readily hybridize with them). *Helianthus agrestis* prefers high humidity environments with wet soils, and known populations from central Florida and Georgia have been described as highly uniform.
- *Helianthus* (annual): a group of 12 annual diploids that represent a monophyletic group (Rieseberg 1991; Stephens et al. 2015; Baute et al. 2016). These species are mostly well-differentiated, with two exceptions (see later discussion of *H. bolanderi-exilis* and *H. neglectus-petiolaris*). Hybridization among section members is common. Most species occur in the southwestern USA and are well adapted to dry and/or extremely dry habitats and sandy soils.
- *Porteri* (annual): contains the single species *H. porteri*, which was recently transferred to *Helianthus* from *Viguiera* (Pruski 1998). *H. porteri* has a limited distribution in northwestern Georgia and may hybridize with several sympatric species.
- *Atrorubens* (perennial): a large group of 30 widely distributed perennial species without clear species boundaries (owing to hybridization, introgression, etc.). Most species occur in the eastern and central USA (except *H. californicus* DC. and *H. nuttallii* Torr. & A. Gray). Plants typically possess rhizomes or tubers.
  - Angustifolii*: a group of eight species limited to the southeastern USA. Morphologically, rhizomes may be well developed to lacking; a basal rosette is typically present; stem leaves are small and leaves often entire; phyllaries are loose, and disk corollas yellow or red. The species for which the series is named (*H. angustifolius* L.) intergrades with *H. floridanus* A. Gray ex Chapm. and *H. simulans* E. Watson, but all species may hybridize. Both *H. carnosus* Small and *H. radula* (Pursh) Torr. & A. Gray represent particularly unique species within the genus.
  - Atrorubens*: a group of four species that range from the Midwest to southeastern USA. Morphologically, rhizomes are usually lacking; a basal rosette is present, with few/small stem leaves, and leaves are often serrate. Phyllaries are appressed and disk corollas red to purple (except in *H. occidentalis* Riddell).
  - Corona-solis*: the largest group of the series, containing 15 diverse species, including the crop species *H. tuberosus* L. (Jerusalem artichoke). Morphologically, all species have rhizomes, coarse/fibrous roots, and well-developed stem leaves; disk corollas are yellow (except in *H. salicifolius* A. Dietr.) and phyllaries loose ( $n = +25$ ); a basal rosette of leaves is lacking. Most species are widely distributed, except for *H. californicus*, *H. eggertii* Small, *H. schweinitzii* Torr. & A. Gray.
- iv. *Microcephali*: a group of four species, including *H. microcephalus* Torr. & A. Gray, which is widely distributed in the eastern USA; the other group members occur in the southeastern USA. Morphologically, rhizomes are usually lacking or poorly developed, while stem leaves are well developed. There is no basal rosette, and disk corollas are yellow and phyllaries loose ( $n < 25$ ).
- *Cilares* (perennial): a group of six western perennial species that develop from tap roots or long lateral roots (no rhizomes). Plants are typically short in stature ( $< 1$  m tall) and the basal rosette of leaves is lacking or poorly developed. Species range from the western USA through northern Mexico.
  - Ciliares*: a group of three species with slender lateral roots, sessile/subsessile leaves, glabrous phyllaries, and glaucous stems. All species are diploid except *H. ciliaris* DC., which is also a noxious agricultural weed (known as “blue weed”) in some states. Species range from the southwestern USA to northern Mexico.
  - Pumili*: a group of three species with stout roots, petiolate leaves, pubescent phyllaries, and non-glaucous stems. Species range through the Rocky Mountains and western USA.

Note that two recently named species that are currently recognized in GRIN-Taxonomy, *H. inexpectatus* D. J. Keil & Elvin ( $n = 34$ ) and *H. winteri* J. C. Stebbins ( $n = 17$ ), are not currently placed in the classification scheme, which was most recently revised by Seiler (2010). The tetraploid perennial, *H. inexpectatus*, is most similar to the diploid *H. nuttallii* Torr. & A. Gray and the hexaploid *H. californicus* DC. (Keil & Elvin 2010); it is therefore suggested to place it in the same section and series as these two species (section = *Atrorubens*, series = *Corona-Solis*). Meanwhile, *H. winteri* is most closely related to (and likely derived from) *H. annuus* (Stebbins et al. 2013, Baute et al. 2015), and it is suggested to therefore place it in the annual *Helianthus* section, though *H. winteri* plants may persist for many years in the mild Californian climate.

### 2.3 Phylogenetic Relationships within *Helianthus*

Given the difficulties in identifying species and species boundaries within *Helianthus*, it should come as no surprise that obtaining a well-resolved phylogeny for the genus has proven equally problematic. While crucial for study of the genus, reconstructing phylogenetic relationships, particularly among the perennial species and polyploid hybrids, has proven a formidable challenge. This is due to several factors, namely: the



group's recent origin (Schilling 1997, Mason 2018) and rapid radiation (leading to a lack of markers that have evolved at pace, as well as incomplete lineage sorting); the high incidence of interspecific hybridization in the genus (Kane et al. 2009); and multiple rounds of whole-genome duplication (Barker et al. 2008).

Early attempts to characterize intrageneric relationships within *Helianthus* have been varied and numerous. For example, studies have used: morphology and/or crossing data (Schilling & Heiser 1981); phytochemistry (Schilling 1983; Spring & Schilling 1989, 1990, 1991); isozyme data (Rieseberg et al. 1991); RFLPs (Gentzmittel et al. 1992, Schilling 1997, Rieseberg 1991); and sequence data (Schilling et al. 1998, Schilling 2001). The phylogenies produced by these studies tended to be discordant and were characterized by poor branch support and widespread polytomies. There was additionally a lack of species resolution and repeated swapping of taxon placement among studies. These problems likely resulted from the use of too few markers (or traits) with too little variability, rendering these efforts unsuccessful in the face of the complex evolutionary history of the genus.

A more recent effort by Timme et al. (2007) used the external transcribed spacer (ETS) region of the nuclear 18S-26S rDNA region to determine a gene tree for 47 *Helianthus* species (of 49 species recognized at the time). The resulting tree identified a monophyletic annual clade (Section *Helianthus*), nestled within a much larger perennial clade. In the annual clade, *H. argophyllus* and *H. bolanderi* were identified as *H. annuus*' closest relatives; note that *H. argophyllus* was not reciprocally monophyletic. Both sections *Atrorubens* and *Ciliares* were polyphyletic, with *Ciliares* divided into two lineages and *Atrorubens* split across many clades; the series within both sections were not recovered as phylogenetically meaningful groups. Both *H. agrestis* and *H. porteri*, the two annuals each representative of a monotypic section, were placed within a basal lineage. However, the most basal clades were generally poorly resolved in terms of the order of divergence. Notably, the distribution of known hybrid species across the phylogeny suggested multiple independent hybrid speciation events.

Although the Timme et al. (2007) gene tree provided better resolution than previous efforts (and included many more species), challenges remained. For example, a large proportion of accessions within species were unresolved and low bootstrap support was prevalent, especially towards the tips. This highlights the difficulties presented by the extensive reticulate evolution within the genus (i.e., due to interspecific hybridization, polyploidization, and horizontal gene flow), and the need for more data to tease apart complex intrageneric relationships: a single gene is

insufficient. To this end, studies have begun to utilize next-generation sequencing data, to work with smaller groups of species, and to explicitly consider hybridization and polyploidy. For example, Moody & Rieseberg (2012) used 11 nuclear loci (ESTs) to resolve the annual clade (section *Helianthus*) when excluding homoploid hybrids; their results support close relationships between *H. annuus* and *H. argophyllus*, *H. bolanderi* and *H. exilis*, and *H. neglectus* and *H. petiolaris*. The authors noted a high degree of incongruence among gene trees however, owing to incomplete lineage sorting and the recent sharing of alleles between species. For example, species monophyly was most elusive for the two most geographically widespread species, *H. annuus* and *H. petiolaris*, both of which have large effective population sizes and high intraspecific diversity (Strasburg & Rieseberg 2008), and for which independent evidence suggests high levels of ongoing genetic exchange (Yatabe et al. 2007). Recurrent gene flow among species is a common feature of the genus, particularly between *H. annuus* and several of the other annual species (Strasburg et al. 2011, Kane et al. 2009, Scascitelli et al. 2010).

Next-generation sequencing data were also used in two successful efforts to characterize phylogenetic relationships: (1) among all diploid, non-hybrid taxa ( $n = 37$  species and subspecies; Stephens et al. 2015); and (2) among taxa cross-compatible with the cultivar ( $n = 22$  species; Baute et al. 2016). Stephens et al. (2015) used a target enrichment approach to garner 170 genes (and +12K parsimony-informative sites) for phylogenetic reconstruction using coalescent and concatenation analyses. By avoiding hybrids and polyploids, they were better able to resolve the relationships among diploids, providing a solid scaffold for further studies (e.g., of polyploid species origins). Note that the origins of confirmed diploid hybrids have been well studied (as discussed previously; e.g., Rieseberg 2006). The two types of analyses (coalescent and concatenation) were largely congruent and able to resolve nearly all taxa as monophyletic; one notable exception was *H. neglectus* and *H. petiolaris*, which formed a polytomy (at the accession and population levels). These two species are not genetically isolated from one another (Raduski 2010), and *H. neglectus* may best be considered a subspecies of *H. petiolaris*. The few areas of conflict between analyses occurred at deeper nodes within the phylogeny (e.g., for *H. agrestis*, *H. cusickii*, *H. gracilentus*, *H. mollis*, and *H. occidentalis*), where gene trees varied and there was no dominant topology; this again suggests the retention of ancient polymorphisms due to rapid radiation and/or high levels of reticulate evolution. The phylogeny produced by Stephens et al. (2015) was generally more consistent with older efforts based on morphology, rather than the ETS-based tree produced by Timme et al. (2007).

*Helianthus porteri* was supported as sister to all *Helianthus* species, which helps explain the historical difficulties in placing this species into the infrageneric classification scheme (as it is an annual, but more similar morphologically to perennial species in section *Atrorubens*). Except for *H. agrestis*, the other annual species were again recovered as a monophyletic group (a near universal finding across studies), with relationships within the clade generally well-resolved; *H. annuus* and *H. argophyllus* were sister species, and both closely related to *H. exilis* (*H. bolanderi* was not included in the study). The annual clade was sister to a large clade containing *H. agrestis* and all perennial species; within this clade, there were two groups of perennials, a southeastern clade (n = 8 taxa) and a clade of primarily large-stature species (n = 11). The southeastern clade was comprised exclusively of species from section *Atrorubens* (series *Atrorubentes* and *Angustifolii*), while the large perennial clade represented a more mixed group, with three species from section *Ciliares* on branches external to a clade of *Atrorubens* species (most from series *Corona-Solis*). As mentioned previously, species that could not be placed precisely (but fell within the larger perennial clade) included *H. agrestis*, *H. gracilentus*, *H. occidentalis*, and *H. mollis*. Mapping life history and growth form onto the tree, “erect perennial” was determined to be the most likely ancestral state, with three independent transitions to an annual life history and three to the basal rosette growth form.

The phylogenomic network constructed by Baute et al. (2016) largely agrees with the tree topology produced in Stephens et al. (2015). Baute et al. (2016) used genotyping-by-sequencing (GBS) to survey 292 accessions of wild *Helianthus* from 22 taxa, including hybrids; the final dataset comprised 4,645 SNPs after quality filtering. Importantly, most named taxa were recovered as unique lineages, with the following exceptions.

- *H. neglectus*/*H. petiolaris*: *H. neglectus* samples largely (but not exclusively) grouped with *H. petiolaris* spp. *fallax*.
- *H. bolanderi*/*H. exilis*: there were no consistent differences between these two species, as also shown by Owens et al. (2016).
- *H. annuus*/*H. winteri*: the *H. winteri* samples fell within the *H. annuus* clade, consistent with *H. winteri* being a young species that originated after *H. annuus* spread to California (Stebbins et al. 2013). An alternative explanation is extensive hybridization between the two.
- *H. divaricatus*/*H. hirsutus*/*H. strumosus*: there was no differentiation between *H. hirsutus* (an autotetraploid) and its diploid progenitor, *H. divaricatus*.
- *H. decapetalus*: with only one exception, both diploid and autotetraploid samples formed a monophyletic clade.

The homoploid hybrid species *H. anomalus* and *H. deserticola* were placed within the *H. petiolaris* clade, congruent with morphological analyses showing these two species are more similar to *H. petiolaris* than *H. annuus* (Rosenthal et al. 2002). Meanwhile, *H. paradoxus* was placed at the base of the annual clade, possibly due to more balanced hybrid ancestry (Rieseberg 2003). Finally, the placement of the hexaploid hybrid *H. tuberosus* was not resolved, but *H. tuberosus* did fall within a clade containing its parental species (the diploid *H. grosseserratus* and tetraploid *H. hirsutus*), as determined by Bock et al. (2014).

## 2.4 The Crop Genepool (*Helianthus* spp.)

As described in the Taxonomy section, the genus *Helianthus* includes circa 50 species native to North America (Schilling 2006; Heiser et al. 1969; Schilling & Heiser 1981), most of which occur primarily within the continental USA, where they are a conspicuous element of the landscape and an inspiration to many. *Helianthus* includes both annual and perennial species, as well as diploids and polyploids. Some species are relatively rare with restricted distributions, while others, such as the common annual sunflower (*H. annuus* L.) and prairie sunflower (*H. petiolaris* Nutt.) are abundant and widespread (Seiler & Rieseberg 1997). Across the genus, species have varied ecologies and morphologies, and occupy diverse habitats, such as climax forests, coastal dunes, disturbed areas, rocky outcrops, tallgrass prairie, and wetlands, among others (Heiser et al. 1969; Kane et al. 2013). Some species even specialize in extreme environments, such as in sandy soil of desert floors (*H. deserticola* Heiser), salt marshes (*H. paradoxus* Heiser), sand dunes (e.g., *H. anomalus* S. F. Blake and *H. neglectus* Heiser), and serpentine soils (*H. exilis* A. Gray). Due to its extensive phenotypic and genotypic diversity, the genus has long served as a model system in ecology and evolutionary biology, receiving particular attention for studies of adaptive introgression and speciation, given the propensity for gene flow among *Helianthus* species (e.g., Rieseberg et al. 1995, 1997, 1999, 2003).

The crop genepool concept, as proposed by Harlan and De Wet (1971), conceptualizes the genepool as containing all genetic resources available for crop breeding and improvement. Crop wild relatives (CWRs) are therefore part of the genepool because they can exchange genes with the crop species, even though they are different biological species. However, the extent to which genetic exchange is possible varies among species. As such, CWRs are subdivided into three groups on the basis of ease of hybridization with the crop:

- **Primary genepool:** contains the crop species itself, as well as any conspecific taxa (e.g., subspecies or

varieties) that are fully cross-compatible (no reproductive barriers).

- **Secondary genepool:** contains all species (typically closely-related congeners) that are capable of hybridizing with the crop species, at least to some extent (*i.e.*, hybrids may show reduced vigour or fertility). Given the presence of reproductive barriers, it can be difficult to utilize species from the secondary genepool in breeding programs.
- **Tertiary genepool:** contains more distantly related species for which there are substantial reproductive barriers to hybridization. Gene transfer is still possible, but with great difficulty as hybrids are typically sterile. Utilization of these species in breeding programs therefore requires specific techniques, such as embryo rescue or the use of bridging crosses (with intermediate species).

Crossing experiments are often used to determine the species composition of the secondary and tertiary genepools, although these can be expensive and time-consuming. More recently, evolutionary studies of species relationships have been used to understand patterns of interspecies fertility (Miller & Khoury 2018).

For sunflower, the primary genepool includes all cultivated, wild, and weedy forms of *H. annuus*; owing to its close relationship with *H. annuus*, from which it is recently derived (Baute et al. 2016), *H. winteri* might also be included in the primary genepool. The secondary genepool for sunflower comprises most of the remaining annual *Helianthus* species (see Table 2.1), except for *H. agrestis* and *H. porteri*, which are instead part of the tertiary genepool.

As described in the Taxonomy section, the annual *Helianthus* species (excluding *H. agrestis* and *H. porteri*) are closely related, forming a single, well-supported clade in the *Helianthus* phylogeny (Timme et al. 2007, Stephens et al. 2015). Meanwhile, *H. porteri*, recently reassigned from *Viguiera*, is sister to all other *Helianthus* species (Stephens et al. 2015); *H. porteri* and *H. annuus* are therefore distantly related, and crosses between the two species also fail to produce seed (Heiser 1963). The exact phylogenetic placement of *H. agrestis* remains unresolved; however, within the most recent relevant phylogeny for *Helianthus* (Stephens et al. 2015), *H. agrestis* is placed as sister to the large perennial clade, which is itself sister to the aforementioned annual clade. *Helianthus agrestis* represents a unique species within the genus; it is highly self-compatible and does not easily hybridize with any other *Helianthus* species, including *H. annuus* (Rogers et al. 1982).

Species within the secondary genepool generally show some degree of cross-compatibility with *H. annuus*.

Details on specific crossing relationships may be found in Rogers et al. (1982). The following section provides a brief description of each wild species in the primary and secondary genepool, showcasing the diversity present in this group of annuals. Descriptions are based on general information from Heiser et al. (1969), Rogers et al. (1982), and Seiler & Rieseberg (1997), with more specific citations included in the text as needed.

The current distribution of wild *H. annuus*, the progenitor of the domesticated sunflower, extends over much of the United States, as well as parts of southern Canada and northern Mexico. However, *H. annuus* is likely indigenous to the central USA, with the hypothesized range prior to human colonization comprising a narrow column from North Dakota south to Texas. In addition to its native distribution, *H. annuus* is now abundant in parts of Australia (Dry and Burdon 1986; Seiler et al. 2008), Europe (Bervillé et al. 2005; Muller et al. 2009), and South America (Poverene et al. 2009; Cantamutto et al. 2010; Casquero and Cantamutto 2016), where it frequently acts as a weed. In contrast to the domesticated sunflower, wild *H. annuus* has multiple inflorescences with small achenes, grows indeterminately and is highly branched, though there is tremendous morphological diversity across the native range (McAssey et al. 2016). Preferring heavy, clay soils and open grasslands (Heiser et al. 1969), wild populations of *H. annuus* may be found growing in a range of open habitats that experience frequent disturbance (Heiser 1954), such as along roads and railway lines, in vacant lots and waste places, and in crop fields. This heliophilic species has been postulated to have originated as a colonizer of natural disturbances (Asche 1993), especially those created by bison, which may also have acted as a dispersal agent for achenes trapped in their fur. Wild and cultivated *H. annuus* remain interfertile, and gene flow between the two is common across the landscape (Linder et al. 1998), with crop-wild hybrids frequently reported in the native range (Arias and Rieseberg 1994; Whitton et al. 1997).

Sunflower commonly acts as an agricultural weed, infesting crop fields and their margins, in both North America (where it is native) and parts of Australia, Europe, and South America (where it is not) (e.g. Al-Khatib et al. 1998; Muller et al. 2009; Casquero and Cantamutto 2016). In the USA, it has been listed as a noxious weed in several states (Iowa, Minnesota, Alaska: USDA, NRCS 2017), as it may decrease crop yields significantly in agricultural fields. For example, for corn, soybean, and sugarbeet fields, a heavy infestation of weedy sunflowers can reduce crop productivity by up to 64%, 97%, and 73%, respectively (Schweizer and Bridge 1982; Geier et al. 1996; Deines et al. 2004). In North America, weedy populations

likely originated as wild sunflowers that colonized agricultural fields, as weedy populations tend to be more closely related to nearby wild populations (occurring in more natural areas) than other weedy populations (Kane and Rieseberg 2008); the role, if any, of crop alleles in contributing to the success of weeds remains unknown. Meanwhile, in other parts of the globe, weedy sunflowers have crop-wild hybrid origins, perhaps originating as seed contaminants in sunflower crop fields. For example, in France and Spain, Muller et al. (2011) found that, while all weeds retained a mitochondrial crop-specific marker, they also possessed a number of alleles not present in the cultivated pool; additionally, the low population structure and high marker diversity found were consistent with multiple introduction events.

*Helianthus anomalus* Blake is a rare sand-dune adapted species that has been found in isolated sites in Utah and northern Arizona, including within the Hopi and Diné First Nations. This is one of three homoploid hybrid species derived from *H. annuus* and *H. petiolaris*, the other two being *H. deserticola* and *H. paradoxus*; the hybrid origins of these species were confirmed using molecular marker data and based on shared chromosomal rearrangements (Rieseberg et al. 1990; Rieseberg 1991; Rieseberg et al. 1993, 1995; Lai et al. 2015; Owens 2016). Ecologically, the hybrid species occupy extreme habitats not normally occupied by their parental species, with *H. anomalus* inhabiting sand dunes, *H. deserticola* sand sheets, and *H. paradoxus* salt marshes. Putative adaptive traits in *H. anomalus* (for life in the sand dunes) include larger seeds, stronger dormancy, smaller leaves, and higher leaf nitrogen concentrations than either parental species (Schwarzbach et al. 2001; Rosenthal et al. 2002; Brouillette et al. 2006). Interestingly, there is also a seed colour dimorphism in *H. anomalus* (Marco Todesco, personal communication): populations may have white or red seeds, purportedly for camouflage in white- or red-sanded areas, respectively.

Using microsatellites, *H. anomalus* was initially reported to be of recent origin, 116,000–160,000 years before present, and multiple origins were proposed as most likely (Schwarzbach & Rieseberg 2002). However, a more recent analysis of SNP data suggests that *H. anomalus* may be significantly older (600,000–800,000 ya), with no evidence for multiple origins (Owens 2016). The SNP analysis also strongly supported a shared origin for *H. anomalus* and *H. deserticola*, the two most closely related homoploid hybrids (Heiser et al. 1969), although independent origins followed by gene flow could not be ruled out (but remains unlikely given strong reproductive barriers between the species; Lai et al. 2005). More recently, *H. anomalus* has shared a rich cultural history with the Hopi community (Nabhan & Reichardt 1983) and may be considered

semi-domesticated in Arizona where populations have notably larger seeds. Apart from their large size (up to 9 mm; Heiser 1978), *H. anomalus* achenes also have the highest oil content of any wild sunflower species (Seiler 1985).

*Helianthus argophyllus* Torr & A. Gray, the “silver-leaf sunflower”, is distinguished by its densely pubescent leaves, stems, and phyllaries with long silky, white, wool-like hairs. This tall-statured plant has often been cultivated as an ornamental owing to its striking, silvery appearance. In the wild, *Helianthus argophyllus* has a small native range, restricted to southern and eastern Texas, and correspondingly small effective population size (Strasburg et al. 2011). However, adventive populations occur in Florida, and *H. argophyllus* may also be found in other countries, such as Australia, where it has escaped cultivation. Within the native range, *H. argophyllus* grows on the sandy soils of the southern Texas coastal plains, including on beaches and breakwaters. Despite its relatively restricted range, the presence of natural barriers to gene flow within the range has led to significant genetic structure within *H. argophyllus*. As determined using molecular markers (64 SNPs), there are three clear genetic groups corresponding to: the northern inland region, southern inland region, and the coast plus barrier islands. There is also evidence for isolation by distance, with geographically proximal populations more closely related than more distant ones (Moyers & Rieseberg 2006).

Among the annual sunflowers, *H. argophyllus* is distinguished as the latest-flowering species, with flowering occurring in response to short daylengths. However, within Texas, two distinct life history syndromes are found: tall and late flowering (with small initial flower heads), and short and early flowering (with larger initial flower heads; likely long daylength sensitive) (Moyers & Rieseberg 2016). The late flowering syndrome occurs predominantly on the mainland, while the early flowering syndrome prevails on the coastal barrier islands. The life history syndromes are genetically based, encompass variation in many other correlated traits (not just flowering time and height), and are likely adaptive (Moyers & Rieseberg 2016). Divergent natural selection may be driving local adaptation in the barrier island populations, while also increasing reproductive isolation: differences in flowering time reduce gene flow between barrier and coastal populations.

*Helianthus bolanderi* A. Gray/*Helianthus exilis* A. Gray is composed of two previously recognized species that might best be considered a single species, *H. bolanderi-exilis*, with geographically based population structure, as determined by two recent genomic studies (Baute et al. 2016, Owens et al. 2016). Both relevant

studies failed to find consistent genetic differences between *H. bolanderi* and *H. exilis*, when examining thousands of SNPs; thus, *H. exilis* is best viewed as an ecotype (or subpopulation) of *H. bolanderi*, as originally proposed by Heiser (1949). Previous treatments had considered *H. bolanderi* and *H. exilis* to be distinct species, owing to differences in morphology, physiology, fatty acid composition (of seed oil), habitat requirements, and cpDNA (Jain et al. 1977, Rieseberg et al. 1988, Rogers et al. 1982). For example, morphologically, *H. exilis* is distinguished by lance-linear shaped leaves, entire leaf margins, and smaller flower heads and fruit; it was originally described as a rare species restricted to poor, serpentine, or serpentine-derived soils in the inner coastal mountains of north-central California. Meanwhile, as originally circumscribed, *H. bolanderi* represented a widespread, ruderal species found from southern Oregon to central California, capable of growing on serpentine soils, but not restricted to them. Its natural habitat was described as the dry soils of fields and foothills, but it may also invade disturbed habitats, such as agricultural fields, ditches, and wastelands (Stebbins 1965).

At one time, *H. bolanderi* was hypothesized to have originated via introgression from *H. annuus* (as it invaded California) into the endemic *H. exilis* (Heiser 1949). This hypothesis has since been refuted (Owens et al. 2016), although *H. bolanderi-exilis* and *H. annuus* are closely related (Stephens et al. 2015); recent molecular phylogenies place *H. bolanderi-exilis* as sister to the clade containing *H. annuus* and *H. argophyllus*. In California, the two species form extensive hybrid swarms where sympatric, and there is evidence for contemporary gene flow (though mainly from *H. bolanderi-exilis* into *H. annuus*). Interestingly, in the non-serpentine environments of the Central Valley, *H. annuus* has largely displaced *H. bolanderi-exilis* over the last 100 years (Carney et al. 2000).

*Helianthus debilis* Nutt. comprises five distinct, geographically isolated subspecies which collectively span the eastern-southeastern United States. Wild populations of *H. debilis* have been little studied in recent decades, and no genetic studies exist of all subspecies, some of which may be at risk owing to habitat loss and fragmentation. However, two of the subspecies are popular as ornamentals and abundantly grown for this purpose.

- *ssp. cucumerifolius* (Torr. & A. Gray) Heiser is popular as an ornamental plant, with seed companies offering a diversity of forms varying in growth habit and flower colour (from primrose to deep red for the ray florets and either yellow or purple for disk florets); ornamental forms typically have larger disks, more numerous rays, and broader phyllaries than the wild type (Heiser et al. 1969). Some of the ornamental types may be derived from hybrid-

ization with ornamental *H. annuus*. The range of wild *ssp. cucumerifolius* has expanded as a result of human contact; native to sandy soiled open areas of southeastern Texas, it may now be found from Louisiana and Georgia through the Carolinas, with sporadic populations appearing up the coast as far as Maine (Rogers et al. 1982). Populations in these states likely represent escapes from cultivation (Heiser et al. 1969).

- *ssp. debilis* is native to east-central Florida, where it is limited to sandy, uninhabited beaches. Though *H. debilis* is typically an annual, *ssp. debilis* may live as a decumbent perennial in warm climates. Trailing branches may develop adventitious roots when in contact with the soil, making *ssp. debilis* an attractive ground cover. The subspecies also blooms most of the year and is a popular ornamental owing to its shiny leaves, lush growth, and low stature. The variety “Flora Sun”, released by USDA in 1994, is widely used for sand dune stabilization, mitigation of wind erosion, and beach beautification, not only on the east coast of Florida, but also on the west coast (i.e., outside of the native range).
- *ssp. silvestris* Heiser is found in northeastern Texas, where it occurs in sandy soils in pine and oak forests. This subspecies grades into *ssp. cucumerifolius* in the southern part of its range.
- *ssp. tardiflorus* Heiser is a particularly rare subspecies found in isolated colonies on sandy beaches from northwestern Florida through southern Georgia and Alabama (Rogers et al. 1982).
- *ssp. vestitus* (E. Watson) Heiser is a rare subspecies endemic to Florida, where it may be found on the barrier islands off the Gulf Coast of Florida. This salt tolerant subspecies grows on the coastal dunes and along sandy beach lines. Native coastal plants in Florida are vulnerable to extreme weather events (hurricanes, etc.), and the west coast is also a hot spot of development and urbanization, putting *ssp. vestitus* at risk. Local beaches may be groomed and modified (destroying native habitat), and competition with introduced species (including *ssp. debilis*) also threatens the long-term preservation of *ssp. vestitus*. Hybridization with *ssp. debilis* is also a significant concern, owing to the prevalence of *ssp. debilis* as an ornamental in Florida (Bradley et al. 2004).

*Helianthus deserticola* Heiser is a rare xerophytic species found in small, isolated populations in the Great Basin Desert (within Utah and Nevada); As discussed, this homoploid hybrid species is well-adapted for life on desert sand sheets (Rosenthal et al. 2002), being highly drought tolerant, with a well-developed tap root that penetrates deeply in sandy soils. Compared to its parental species, *H. deserticola* flowers earlier, has smaller leaves, and takes up less boron, all traits predicted to confer a fitness advantage in desert

environments (Gross et al. 2004). As with *H. anomalus*, high seed dormancy also ensures the long-term survival of *H. deserticola*, as seeds can outlast multi-year droughts. Finally, the timing of *H. deserticola*'s origins remains unclear (similar to *H. anomalus*); early work (based on cpDNA haplotypes & microsatellites) dated its origin to 63,000–170,000 years ago (Gross et al. 2003), but genomic data have suggested an older origin, shared with *H. anomalus*, from 600,000–800,000 years ago (Owens 2016).

*Helianthus neglectus* Heiser/*Helianthus petiolaris* Nutt.: the “neglected sunflower”, *H. neglectus*, is so named because it is among the more recently discovered *Helianthus* species. As per its initial description (Heiser 1958), *H. neglectus* is a narrowly distributed species found within southeastern New Mexico and southwestern Texas, closely related to the widely distributed prairie sunflower, *H. petiolaris*, but differing from it slightly in habitat preference and morphology. Genetically, the two “species” also differ by one or two reciprocal translocations (Chandler et al. 1986; Heiser 1958). However, Heiser (1958) noted that the species status of *H. neglectus* was “somewhat arbitrary”, and recent molecular work has called the distinction of *H. neglectus* as a separate species from *H. petiolaris* into question (Raduski et al. 2010; Baute et al. 2016). For example, *H. neglectus* harbours substantial genetic diversity, more than that contained in any other annual species, including *H. petiolaris* or *H. annuus* (both widespread species) (Baute et al. 2016). Arguing that it would not be possible for *H. neglectus* to maintain such high diversity in isolation (due to its small range and effective population size), Raduski et al. (2010) suggest that *H. neglectus* is best viewed as a morphologically and ecologically distinct geographic subspecies of *H. petiolaris* (perhaps most closely related to *H. petiolaris* ssp. *fallax*; Baute et al. 2016). This conclusion is borne out by the lack of significant genetic divergence between *H. neglectus* and *H. petiolaris* (Baute et al. 2016; Stephens et al. 2015), and high levels of interspecific gene flow between the two “species” (Strasburg & Rieseberg 2008; Kane et al. 2009). Pollen viability is also high in *H. neglectus* x *H. petiolaris* F1 hybrids (Chandler et al. 1986; Heiser 1958) and comparable to that of F1 hybrids among the *H. petiolaris* subspecies (Heiser 1961; Heiser et al. 1969).

After *H. annuus*, the prairie sunflower, *H. petiolaris*, has the second largest range of any sunflower species; it is widely distributed across west-central North America and adventive as a weed elsewhere (e.g., in California and the eastern US). It has also been introduced to many countries outside of North America (Seebens et al. 2017), often as a seed contaminant, and is considered naturalized in some countries, such as Argentina (Cantamutto et al. 2008; Gutierrez et al. 2020). In North America, *H. petiolaris* and *H. annuus*

are broadly sympatric, but exhibit distinct habitat preferences (Heiser 1947): *H. annuus* prefers more fertile and mesic soils, while *H. petiolaris* frequents drier, sandier soils with less organic matter. Strong prezygotic and postzygotic reproductive barriers exist between the two species (Buerkle & Rieseberg 2001; Lai et al. 2005; Rieseberg et al. 1995; Ungerer et al. 1998), which are morphologically and genetically distinct, yet natural hybridization is common (Heiser 1961, 1978), with many contemporary hybrid zones described in the landscape (Yatabe et al. 2007). Molecular evidence suggests that the two species have long exchanged genes, with slightly higher rates of introgression from *H. annuus* into *H. petiolaris* than vice versa (Strasburg & Rieseberg 2008). Three contemporary species represent stabilized *H. annuus* x *H. petiolaris* hybrids (*H. anomalus*, *H. deserticola*, and *H. paradoxus*; Rieseberg 2006), also illustrating the historical propensity for hybridization between these species.

Two subspecies have been described for *H. petiolaris*: ssp. *fallax* and ssp. *petiolaris*. The former occurs in scattered populations across the Southwest (i.e., in Arizona, Colorado, New Mexico, and Utah) at higher elevations (1,200–2,400 m), while the latter is most abundant in the Southern Great Plains east of the Rockies (i.e., from central Texas to southern South Dakota) at elevations up to 1,500 m. Fragmented populations of ssp. *petiolaris* also extend west to California, north to Canada, and east of the Appalachians. Within ssp. *fallax*, repeated adaptation to sand dune ecosystems has occurred in both Colorado and Texas (Todesco et al. 2020). Dune ecotypes are phenotypically distinct from non-dune types found on nearby sand sheets, possessing distinct adaptations, such as larger seeds, faster seedling growth, earlier flowering, and more robust stems. In Colorado, the dune ecotype originated only recently (<10,000 years ago), after the last ice age (Andrew et al. 2012), yet reproductive barriers have already evolved between the ecotypes, which are considered incipient species (Ostevik et al. 2016). Interestingly, a recent large-scale molecular analysis (based on resequencing data; Todesco et al. 2020) found several large regions of genetic differentiation between the ecotypes. These non-recombining haplotype blocks were associated with seed size, days to bud, and soil fertility, suggesting they played an important role in ecotypic divergence.

*Helianthus niveus* (Benth.) Brandege is found in semi-arid to very arid areas from the southwestern US through northern Mexico and Baja California, where it grows in xeric sandy soils and on sand dunes. *H. niveus* is known for its drought tolerance, high seed oil content, and robust disease resistance (Seiler 1985), all traits of considerable agronomic potential. Within *H. niveus*, three subspecies have been described:

- *ssp. canescens* (A. Gray) Heiser is an annual (rarely perennial) erect-stemmed plant found in sandy soils across the southern US, from California to southwest Texas, as well as northern Mexico (Chihuahua and Coahuila). In the eastern part of its range, *ssp. canescens* co-occurs with *H. petiolaris ssp. fallax*, which it closely resembles morphologically. Zhang et al. (2019) suggest that this phenotypic resemblance is a result of ongoing interspecific gene flow, with a large proportion (~17.6%) of the *ssp. canescens* genome affected by introgression.
- *ssp. niveus* is a decumbent, somewhat shrubby, perennial plant which grows from a long tap root; it is found exclusively in the sand dunes of Baja California, Mexico, where it flowers almost year-round. As discussed by Heiser et al. (1969) and by Zhang et al. (2019), there is a good case for designating *ssp. niveus* as a separate species, given its geographic isolation (from other *Helianthus* species) and lack of reproductive compatibility with the other two subspecies, and the results of phylogenetic, structure analysis and crossability among the subspecies (Zhang et al. 2019). Interestingly, *ssp. niveus* can, however, be easily hybridized with many of the perennial sunflower species, suggesting it may retain certain ancestral characteristics and/or be considered “primitive” within *Helianthus*.
- *ssp. tephrodes* (A. Gray) Heiser is a perennial (sometimes annual) erect or decumbent plant from a stout tap root that occurs in the sandhills of southern California and Arizona, as well as in western Sonora, Mexico. One of the few plant species native to the Algodones Dunes of the Sonoran desert, a particularly harsh environment with low annual rainfall and high summer temperatures (Mandel et al. 2013); germination may be tied to seasonal winter rain events (Bowers 1996). Given its rarity and recent habitat destruction (owing to off-road vehicle use in the dunes), *ssp. tephrodes* is considered a species of special concern for the [United States Fish and Wildlife Service \(USFWS\)](#) and is listed as endangered in the state of California.

Zhang et al. (2019) recently evaluated patterns of phenotypic and genetic variation within *H. niveus*, including intraspecific genetic structure, using new collections made for all three subspecies ( $n = 10$  populations), including two newly discovered morphotypes of *H. niveus ssp. niveus* found in the more southern part of its range. The morphotypes, “*lanatus*” and “*rugosus*”, are both annuals, with distinctive traits not typically seen in *ssp. niveus*. Although phenotypically unique, the morphotypes were found not to differ genetically, nor to be reproductively isolated, from other populations of *ssp. niveus*; they therefore represent local ecotypes well-adapted to extreme dune (*lanatus*) and drought (*rugosus*) environments. Confirming Heiser’s suspicions (Heiser et al. 1969),

*ssp. niveus* was found to be reproductively isolated, phenotypically and genetically distinct, and to have a larger genome than the other two subspecies. As such, Zhang et al. (2019) advocated for the reclassification of *ssp. niveus* as a fully-fledged species, separate from *ssp. tephrodes* and *ssp. canescens*; Also, Zhang et al. 2019. pointed out that current data are insufficient to determine if *ssp. canescens* should be merged with *ssp. tephrodes*, or considered a subspecies of the latter.

*Helianthus paradoxus* Heiser is a rare halophytic species found in scattered populations in far western Texas and in New Mexico. While initially known from only a single location on the Laguna Indian Reservation in Pecos County, Texas (Heiser 1958), where it still exists, further *H. paradoxus* populations have since been identified. Some of these populations have been impacted by development (Rogers et al. 1982), and currently 12 documented populations exist, nine in New Mexico, two in Texas, and one in Mexico (Sivinski 2016; Roth 2019; Marek personal communication, 2023). Owing to its rarity, and highly specific habitat needs, *H. paradoxus* was listed as Threatened under the US Endangered Species Act in 1999; at the state-level, *H. paradoxus* is considered endangered in New Mexico and threatened in Texas. A recovery plan was released in 2005 (USFWS 2005), and current populations are being monitored (Roth 2019). While some populations are reasonably secure, such as that within the Bitter Lake National Wildlife Refuge (on federal land in New Mexico) and the sites managed by the Texas Nature Conservancy (Diamond Y and East Sandia Spring Preserves), others are located on privately owned lands and are considerably more vulnerable.

*Helianthus paradoxus* grows exclusively in permanent salt marshes with soil sodium concentrations of 2,000 to 20,000 ppm (Rogers et al. 1982; Welch & Rieseberg 2002). Soils at root-level must be continuously saturated (USFWS 2005), and suitable habitats include the ciénegas (desert wetlands) associated with springs or seeps, or along the margins of streams, ponds, or reservoirs. Germination is dependent on natural temporal cycles in salinity: a higher water table in late fall to early spring leaches salt from the soil surface, creating a brief window when low-salinity conditions permit germination and seedling establishment (Van Auken & Bush 1995, 1998). As such, population abundance can fluctuate widely from year-to-year. Within the species’ range, the amount of suitable habitat for *H. paradoxus* is declining, owing to groundwater depletion, development, competition with non-native plants (such as saltcedar, *Tamarix* sp.), grazing, and alterations to natural fire regimes.

Although generally allopatric to *H. annuus* (owing to different habitat requirements between *H. paradoxus* and its parent species), hybridization with

*H. annuus* represents a threat in more marginal *H. paradoxus* habitats. Natural hybrids have been observed, presenting the possibility of introgression from *H. annuus*, although these tend to have reduced pollen viability and low fertility (Heiser 1978). Morphologically, this homoploid hybrid species tends to be intermediate to its parental species (*H. annuus* x *H. petiolaris*) (Rosenthal et al. 2002), although several transgressive traits have been documented, some of which likely play a role in salt tolerance (e.g., greater Ca uptake and leaf succulence) (Welch & Rieseberg 2002; Lexer et al. 2003). Congruently, the *H. paradoxus* genome is fairly evenly admixed between the two parental genomes (*H. annuus* and *H. petiolaris*), as compared to *H. anomalus* and *H. deserticola* which have *H. petiolaris* as the dominant parent (62% and 63–65%, respectively) (Owens 2016).

*Helianthus praecox* Engelm & A. Gray, the Texas sunflower, is so named because it is a narrow endemic that is restricted to sandy soils on the coastal plains of southeastern Texas. As seen in recent molecular phylogenies, *H. praecox* is the sister species of *H. debilis*, which it also resembles morphologically, and together the two species are sister to *H. petiolaris* (Stephens et al. 2015). Natural hybrids are known in areas of sympatry between *H. praecox* and both *H. annuus* and *H. debilis*, but no genetic studies to date have quantified the extent of introgression among these congeners. Within *H. praecox*, three geographically isolated subspecies have been described, but little is known about the ecology of each:

- *ssp. hirtus* (Heiser) Heiser: has the most limited distribution of the subspecies, confined to a small area within Carrizo Springs; as such, *ssp. hirtus* may be vulnerable to extirpation in the long-term, and it is susceptible to threats such as genetic swamping by more common local congeners, as well as habitat destruction (Rieseberg & Doyle 1989).
- *ssp. praecox*: occurs on Galveston Island and the adjacent mainland.
- *ssp. runyonii* (Heiser) Heiser: occurs on the coastal prairies of southern Texas, from Aransas County to Cameron County.

*Helianthus winteri* J.C. Stebbins: the recently described “Winter’s sunflower” can be found in southern Fresno and northern Tulare Counties in the southern Sierra Nevada foothills of California (Stebbins et al. 2013). It is distinguished from the closely related *H. annuus* by its tendency to perenniality, nearly continuous year-round blooming, and secondary growth throughout the primary stem (acquired while maturing); this last feature results in a visibly woody trunk in stems that persist for multiple years. When grown in a common garden (Moyers & Rieseberg 2013), *H. winteri* also flowers later and grows taller than typical *H. annuus*. Genetically, *H. winteri* is closely related to nearby

*H. annuus* populations ( $F_{ST} = 0.034$ ) and shows reduced heterozygosity (Baute et al. 2016), consistent with a founder event or population bottleneck. Though closely related, the two species are distinct genetically, with 3.5% of the transcriptome showing differential expression, for example (Moyers & Rieseberg 2013).

In a recent molecular phylogeny (Baute et al. 2016), *H. winteri* samples were found to group within the larger *H. annuus* clade, consistent with *H. winteri* being a young species that originated after *H. annuus* expanded its range to California. As *H. annuus* is hypothesized to have arrived in California only in the last few thousand years (Dorado et al. 1992; Heiser et al. 1969), likely in association with indigenous peoples, this would indeed suggest a very recent origin for *H. winteri*. Within California, *H. winteri* is currently described from nine sites (Stebbins et al. 2013), all of which are relatively open, steep areas on ungrazed hillsides with southern exposure. The sites also have poor, xeric soils that are extremely shallow (10–70 cm) in depth; as the region also experiences seasonal droughts and patchy rainfall, water stress may be a common feature of the *H. winteri* habitat. In this harsh environment, strong selective pressures may have produced the abrupt shifts in life history and development posited for *H. winteri*, with traits such as perenniality and woodiness representing putative adaptations to drought.

## 2.5 Crop Domestication

Sunflower is native to North America, where its progenitor, wild *H. annuus*, still exists today in parts of Canada, the US, and Mexico. According to the most accepted theory, Native peoples in the continental United States first began cultivating this useful plant more than 4,500 years ago. Sunflower had many traditional uses, including for food, medicine, and ceremonial purposes. For example, seeds were eaten raw or roasted and ground into flour or meal to make cakes, crackers, and wafer-like bread (Heiser 1951). The meal might also be rolled into balls for a portable snack or mixed into a nutritious dish with the addition of beans (*Phaseolus* L.), squash (*Cucurbita* spp.), and cornmeal (Wilson 1917). Sunflower oil was also extracted and used for cooking and in ceremonies. Other, non-food uses included the extraction of anthocyanins (from achene coats) to produce a purple dye for basketry and textiles (Whiting 1939), and exploitation of the sturdy stalks for use in construction. Further detail on traditional uses is available in Heiser (1951).

Wild *H. annuus* was originally restricted to the central and southwestern USA prior to the arrival of humankind on the continent but was gradually spread eastwards by native peoples (Seiler 2010). Concomitantly, the artificial selection continually imposed by



early farmers began gradually transforming the wild sunflower (now associated with human settlements) into a single-stemmed plant bearing large seeds in a single large inflorescence (or “head”), very different from the small-seeded, highly branched wild progenitor, with its many inflorescences. This transformation was documented by early European explorers who observed tall, single-headed landraces growing in native communities upon arrival in the 1500s (Putt 1997). Written records and archaeological evidence suggest that this monocephalic sunflower, similar to today’s cultivated types, has been part of Native American culture for at least 30 centuries. Thus, sunflower represents one of the few crops domesticated in temperate North America (Smith 2006).

Archaeological, historical, and linguistic evidence persuasively situates sunflower domestication in the central and eastern US between four and five thousand years ago (Seiler 2010). For example, large achenes (>7 mm in length) have been found at several archaeological sites in the central and eastern US, such as at the Higgs site in eastern Tennessee (dated at 2,850 BP) and the Marble Bluff Rock shelter in northwest Arkansas (2,843 BP) (Smith 2006). Meanwhile, only small (<7 mm) seeds have been recovered from sites in the southwest US and Mexico. Previous work by Heiser (1954) established a length of 7 mm as the upper size limit for wild *H. annuus* achenes, with any larger achenes considered domesticated forms. The oldest evidence of domesticated sunflower comes from the Hayes site in Tennessee, where carbonized sunflower achenes were dated to 4,625 BP.

The possibility of a second independent domestication event in Mexico was raised by Lentz et al. (2001), who described a single achene specimen found at an archaeological site near San Andres, Tabasco in Mexico; this specimen was dated at 4,130 BP. However, upon further examination of the specimen, Heiser (2008) deemed it not to be a sunflower achene, but rather a bottle gourd seed (*Lagenaria siceraria*); this finding was supported by Smith (2006), refuting the multiple origins hypothesis. However, Lentz et al. (2008) have since reported the discovery of three more putative Mexican sunflower achenes from the Cueva del Gallo site in Morales; these large specimens (> 7 mm) were dated to ~2,600 BP but were destroyed in the dating process and so made unavailable for independent confirmation of their identity. While this again raises the possibility of a second domestication event in Mexico, genetic studies of sunflower domestication conducted to date find evidence for only a single domestication event in the eastern US. For example, surveys of neutral markers (e.g., SSRs) have shown domesticated types (both primitive landraces and improved materials) to contain a subset of the diversity found in wild *H. annuus* from the east-central

US, and to be genetically distinct from wild *H. annuus* collected in contemporary Mexico (Harter et al. 2004, Wills & Burke 2006).

The most compelling molecular evidence for a single origin to date comes from Blackman et al. (2011), who sequenced three candidate domestication genes and genotyped 12 neutral SSR markers across a diverse sampling of Mexican landraces and Mexican wild *H. annuus* populations surveyed over a broad geographical range. The three genes and neutral markers all exhibited patterns of variation consistent with a single origin in eastern North America; the results furthermore suggested that all extant cultivated sunflower germplasm (sampled in the study) is derived from this single domestication event. Note, however, that this does not preclude the one-time existence of an independent Mexican crop lineage, now extinct. Despite an exhaustive search, Blackman et al. (2011) may have also missed modern domesticates descended from such an independent Mexican lineage (especially if now rare). Hopefully, future archaeological studies in Mexico will yield ancient DNA samples that could be sequenced to look for evidence of a separate Mexican lineage.

## 2.6 Sunflower Domestication Syndrome

Domestication refers to the genetic modification of a wild species into an altered form suitable for human needs (Doebley et al. 2006). As such, plant domestication is best viewed as a gradual process, rather than a discrete event (Zeder et al. 2006), and the many plant species used by humans today may therefore be arranged on a spectrum, varying in their level of domestication (see e.g., Dempewolf et al. 2008 for examples from the Asteraceae). As the domestication process proceeds, cultivated forms diverge further from the wild type, sometimes into extremely modified forms. The suite of traits that distinguishes domesticates from their wild progenitors is known as the “domestication syndrome” (Hammer 1984). In plants, for example, food crops typically have larger fruits or grains; more determinate growth and stronger apical dominance; and limited natural seed dispersal and seed dormancy, among other traits (Doebley et al. 2006).

In sunflower, the domestication syndrome includes alterations to plant morphology, physiology, and phenology. In both oil- and confectionary-types, branching has been lost, and a single large head has replaced the many small inflorescences typical of wild *H. annuus*. Seed size has also increased for all cultivated types, and achenes no longer disperse, rather remaining until harvest to maximize yield (Burke et al. 2002, 2005). Plant height has been reduced (with even some dwarf forms in use) and is highly uniform

to facilitate mechanical harvest. To reduce reliance on pollinators, cultivated sunflower is also self-compatible (the wild progenitor is an obligate outcrosser) (Wills & Burker 2007). Finally, cultivated sunflower seeds have lost seed dormancy (Seiler 1998), to ensure easy and uniform sowing by growers, and other life cycle and flowering time shifts have taken place, with the goal of shortening and standardizing the time to flower. The specific timing of flowering may vary among elite cultivars bred for different geographic areas (and latitudes) and local environmental conditions, with both day-neutral and long-day photoperiods represented (Goyné & Schneiter 1987, Yanez et al. 2005, Fonts et al. 2008, Wien 2008). Similarly, other morphological traits, such as head shape and tilt or inclination may vary as per the needs in specific areas (e.g., to reduce sunburn, bird damage, and head rot disease incidence) (Marinković et al. 2003, Kaya 2015).

Genetically, domestication was not cohesive in sunflower, owing to selection for different uses (oil vs. confectionary) and the subdivision of germplasm into different heterotic groups (Baute et al. 2015). Molecular studies of sunflower domestication have revealed a large number of genes involved, with the majority of genes having small or moderate phenotypic effects (Burke et al. 2002, Wills & Burke 2007, Baute et al. 2015, Radanovic et al. 2017). Moreover, as with other crop species, sunflower shows evidence of multiple breeding and domestication bottlenecks (Tang & Knapp 2003, Liu & Burke 2006), despite its relatively high phenotypic diversity. For example, the consensus among population genetic assessments is that cultivated germplasm retains only about two-thirds (50–67%) of the genetic diversity present in wild *H. annuus*, with higher levels of genetic diversity observed in landraces versus elite cultivars (Kolkman et al. 2007, Mandel et al. 2011, Hübner et al. 2019). Furthermore, Mandel et al. (2011) determined that the bulk of cultivar diversity is present in wild sunflower populations from the east-central USA, the same region in which domestication occurred.

## 2.7 Early Breeding Work and Development of High-Oil Cultivars

After domestication in North America, cultivated sunflower was brought to Europe in the 1500s, where it was initially adopted as a garden ornamental. Historical records suggest that Spanish explorers were responsible for this introduction in 1510 (Zukovsky 1950), although Heiser (1950) credits the herbalist Dodonaeus with introducing the sunflower in 1568; note that the sunflower illustrated by Dodonaeus was a single-headed type resembling a modern cultivar. From Spain, sunflower travelled to Italy and France, where botanists and physicians took an interest in this

impressive, large-statured plant; this resulted in further dispersal of the sunflower to gardens in Belgium, England, Germany, the Netherlands, and Switzerland (Putt 1997). By the end of the 1600s, cultivated sunflower had continued its spread further eastwards in Europe. Along the way, sunflowers also attracted attention as an edible plant, with the petioles and young flowers eaten as vegetable delicacies. The practice of consuming sunflower seeds was first recorded in 1740 and later became common (Semelczi-Kovacs 1975), but the seeds were not routinely used as a source of oil at this time.

Also in the 1700s, Peter the Great is believed to have introduced sunflower into Russia, after first encountering the plant in the Netherlands (Zukovsky 1950). First grown as an ornamental in Russia (as in Europe), sunflower was later cultivated specifically for oil, potentially as early as the late 1700s (Putt 1997). Yet it took until the 1830s and 1840s for the Russian manufacture of sunflower oil to begin on a commercial scale (Atkinson et al. 1919, Clydesdale & Hart 1948, Quesenberry et al. 1921). Sunflower oil became increasingly popular, most likely because its use was not specifically forbidden by the Holy Orthodox Church of Russia during Lent, when many other oils were prohibited (Heiser 1955, Heiser 1976). As a result, sunflower cultivation expanded rapidly, and, by the beginning of the 1900s it was a major crop in Russia, with annual production at 21.5 million hectares from 1911–1916, for example (Hensley 1924). Importantly, two types of seeds were grown: a thin-hulled round type used for oil extraction (200–300 g/kg of oil) and a larger thick-hulled type for direct consumption (150–200 g/kg of oil) (Putt 1997).

In step with this increase in cultivation, Russian sunflower breeding commenced in earnest in the late 1800s, with a particular focus on oil content and sunflower moth resistance (*Homoeosoma nebulella* Hb.). By 1925, breeding programs were underway at several agricultural institutes and experimental stations, the most important of which was located at Krasnodar. Here, V. S. Pustovoit, the “father of modern sunflower breeding”, devoted his breeding program to enhancing oil content while preserving (or even improving) seed yield. While seed oil content averaged 330 g/kg in the 1940s, under Pustovoit’s guidance this increased to upwards of 500 g/kg in some cultivars by 1965. The improved, high-oil cultivars produced by Pustovoit eventually spread to Europe and other parts of the world, stimulating sunflower production elsewhere. Today, the bulk of the modern cultivated germplasm available worldwide has its roots in the Russian high-oil breeding programs (Korell et al. 1992; Burke et al. 2002).

## 2.8 Global Dispersal of Crop Sunflower

Sunflower returned to North America via Russian immigrants, who arrived beginning in the late 1800s with cultivated sunflower seeds in hand. Mennonite communities played a particularly important role in reintroducing cultivated sunflower to the United States and Canada; for Mennonites this was a culturally significant crop, grown in kitchen gardens to produce edible seeds for human and animal consumption (Putt 1997). Other avenues of reintroduction include the US consul in St. Petersburg, who sent cultivars to the USA in 1893, and American seed companies, which began offering cultivar seeds (e.g., for “Russian Mammoth”, a particularly large variety) in catalogues about the same time (Semelczi-Kovacs 1975). Much of the early use in North America (1900 to 1940s) was for silage (i.e., animal feed) and scratch feed for poultry.

The advent of World War II led the Canadian government to investigate the oilseed potential of cultivated sunflower, as a means of reducing national dependence on imported sources of edible oil; for this purpose, a breeding program was established in the 1930s (Putt 1997). To produce oil, the tall, late-maturing cultivars grown for silage were inappropriate, and both Mennonite cultivars and Russian imported lines were utilized instead, as these were shorter and earlier (i.e., more amenable to mechanical harvest). One cultivar in particular, a Russian import named S-490, was eminently suitable, being of short (almost dwarf) stature and with high seed oil content; S-490 was later increased and licensed as Canada’s first cultivar, “Sunrise”, in 1942. Around this time, work by the Canadian breeder Eric D. Putt revealed the benefits of heterosis, or “hybrid vigour”, in sunflower (Putt 1940, Unrau 1947); heterosis refers to the phenomenon whereby the hybrid progeny of inbred lines out-perform the parental lines, surpassing them in yield. Crossing “Sunrise” with an early Mennonite inbred line, the first hybrid, “Advance,” was released to the Canadian public (Unrau & White 1944), followed by “Advent” (added rust resistance) and “Admiral” (slightly earlier flowering). However, the commercial production of early hybrid seed was inefficient (owing to problems with self-pollination), and the full benefits of heterosis was not practically realized (Putt 1962).

The landscape for sunflower production in North America changed radically in the 1960s owing to two important developments.

(1) The first was the introduction of high-performing USSR cultivars, derived from Pustovoi’s breeding program, which continued to underpin major perfor-

mance enhancements in sunflower breeding. These cultivars were comparable to Advent and Admiral (in terms of earliness and yield) but had much higher oil content (Putt 1965). One cultivar in particular, “Peredovik”, was licensed in Canada in 1964 and represented a boon for the industry, vastly increasing the efficiency of processing and therefore the profitability of sunflower crops. At this time, sunflower was adopted more broadly as an oilseed crop in the USA, as the new high-oil cultivars made the crop more economically attractive. By 1967, commercial crushing began in the US (in North Dakota and Minnesota), USDA expanded its sunflower research program, and the National Sunflower Association was founded to promote the crop.

(2) In 1968, the second important development occurred, with the discovery of cytoplasmic male sterility (CMS) (Leclercq 1968) and the subsequent identification of fertility-restoring genes (Kinman 1970). Using these discoveries allowed sunflower breeders to overcome the challenges of early hybrids (e.g., Advance) and to efficiently produce hybrid seed (via an exclusively female parent). The CMS system was rapidly adopted, adding further value to the sunflower industry in addition to that already imparted by USSR-derived high-oil cultivars.

These twin breakthroughs fostered a new age of trait development for sunflower, allowing seed companies to develop distinct varieties and focus on other breeding goals (disease resistance, etc.). The healthful properties of sunflower oil (as compared to saturated fats) were also recognized around this time, leading to further gains for the sunflower industry in the 1970s, as sunflower oil became increasingly popular.

Outside of Russia and Eastern Europe, North America is widely regarded as the first area to cultivate sunflower commercially, but significant interest also existed on other continents. For example, China and India saw commercial use beginning in the 1920s (Jamieson & Baughman 1922). Similarly, European immigrants brought cultivated sunflower to Argentina as early as the 1920s, where it was used for seed and oil production; by 1938, sunflower oil accounted for 66% of the total edible vegetable oil produced in Argentina (Putt 1997), a trend which continues today. Major sunflower production centers also developed in Europe. Today, the crop is truly global, produced in temperate zones worldwide. The world production of sunflower in 2021 covered over 27 million hectares in 60 countries. As a comparison, palm oil world production in 2021 covered 29 million hectares (FAOSTAT 2023).



### 3 EX SITU CONSERVATION IN THE GLOBAL SYSTEM: COMPOSITION

A sunflower conservation strategy questionnaire was circulated to 28 institutes holding “large” collections (>100 accessions each) and 32 institutes holding “small” collections (10–100 accessions each). The questionnaire was comprehensive, collecting details on each institute’s: current *Helianthus* holdings (both cultivated *H. annuus* and other *Helianthus* species, if applicable); *ex situ* conservation facilities; germplasm management and collection documentation practices; patterns of distribution and use; involvement in networks and partnerships; and vulnerabilities for long-term conservation. For more information, please refer to Appendix 1, which presents the questionnaire in its entirety. For a list of the institutes surveyed, please see Appendix 2. The questionnaire was initially circulated beginning in June 2021 and closed in mid-September 2021, upon receiving sufficient responses. A total of 17 large collections returned questionnaires (61% return rate). Ten of the “small” collections returned a full survey (a 37.5% response rate), with two additional collections noting that they conserve only *H. tuberosus* (NOR017, SWE089), and two more respondents (MEX201, SWE054) noting they no longer maintain *Helianthus* collections.

The *Helianthus* collections described by questionnaire respondents were established from 1948–2017, ranged from 11–5,248 accessions, and conserved 1–53 *Helianthus* species. A total of 14 collections (or nearly half) held only a single *Helianthus* species, either *H. annuus* L. (the oilseed and confectionary crop) or *H. tuberosus* L. (the tuber crop, Jerusalem artichoke). Most questionnaire respondents represented governmental organizations (n = 25); the remaining respondents included two government-university partnerships, one university and one “public research institution”. No private organizations or NGOs were represented. For the most part (n = 22, or 76%), questionnaire respondents reported that

their institution operated under a national conservation plan or strategy. In terms of decision-making specific to the *Helianthus* collection, genebank priorities were most often set (at least in part) by the collection curator(s) (62% of respondents), or the organization/department management (24%). Other decision-makers described by respondents included: affiliated organizations (e.g., other national genebanks or active *Helianthus* collections), germplasm source countries, governing committees, scientific committees, and multidisciplinary national networks.

In the consolidated dataset from the survey data, a total of 30,903 accessions of *Helianthus* species (including the two cultivated species) were identified at 29 institutes. An additional 193 accessions had no species identity assigned, and 24 accessions were unspecified hybrids. Listed species names were standardized to currently accepted names (see Appendix 3 for a species list, and also GRIN Taxonomy). Overall, there were 74 taxa conserved by survey respondents for a total of 55 species.

Accession information provided by other curators and retrieved from the literature (Terzić et al. 2020) was used for two large collections that did not respond to the questionnaire: IND001 and UKR001. Accession level information on sunflower genetic resources conserved worldwide was also compiled from two international databases: *Genesys* and *WIEWS* (FAO’s World Information and Early Warning System on Plant Genetic Resources for Food and Agriculture). In compiling the data in one combined dataset, taxa were standardized using the species list for *Helianthus* described given in Appendix 3 and duplicates (the same accession reported in both databases) between the two databases removed to avoid double counting the same accessions.

To estimate the total number of *Helianthus* accessions conserved globally, data were merged on an institute-by-institute basis from all three listed sources: the sunflower questionnaire, the supplementary data (obtained from curators or the literature), and the international genebank database search. For each institute, accession data were preferentially taken from the questionnaire or supplementary datasets over that from the database search (Appendix 4). Three collections were known only from the survey (BGR029, IND041, SRB002): i.e., their accession data were not reported to either Genesys or WIEWS. The collections of all other questionnaire respondents were also represented in the database search results, to varying extents (accession numbers differed in 69% of cases). For several institutes, the size of their

*Helianthus* collection differed significantly between their questionnaire response and the genebank database results: ARG1348 (n = 909 accession difference), FRA015 (n = 1,220), and ROM002 (n = 1,698). This highlights the dynamic nature of collections and reinforces the importance of the questionnaire for obtaining accurate, up-to-date collection information.

In the compiled data, a total of 40,501 accessions were identified from 107 institutes. Collections with 100 or more accessions are shown in Table 3.1, and the full list is provided in Appendix 4. Each institution was assigned to one of five geographical regions: America (1), Europe (2), Asia (3), Africa (4), and Australia (5).

**Table 3.1** Overview of the composite dataset of *Helianthus* plant genetic resources conserved *ex situ*, including the data source, FAO code, region where institute located, total number of accessions, number of accessions for select species and CWRs, and number of species described for each institute. Only collections with 100 or more accessions are shown. The full list is in Appendix 5.

FAO INSTOCDE	Data source	Region	<i>Helianthus annuus</i> L.	<i>Helianthus tuberosus</i> L.	<i>Helianthus</i> spp.	<i>Helianthus</i> non specified hybr.	Accessions of CWR	Accessions all species	Number of species
USA020	Survey	America	3710	90	12	10	1426	5248	53
BGR029	Survey	Europe	4625	70	0	0	195	4890	31
IND041	Survey	Asia	3444	0	0	0	24	3468	6
FRA015	Survey	Europe	2870	194	10	0	316	3390	49
RUS001	Survey	Europe	2608	12	0	8	81	2709	30
BRA014	Databases	America	1834	1	11	8	198	2052	17
BRA003	Survey	America	1620	5	3	3	259	1890	28
ROM002	Survey	Europe	1828	3	0	0	29	1860	14
IND001	Supplementary	Asia	1570	2	8	0	16	1596	11
AUS165	Survey	Australia	1296	1	26	3	108	1434	23
POL003	Databases	Europe	1113	1	28	0	0	1142	2
HUN003	Databases	Europe	1056	0	0	0	8	1064	7
MAR088	Survey	Africa	1014	0	0	0	0	1014	1
ARG1348	Survey	America	922	0	0	0	0	922	1
CAN004	Survey	America	603	174	0	0	4	781	4
UKR012	Survey	Europe	600	16	7	0	68	691	22
DEU146	Survey	Europe	468	90	105	0	16	679	12
TUR001	Databases	Europe	666	0	0	0	0	666	1
UKR001	Supplementary	Europe	510	2	0	0	74	586	29
SRB002	Survey	Europe	76	145	0	0	303	524	28
BGR001	Survey	Europe	420	0	30	0	10	460	7
TUN029	Survey	Africa	400	0	0	0	0	400	1
URY003	Databases	Europe	299	0	0	0	0	299	1
ESP004	Survey	Europe	195	0	0	0	0	195	1
JPN183	Databases	Asia	61	126	0	0	0	187	2
PAK001	Databases	Asia	184	0	0	0	0	184	1
MEX006	Databases	America	150	0	0	0	0	150	1
ECU023	Survey	America	122	0	0	0	0	122	1
ETH085	Databases	Africa	113	0	0	0	0	113	1
BLR011	Databases	Europe	105	0	0	0	0	105	1
BLR026	Databases	Europe	101	0	0	0	0	101	1

The data analysis reported in the rest of this strategy was conducted on this combined, consolidated dataset at the species level. Appendix 5 summarizes the number of accessions conserved *ex situ* and the number of institutes conserving them for each of the 55 *Helianthus* species in the consolidated dataset.

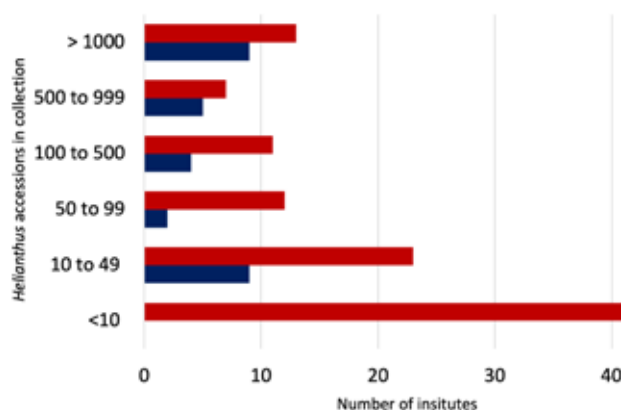
The distribution of accessions among the 107 institutes is illustrated in Figure 3.1, which shows that about 60% of the collection holders had fewer than 50 accessions. Nineteen institutions conserve about 90% of the total accessions and *H. annuus* accessions held globally, 61% of the *H. tuberosus* accessions held globally, and 89% of the CWR accessions held globally (for all other wild species). Thus, the current global system is characterized by a small number of institutions that hold nearly all globally conserved accessions.

The adequacy of the regional and global sampling in the survey was assessed and the results given in Table 3.2 in terms of the proportion of the regional and global number of accessions that were included in the survey respondents. Among the questionnaire respondents, a total of 25 countries were represented. Although many responses were received from European nations, at least one response was received from all five regions (described below). As such, the questionnaire respondents generally reflected the global distribution of sunflower as a crop. Overall, the survey respondents conserved about 77% of the total number of accessions held globally. The survey respondents generally represented a very good sample of the collections within their region; the exception was Asia, where survey respondents conserved the lowest proportion of the total regional accessions (60%), due mainly to the limited number of respondents. There was also a limited number of respondents from Africa, but they had larger collections.

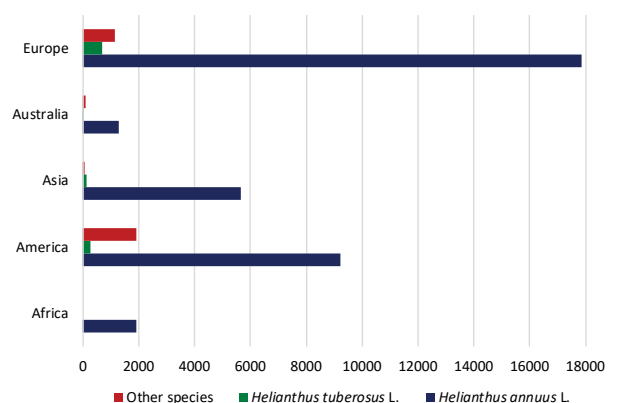
Over all institutions listed in Appendix 4, there were 35,955 accessions of *H. annuus*, 1,090 accessions of *H. tuberosus*, and 3,178 accessions of other *Helianthus* species, 246 accessions not identified at the species level, and 32 non-specified hybrids. A total of 76 institutes (or 71%) held only a single *Helianthus* spe-

cies; among these, 62 institutes held only *H. annuus*, while the remaining 14 held only *H. tuberosus*. In the survey, *Helianthus annuus* was the most conserved, species with a total of 27 institutes holding *H. annuus* accessions, whether cultivated or wild (or both). The remaining two institutes (NOR017 and SWE089) held only *H. tuberosus* accessions. Regionally, very few accessions of species other than *H. annuus* are conserved outside the Americas and Europe (Figure 3.2).

A total of 29,242 *H. annuus* accessions were documented in the questionnaire and supplementary data, and a detailed breakdown of *H. annuus* accession holdings by institute is given in Table 3.3.



**Figure 3.1** Proportion of institutes conserving more than 1,000 accessions, 500 to 999 accessions, 100 to 499 accessions, 10-49 accessions, and fewer than 10 accessions; including all institutions responding to the survey plus supplementary data.



**Figure 3.2** Number of accessions of *H. annuus*, *H. tuberosus*, and all other *Helianthus* species for each region individually.

**Table 3.2** Number of *ex situ* conserved sunflower genetic resources in the five world regions and globally (data from databases and survey), and percentage of accessions in the region that were conserved by the survey respondents (data from survey).

Region	Total number of institutions regionally	Number of accessions conserved regionally	Total number of institutions in survey regionally	Number of accessions in the survey regionally	% of accessions regionally conserved by survey respondents
Africa	18	1913	4	1524	80%
America	19	11437	5	8963	78%
Asia	19	5839	3	3532	60%
Australia	1	1434	1	1434	100%
Europe	50	19878	16	15667	79%
Globally	107	40501	29	31120	77%

When subdivided by type, accessions derived from research programs (advanced lines, improved varieties, breeding and/or research materials, and specialized genetic stocks) accounted for 53% of all the accessions of *H. annuus* conserved by the survey respondents.

Across all survey respondents, the proportion of breeding and/or research related accessions ranged from 0–98% (of the total), with seven institutes for which >70% of all accessions were breeding and/or research materials. This is a very high proportion of the total global accessions conserved, but this is not unexpected given the history of breeding and germplasm exchange for cultivated sunflower.

Obsolete and/or traditional cultivars and landraces were less well represented. More research is needed to better understand the unique genetic diversity of landraces and traditional open-pollinated varieties

(OPVs), but together these only represent 14% of the total number of accessions conserved among the survey respondents and only nine of the respondents held more than 100 accessions of these two types.

It must be acknowledged that cultivated sunflower does not fit nicely into the categories presented in Table 3.3, and many survey respondents struggled to allocate accessions to categories that, in hindsight, were not clearly defined in the survey.

In the survey questions it was assumed that respondents had a shared understanding of sunflower landraces as *H. annuus* cultivated by early farmers of the native American tribes. But it seems that this definition is not shared among all the survey respondents, as many respondents applied a broader definition of landraces than the one used in the questionnaire.

**Table 3.3** Number of *Helianthus annuus* accessions by institute and germplasm type (source Sunflower Collections Survey 2021 and supplementary data, n = 28).

Institute code	Total	Landraces	Obsolete/traditional cultivars	Advanced/improved cultivars	Breeding/research materials	Specialist genetic stocks	Wild or weedy populations	Unknown or other
BGR029	4,625	0	0	0	4,500	0	125	0
USA020	3,710	199	300	0	1,043	88	1,063	1,017
IND041	3,444	0	5	350	300	97	44	2,648
FRA015	2,870	115	618	599	668	170	700	0
RUS001	2,608	0	943	50	1,275	0	340	0
ROM002	1,828	50	11	98	1,570	34	65	0
BRA003	1,620	0	0	0	0	0	0	1,620
IND001	1,570	0	341	169	281	87	455	237
AUS165	1,296	10	0	248	582	79	112	265
MAR088	1,014	100	0	0	903	0	0	11
ARG1348	922	34	117	322	351	0	98	0
CAN004	603	20	10	152	418	0	3	0
UKR012	600	203	60	5	61	261	2	8
UKR001	510	0	16	168	244	56	26	0
DEU146	468	143	0	153	143	0	18	11
BGR001	420	8	0	0	0	0	0	412
TUN029	400	0	400	0	0	0	0	0
ESP004	195	195	0	0	0	0	0	0
ECU023	122	0	0	0	0	0	0	122
CZE122	93	2	0	58	33	0	0	0
ZMB048	70	0	0	0	0	0	0	70
SRB002	76	0	0	0	0	0	76	0
ZWE049	44	44	0	0	0	0	0	0
LSO015	40	40	0	0	0	0	0	0
ROM007	39	35	0	0	4	0	0	0
ALB026	22	7	0	0	0	0	0	15
MMR015	20	0	0	0	0	0	0	20
GBR004	11	0	0	0	0	0	11	0
ITA368	2	0	2	0	0	0	0	0
Total	29,242	1,205	2,823	2,372	12,376	872	3,138	6,456
Percentage	100%	4%	10%	8%	42%	3%	11%	22%

Some respondents considered landraces also cultivated varieties of *H. annuus* that have adapted to a specific ecogeographical region also when this area is not the primary center of diversity and domestication. Indeed, several respondents indicated that landraces and traditional cultivars were not distinguished in the records of their institute; hence, there may be a certain amount of overlap between these two categories.

Also, survey respondents were asked to quantify the number of traditional varieties. In this case, a shared understanding of sunflower “traditional varieties” was assumed as OPVs (developed in the era pre-hybrid breeding), but excluding the landraces cultivated originally by early farmers of the native American tribes. Instead, it seems that some curators have divided their OPVs between the traditional and modern/improved categories. Many of the OPVs were created in Russia and it is not very well understood to what extent there are older, unique OPVs specific to particular regions/countries. Thus, in areas of the world where there has been introduction and breeding for a long time, such as Europe, distinguishing between the types of obsolete or traditional varieties would be difficult. In hindsight, in the survey it would have been better to give a specific definition for each of these categories of germplasm, and to ask specifically about the number of accessions that were OPVs versus hybrid parental lines.

Generally, there is a lack of understanding of the unique diversity of sunflower cultivated material, since much of this diversity now resides in private collections. Thus, conservation and research on locally adapted genetic resources can be considered a gap for the cultivated sunflower that needs to be addressed.

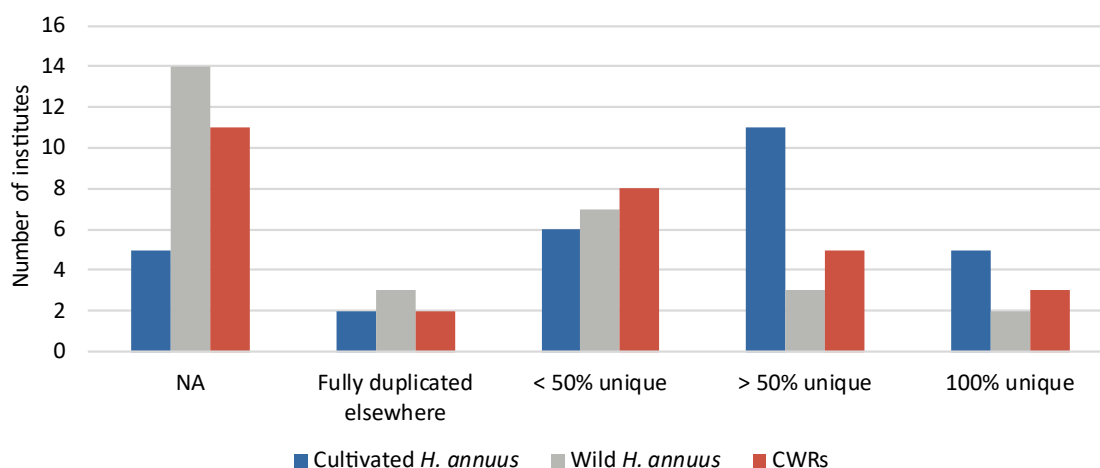
The respondents were asked about the origin of the accessions that they were conserving. The number of countries that were the source for the accessions

ranged from 1 to 61, with five of the institutions (AUS165, DEU146, FRA015, RUS001, and USA020) indicating that they conserved accessions that were received from more than 30 countries. Overall, for ten institutions >60% of accessions were derived from international donors, while for twelve institutions >60% of their accessions were derived from national sources, collections, or donations. This demonstrates the high degree of historical germplasm exchange for sunflower, although eight institutions did indicate that 100% of their accessions were of national origin. This history of sharing accessions (both of cultivated and wild materials) between institutes means there are likely substantial overlaps among *Helianthus* collections. Materials of national origin (e.g., cultivated lines or breeding materials developed in the country where they are conserved) are likely to be more unique.

The survey respondents were also asked to rate the degree of uniqueness for the accessions they conserved. Figure 3.3 summarizes the responses for cultivated and wild sunflower, as well as CWRs. Very few institutes (2 or 3) rated their accessions as 0% unique. For the cultivated sunflower accessions there were 5 institutes that rated their accessions as 100% unique. Overall, 11 institutes concluded that the cultivated sunflower accessions were more than 50% unique and 7–8 institutes concluded that accessions they conserved from the wild sunflower and CWR were less than 50% unique. This is likely an indication of the high degree of duplication for wild accessions, for which there are fewer accessions overall globally (Appendix 4).

### 3.1 Sunflower wild relatives

In terms of sunflower wild relatives, the 14 survey respondents conserving *Helianthus* species other than the cultivated ones held 90% of the accessions of the *Helianthus* species that are conserved globally. Most



**Figure 3.3** The number of institutes that indicated the accessions of cultivated and wild *H. annuus* as well as the CWRs were 0% (fully duplicated elsewhere), <50%, >50%, or 100% unique, NA = not applicable. n = 29. Source: 2021 survey.



of these accessions are held by USA020 (1,426 accessions from 51 species), FRA015 (316 accessions from 47 species), SRB002 (303 accessions from 26 species), BRA003 (259 accessions from 26 species), and BGR029 (195 accessions from 29 species). The USDA collection at USA020 has the largest and most diverse collection of these other *Helianthus* species.

Appendix 6 shows for each *Helianthus* taxon its *in situ* conservation status according to available assessments. In general, 19 of the species were of Least Concern, with stable population trends. Marek et al. (2019) pointed out that the majority of sunflower CWRs are abundant in North America, but that there are also species with a more limited distribution. Modeled distribution, extent of occurrence, and area of occupation (IUCN, 2012) for 71 taxa are available from Khoury and Carver (2020).

According to data in the combined dataset (survey and databases), when analyzed at the taxon level (Appendix 5) there are five annual species, three diploid perennials, and two perennials with over 100 accessions conserved at 10 to 16 institutions and these species are better represented and securely conserved in the global system (see details in Appendix 5).

Several species are only conserved by a limited number of institutions. This is largely due to practical difficulties, as many wild species are challenging and expensive to regenerate. In particular, many of the perennials have highly-specific edaphic needs and cannot be grown to seed outside the US. These are well conserved by the USDA and available to anyone requesting germplasm. Curators participating in the consultations for this strategy document suggested that a global system where only a few major institutes, with adequate resources and located where species grow well, conserve wild species and make them available for distribution is the most sustainable since it is not practical for smaller institutes to keep them. However, it must also be noted that there is a trade-off between efficiency and security, as a system where accessions of a species are conserved only in one or a few institutions is less secure than a system where these are conserved in multiple institutions.

Only two described species are not currently conserved *ex situ*: *Helianthus inexpectatus* D. J. Keil & Elvin, and *Helianthus x intermedius* R. W. Long. Additionally, in our analysis we find only one record of *ex situ* accessions for *Helianthus annuus* subsp. *texanus* Heiser. This is likely due to the fact that, although there is evidence that the Texas populations of *H. annuus* are genetically distinct, these are currently considered ecotypes rather than a subspecies (Todesco et al 2020). Some wild *H. annuus* from southern Texas conserved at USA20 could be considered as subsp. *texanus*, if this

was recognized as subspecies (Marek personal communication 2023).

*Helianthus inexpectatus* is a recently described tetraploid perennial species from southern California (Keil & Elvin 2010), where it is known from only a single small population; it has not been included to date in any broader treatises on the genus. *H. x intermedius* is a natural hybrid of *Helianthus grosseserratus* M. Martens and *Helianthus maximiliani* Schrad. initially recognized by Heiser et al. (1969).

In addition to the three species described above, one particular subspecies of *Helianthus niveus* (Benth.) Brandegees, *H. niveus* subsp. *niveus*, is also not currently listed as conserved *ex situ*. This subspecies, which is restricted to Baja California, is quite distinct from the other two recognized subspecies of *H. niveus* (subsp. *canescens* (A. Gray) Heiser and subsp. *tephrodes* (A. Gray) Heiser), not only phenotypically, but also genetically and reproductively (Zhang et al. 2019). As such, it merits conservation, but given current limitations on accessing natural populations in Mexico, it has rarely been collected to date.

As a group, the annual *Helianthus* species are generally not well conserved, with seven of the twelve species having poor representation in the global system. There are several perennial species (typically with restricted ranges) that are poorly represented, such as *H. winteri* J. C. Stebbins, *H. carnosus* Small, *H. x multiflorus* L., *H. arizonensis* R. C. Jacks, *H. verticillatus* Small, and *H. x daronicooides* Lam.

As highlighted in the sunflower survey results, sunflower CWRs are generally well-conserved globally, in large part due to the efforts of USDA. As part of its mandate, the US National Plant Germplasm System (NPGS) (managed by the Agricultural Research Service [ARS] of USDA) seeks to safeguard the genetic diversity of agriculturally important plants for the US, including sunflower. This includes the collection and conservation of CWR diversity; in the case of sunflower, all currently recognized *Helianthus* species ( $n = 54$ ) are conserved within the NPGS system. As these species are almost all native to the US (with a majority also endemic there), USDA has taken the lead with regards to their *ex situ* conservation, holding some 1,538 CWR accessions. However, it must be noted that *Helianthus niveus* subsp. *niveus* is native to Mexico, has not been much collected, and it likely should be viewed as a separate species (Zhang et al. 2019).

The adequacy of the USDA CWR collection for sunflower is also explored in a recent conservation gap analysis for a national inventory of 600 CWR taxa native to the US (Khoury et al. 2020). This analysis compiled occurrence information for each taxon, and

modeled their distribution, then used ecogeographic tools to identify significant conservation gaps. Sunflower fared well as compared to other crops, having a final conservation score higher than all but two other crops. While some *Helianthus* species are represented by few accessions within the USDA-NPGS, these represent species with highly restricted distributions. As compared to *H. annuus*, many wild species have limited geographic distributions, likely due to edaphic factors. As such, only a small number of accessions are needed to capture the limited diversity in the wild (for narrow endemics such as *H. carnosus*, *H. winteri*, etc.). Nonetheless, the curator of the USDA collection identified the need for further collections in Canada and the Eastern US (to some extent) to sample within-species diversity more broadly for several CWRs. The most significant collection gap within the USDA collection, however, was felt to be the lack of germplasm from Mexico, which represents the southern range limit of several *Helianthus* species.

*Helianthus* diversity is concentrated towards the north within Mexico, particularly in the states of Baja California, Chihuahua, Coahuila, and Sonora. Perennial species are especially diverse here, but there are also large populations of the annuals *H. annuus* and *H. neglectus* at lower elevations, as well as *H. petiolaris* at higher elevations (such as within the Northern mountains in Chihuahua and Sonora). A 2015 survey (conducted by Dr. Dylan O. Burge) identified unique peripheral populations for these annual species near their southern range limit, within a zone extending ~150 km south from the Mexico-US border. The survey also noted unique diversity on the US side of the border (e.g., atypical *H. petiolaris* populations and interesting hybrid swarms), but the most novel materials (compared to previously described populations) were observed within Mexico. For example, two novel annual morphotypes ("*lanatus*" and "*rugosus*") of *H. niveus* ssp. *niveus* were documented in Baja California, with distinctive traits not typically seen in ssp. *niveus*. This observation prompted a follow-up survey in 2016 to catalogue the morphotypes, as well as a combined analysis of all three *H. niveus* subspecies (Zhang et al. 2019). These genetic and phenotypic analyses identified *H. niveus* ssp. *niveus* as a fully-fledged species, distinct from the other two *H. niveus* subspecies.

Outside of this "high diversity" zone in Northern Mexico, there has been little in the way of exploration for wild sunflower populations in Mexico. Species and genetic diversity are expected to decline further south, as fewer *Helianthus* species occur (and those that do, approach their southern range limits). A few perennial species are known to be distributed further south into Mexico, and there may also be naturalized populations of *H. annuus*. The northern states in Mexico may have particularly diverse sunflower populations owing to

high habitat heterogeneity in this topographically complex region. This habitat diversity has translated into high genetic and species diversity in other plant genera occurring in the same region (e.g., Ponderosa pine).

Mexican populations of both annual and perennial *Helianthus* species are particularly important to document and conserve as they occur near their southern range limits. Populations at warm-edge range limits may contain useful diversity (e.g., alleles for heat or drought tolerance) for adapting sunflower crops to future climates. Understanding *Helianthus* diversity within Mexico is also critical to forming a complete picture of the genus, particularly for those species with ranges extending outside of the US. *Helianthus paradoxus* represents a cautionary tale. Within the US, *H. paradoxus* is scarce, with only a few documented populations. This scarcity, in combination with threats to existing populations, led to the classification of *H. paradoxus* as a federally threatened species in 1999 by the US Fish and Wildlife Service. However, *H. paradoxus* is now known to be an order of magnitude more abundant in Mexico. For many years, evidence of its existence was "hiding in plain sight" as a series of voucher specimens collected in the 1960s by researchers from the Universidad Nacional Autónoma de México (UNAM). Without an in-country sunflower expert, these specimens long went unnoticed, but were recently rediscovered; field surveys have since confirmed the presence of *H. paradoxus* in Mexico. The Mexican populations are morphologically distinct from those in the US, prompting a call to designate them as a separate subspecies, *H. paradoxus* ssp. *mexicanus* (Sivinski 2016).

Future field research and extensive collections are needed to fully document *Helianthus* species in Mexico, including their abundance and distribution, genetic diversity and population structure, and morphological variation. Given that these populations are likely highly unique (both phenotypically and genetically), it is a top priority to also preserve germplasm from across the range of each species (capturing ecogeographic variation) in *ex situ* collections.

Generally, there are still gaps in the *ex situ* conservation of wild *Helianthus* species, and this is a significant risk for the long term improvement of the cultivated *Helianthus* species. These gaps need to be addressed within the global system with an increased focus on collection, *ex situ* conservation, and safety duplication and with a greater focus on securing the species in protected areas. This could be done with complementary *in situ* and *ex situ* conservation, with priorities for *ex situ* conservations set by the conservation status of the *in situ* populations, and with opportunities to periodically re-sample from the populations when needed.



Seed packets containing sunflower seeds that are being deposited by IPK in the Svalbard Global Seed Vault. Photo: IPK

## 4 EX SITU CONSERVATION IN THE GLOBAL SYSTEM: CONSERVATION

When asked about the purpose of their *Helianthus* collections, long-term germplasm conservation was cited by most questionnaire respondents (85%) as an important objective. Providing germplasm for academic or educational use was another common objective (67%), as was hosting a working collection for public breeding or research programs (63%). Other uses included working collections for private breeding or research use (33%), as well as reference collections (15%). Additionally, one respondent listed the reintroduction of older varieties, and promotion of their use, as a key objective.

To assess how securely accessions are conserved *ex situ*, institutes were asked to describe the storage conditions and genebank facilities for their *Helianthus* collections. Data were analyzed for 25 questionnaire respondents, excluding the two institutes holding only cultivated *H. tuberosus* (NOR017 and SWE089). All accessions were conserved as seeds.

**Short-term storage facilities** were described for only four institutes. These included warehouses or other rooms (n = 3) and a refrigerator (n = 1). Temperature was controlled in three cases (range = 4–19°C) and humidity in two cases. Packaging for seeds was a mixture of paper envelopes or bags (n = 4) and cloth bags (n = 1); note these categories are not mutually exclusive.

**Medium-term storage facilities** were described, at least in part, for 13 institutes. In all cases these facilities were climate-controlled, with most institutes using cold chambers (n = 12) and one institute using a freezer. Temperature was controlled at an average of 2.9°C (range = -4°C to 8°C). Humidity was controlled in three cases (range = 17.5–55%). Packaging was diverse: sealed, vacuum-packed aluminum packs (n = 5); glass containers (5); paper envelopes or bags (3); sealed aluminum packs (1); plastic containers (1); and cloth bags (1).

**Long-term storage facilities** were described for 19 institutes; all were climate-controlled. Facilities included cold chambers (n = 12) and freezers (n = 7). Temperature was controlled at a range of -20°C to 4°C. Humidity was controlled in nine cases (range = 5–30%). Packaging was again diverse: sealed aluminum packs (n = 9); sealed, vacuum-packed aluminum packs (8); glass containers (4); glass containers (4); plastic containers (2); paper envelopes or bags (2); and metallic cans (1).

Using information on the number of accessions held by each institute, most accessions were found to be conserved under long-term storage conditions (Table 4.1), followed by medium-term storage conditions and short-term storage conditions. Note that these categories are not mutually exclusive, and while a slight majority of genebanks (56%) maintained accessions only in one storage type (either short-, medium- or long-term), in many cases accessions were maintained in more than one mode, depending on genebank purposes. For example, as an active distributor of seeds, USDA (USA020) was the only institute preserving some fraction of accessions in all three storage modes. More commonly (n = 10 institutes), institutes kept a portion of accessions in two storage modes (usually medium- and long-term storage).

To ensure the safety of conserved accessions, institutes utilized a variety of approaches to monitor that target temperatures and/or humidity were met (Table 4.2). For short- and medium-term storage, a daily visit to check on the collection, as well as internal temperature monitors (for the cold chambers or freezers), were the most common monitoring tools. For long-term storage, use of internal temperature monitors was again common practice, and the use of an automated monitoring system was also common. As expected, accessions in long-term storage were most carefully monitored, and redundant checks were often used. Over all storage modes, internal temperature monitors were the most used tool, followed by a daily visit from genebank/security staff and an automated monitoring system. Only one genebank did not routinely monitor conserved accessions in any way.

As sunflower produces orthodox seeds, seed viability is best preserved by drying achenes prior to storage. Indeed, achenes were typically dried before storage, especially for medium term storage (85% of respondents) and long-term storage (95% of respondents).

A range of facilities were available to genebanks to support their germplasm conservation activities:

- Separate work areas for ‘dirty’ and ‘clean’ seed handling procedures (64% of institutes)
- Separate work areas for seed packaging for storage and distribution (80%)
- Dedicated laboratory and trained staff for seed viability testing (84%)
- Dedicated laboratory and trained staff for seed health testing (28%)
- Low temperature seed dryer (68%)
- Suitable field sites for regeneration and multiplication (88%)
- Greenhouse/glasshouse facilities for regeneration and multiplication (64%)

In general, most of the institutes were well-equipped with facilities for multiplying and regenerating seed, whether field sites or greenhouse/glasshouse space. Proper facilities for seed packaging and viability testing were available to most, but provisions for seed health testing were less common.

**Table 4.1** *Ex situ* conservation overview by storage facility type.

	Short-Term Storage	Medium-Term Storage	Long-Term Storage
Proportion of Accessions (%)	17.7	44.6	63.2
Sum of Accessions	4,994	12,609	17,864
Count of Institutes	4	13	20
% of Institutes	16	52	80

**Table 4.2** Facility monitoring tools and/or protocols used by genebanks.

	Long-Term Storage	Medium-Term Storage	Short-Term Storage	Total
Automated monitoring system	11	6	0	17
Daily visit by genebank or security staff	9	9	1	19
External sounding alarms	5	5	0	10
Internal relative humidity monitors	4	3	0	7
Internal temperature monitors	11	9	2	22
None	1	0	0	1
TOTAL RESPONDENTS	19	13	3	25

## Germplasm health, viability and regeneration

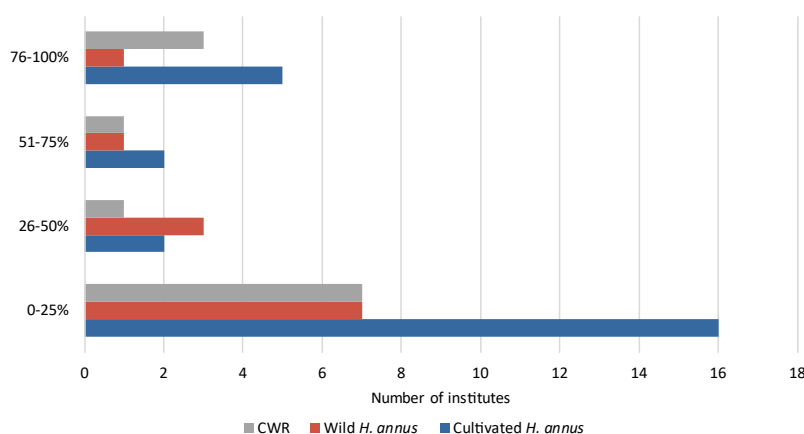
Institutes were asked to describe quality-control activities for viability testing and health testing of their *Helianthus* collections. In general, the information provided was incomplete, and the number of respondents reporting that they performed regular testing was low. For example, only a slight majority of institutes (56%) performed regular germination testing and even fewer institutes performed health testing (24%). For germination testing, twelve institutes described the testing frequency, with other institutes either not providing details or noting that intervals were species-specific. These ranged dramatically from every six months to every 15 years. Methods used included those provided by the International Seed Testing Association (ISTA), the Association of Official Seed Analysts (AOSA), or national standards. Two genebanks reported the use of Tetrazolium as an additional way of assessing viability. Health testing was generally performed only as needed. For example, two institutes noted that health testing was required for new materials entering the collection, while two other institutes noted that health testing was performed only as requested by users, to fulfill legal requirements for distribution.

When asked about the regeneration of accessions, eighteen institutes provided a standard regeneration interval they followed (or attempted to follow under ideal circumstances) to maintain the viability of their *Helianthus* accessions. Depending on the institute, these ranged dramatically from one to 40 years. Regenerating accessions at adequate intervals to maintain viability is a challenge for many institutes, owing to limited funds and/or staffing shortages. For example, four institutes noted that they had not regenerated any *Helianthus* accessions to date (*i.e.*, since the establishment of their *Helianthus* collection). Seven institutes indicated that the interval was from

1 to 5 years, while an additional seven institutes indicated the interval was from 6–10 years.

Institutes with shorter regeneration intervals tended to be well-funded working collections holding mostly cultivated materials; in these collections, materials are actively multiplied each year, for example for use in breeding programs. However, it is important to note that overly frequent regeneration can also be problematic in some cases, particularly in the maintenance of genetically diverse wild materials. This is because of genetic drift during regeneration events, which can cause shifts in the genetic make-up of the accessions (both altered allele frequencies and allele losses). Only three institutes indicated the intervals were more than 10 years and two monitored the viability and quantity of seed to determine the need for regenerations. For example, the USA020, which maintains the largest collection of CWRs globally, only regenerates accessions when necessary (*i.e.*, when inventory and/or viability decrease below acceptable levels) and not at a set interval. Regeneration from most-original seed is also prioritized whenever possible.

Genetic erosion and shifting allele frequencies are important regeneration concerns; nevertheless, as seeds age, regeneration becomes necessary to preserve older accessions exhibiting viability loss. Almost all institutes have a regeneration backlog, with only two institutes reporting no urgent regeneration needs. The number of institutions with regeneration backlogs from 0–100% are given in Figure 4.1. Most of the institutions had backlogs of less than 25% of three types of accessions. Five institutes (ECU023, TUN029, ZAMB048, ZWE049, and MMR015) reported that 80–100% of their accessions (all cultivated materials) may be at imminent risk of loss, owing to regeneration backlogs. Two institutions (AUS165 and BGR029) reported their regeneration backlog for the wild accessions was from 85–100%. Thus, there were signif-



**Figure 4.1** The number of institutions that had 0-25%, 26-50%, 51-75%, and 75-100% of accessions that require urgent regeneration for the cultivated and wild *H. annuus* and the CWRs. Source: 2021 survey.

icant regenerations backlogs for only a few institutes in the global system but only two institutions utilized monitoring of viability and seed quantity to identify accession in need of regeneration. This approach is more secure and reduces the need to routinely regenerate to avoid loss of viability.

### Safety duplication

Safety duplication refers to the backing-up of accessions at a minimum of at least one independent, offsite location. It is crucial to safety duplicate all unique accessions, as individual genebanks may suffer damage or losses of conserved materials, for example due to a lack of funding, natural disaster, or human conflict. International genebank standards (FAO, 2014) recommend placing duplicate accessions at a separate and geographically distant location, ideally in a different country. Institutes holding safety-duplicated accessions may either fully integrate these into their own collections, or take a “black-box” approach, simply storing the materials without any entitlement for use or distribution.

In the sunflower conservation strategy questionnaire, 14 respondents noted they have either fully or partially safety duplicated their *Helianthus* collections in at least one site, 10 respondents had not safety duplicated, and two institutes were not sure if their collections are backed-up. Note that one institute (BRA003) is itself a safety duplication location, which holds a back-up for an active sunflower collection at another research institute in EMBRAPA; as such, the sunflower accessions conserved there are not dupli-

cated elsewhere. Only two respondents conserved safety duplicates for other genebanks in the global system.

Of the 14 institutes with at least one site for safety-duplication, ten had duplicated accessions at another site outside of their country (four of these ten had used the Svalbard Global Seed Vault as the only safety duplication site). The proportion secured in a safety duplication was more than half of the collection for only four respondents, one had more than 50% conserved at two sites and three had more than 50% conserved at one site.

In terms of constraints to safety duplication, several questionnaire respondents cited limited seed stocks as a primary reason. Regulatory challenges were also common, with countries such as Argentina, Australia, and Ecuador having strict national policies for genetic resources. In other cases (e.g., Morocco), national policies are currently under development, and germplasm may not yet be moved out of the country. The collection in Spain (ESP004) aspires to send a safety duplicate to Svalbard but is currently facing delays with the legal procedures that must be met to ship the materials. Finally, for CZE122, a safety duplicate of the collection was at one time placed at a national research institute in the Czech Republic, but the institute no longer exists (and the duplicate accessions were lost).

This low level of safety duplication is a risk for the global system that needs to be addressed urgently.



Sunflowers in Argentina.  
Photo: Luis Salazar/Crop Trust

## 5 EX SITU CONSERVATION IN THE GLOBAL SYSTEM: DOCUMENTATION

Documentation of genebank collections is essential for collection management and use. Without basic passport data for each accession (that is reasonably up-to-date), collections cannot be surveyed, compared, or rationalized, and the history (and potential uniqueness) of accessions can be impossible to trace. Furthermore, potential germplasm users need to be able to easily access passport data to select accessions suitable for their purposes; the inclusion of characterization and/or evaluation data is of considerable additional value for users.

Not all responding institutes (89%) use a computerized database to manage accession information. Commonly used information management systems include proprietary databases (n = 12; e.g., Alelo, BIOGEN, DB Germa, GBIS/I, SDIS, and Siregal), Microsoft Office software (n = 9; e.g., Microsoft Access, Excel, and FoxPro), and GRIN-Global (n = 4). The database management system Sybase is currently used by GBR004, but they are switching to the EarthCape platform in the next two to three years. Systems vary in quality and not all institutes found their selected database to be adequate for their needs (n = 7); most of these institutes described active plans to update their databases. One

institute currently without a computerized database (ECU023) is in the process of migrating to GRIN-Global.

Fifty-nine percent of responding institutes make their accession data publicly accessible, at least in part (Figure 5.1). However, these data may not always be available online outside of the institute (only 41% of institutes share this information online in a searchable format). In cases where accession data are not publicly available, they may often be obtained from a written catalogue, or electronically from the institute's searchable database, with the help of the collection curator. However, 19% of institutes indicated that at least some accession data are considered private.

Collection data for a significant number of institutes are also included in other national, regional, and/or international databases. For example, 85% of institutes upload at least part of their sunflower accession data to international databases, such as Genesys and WIEWS. However, these data may not always be up to date. Only nine (36%) institutions used national databases and seven (28%) used regional databases to share accession level information.

Accession-level data may include: passport, characterization, and evaluation data; information on taxonomy, genotypes, and distributions; and images of the accessions (Figure 5.2). By far the most commonly available accession data are passport (92% of institutes) and taxonomy (84%) information. Characterization data are available, for at least some traits, for 52% of collections, while evaluation data are available for 32% of collections.

The agro-morphological descriptors in common use for sunflower by the respondents include:

- IBPGR sunflower descriptors (1985) (52%)
- FAO/IPGRI multi-crop passport descriptors (MCPD 2015) (48%);
- Institute-specific descriptors (22%)
- UPOV descriptors (22%);
- USDA sunflower descriptors (9%);
- Others (9%)

The other descriptors in use include: IPK-adapted descriptors from various sources (DEU146) and DUS (Distinctness, Uniformity, and Stability) descriptors created by relevant departments of the Indian national government (IND041).

Resistance to both abiotic and biotic stresses will be critical to adapting sunflower crops to future conditions. Institutes described evaluation data for the following abiotic stresses: drought, heat, lodging, low temperatures, and salt. For biotic stresses, evaluation data included resistance to three pests (banded sunflower moth, red seed weevil, and sunflower beetle) and a variety of diseases: *Albugo* stem spot, *Alternaria*, anthracnose, BB, blast, broomrape (frequency & attack rate), downy mildew (races 2–4), *Phoma* blight, *Phomopsis*, powdery mildew, rust (multiple races: rust race 3, rust race 4), *Sclerotinia* basal stem rot and head rot, and white rust.

For the cultivated accessions, sixteen of the survey respondents had agro-morphological characterization data, while fewer had genotypic characterization data, and evaluation data for abiotic or biotic stress tolerance (Figure 5.3). Notably, both characterization and evaluation data are rarer for wild accessions than for cultivated ones (Figure 5.4). The case was similar for evaluation of abiotic and biotic tolerance of wild accessions. Few accessions of the wild species have been characterized or evaluated. For the cultivated species, more institutions had characterized or eval-

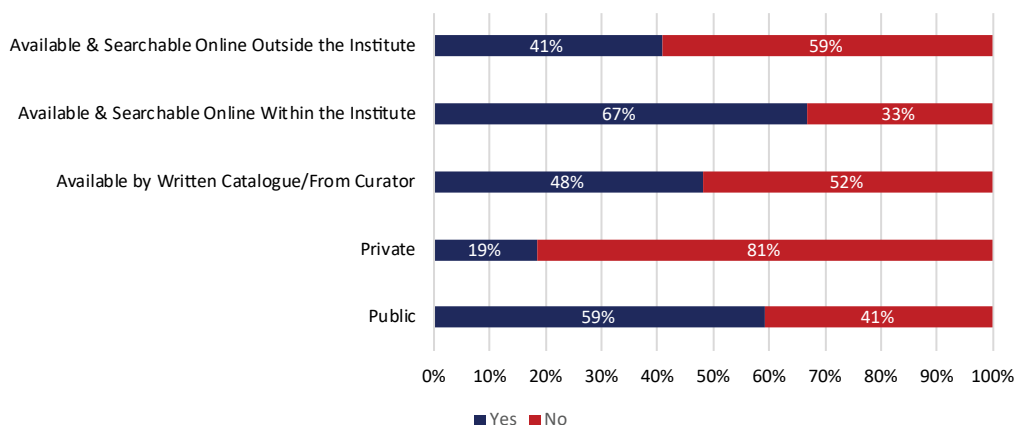


Figure 5.1 How accession-level data are shared by respondents to the survey (n = 27). Source: 2021 survey.

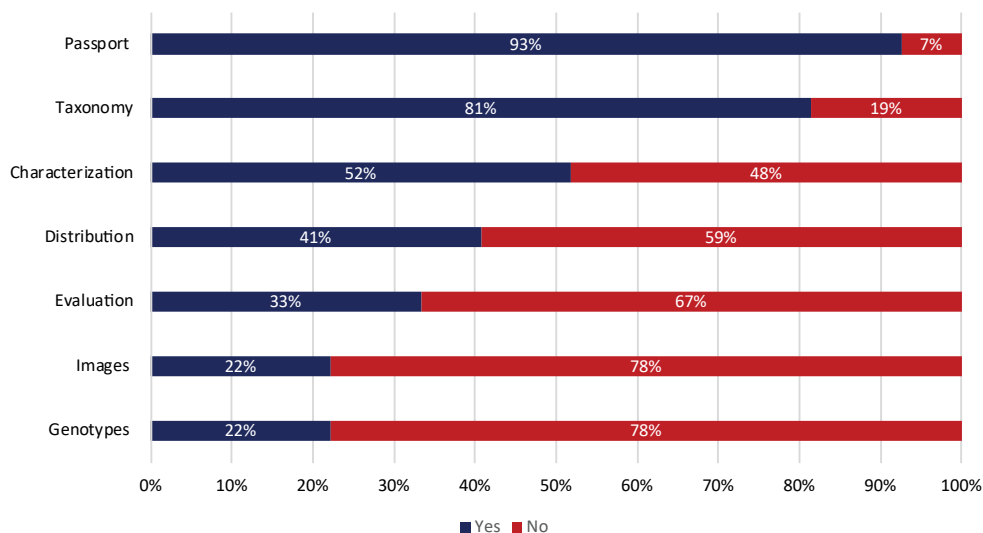
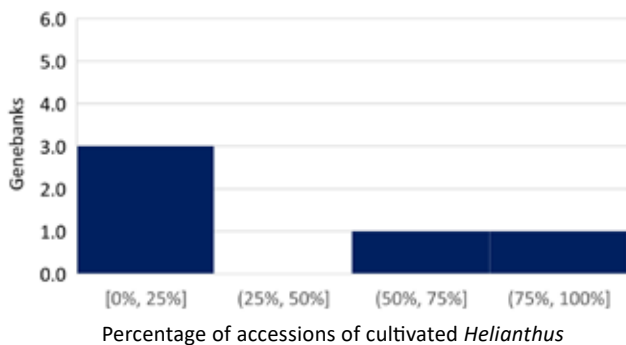


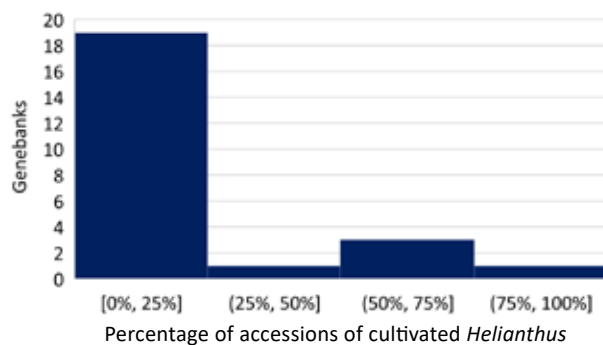
Figure 5.2 Types of accession level information available (proportion of survey respondents, n = 27). Source: 2021 survey.



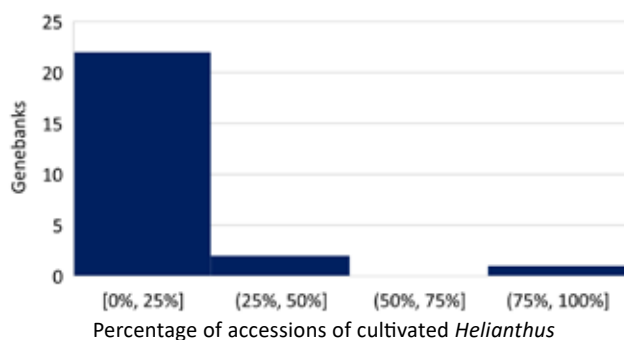
a) Percentage of accessions of cultivated *Helianthus* with agro-morphological characterization of data



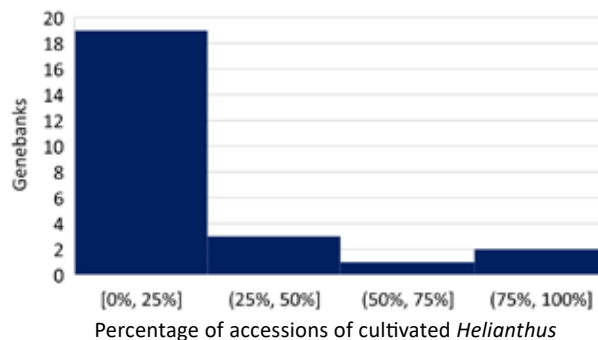
b) Percentage of accessions of cultivated *Helianthus* with genotypic characterization data



c) Percentage of accessions of cultivated *Helianthus* with abiotic stress tolerance data

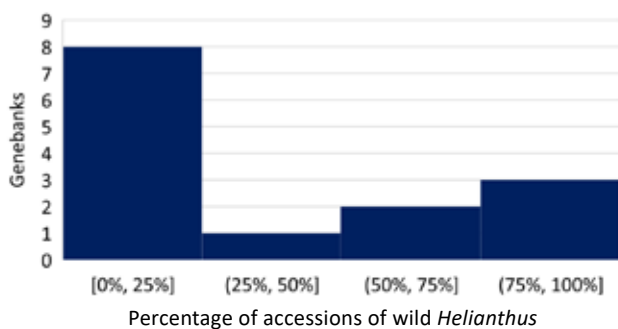


d) Percentage of accessions of cultivated *Helianthus* with biotic stress tolerance data

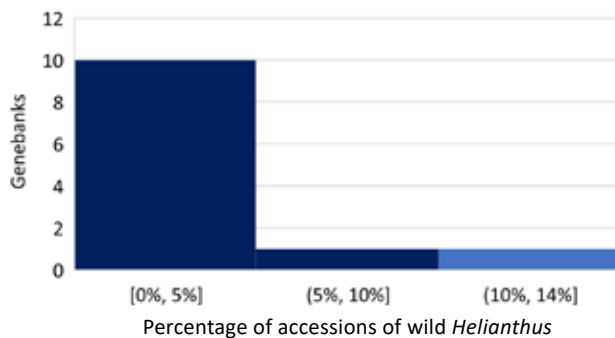


**Figure 5.3** a, b, c, d. Histograms showing the distribution of answers regarding the percentage of the accessions of cultivated *Helianthus* with different categories of characterization and evaluation data. Responses in the survey were binned in four categories (n = 27). Source: 2021 survey.

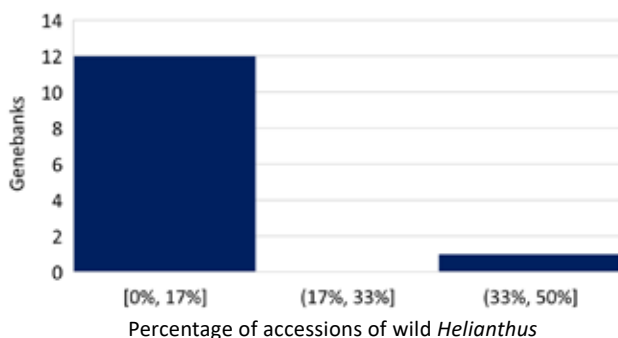
a) Percentage of accessions of wild *Helianthus* with agro-morphological characterization of data



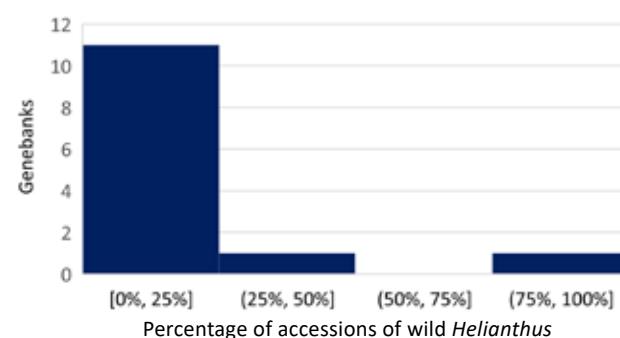
b) Percentage of accessions of wild *Helianthus* with genotypic characterization data



c) Percentage of accessions of wild *Helianthus* with abiotic stress and tolerance data



d) Percentage of accessions of wild *Helianthus* with biotic stress and tolerance data



**Figure 5.4** a, b, c, d. Histograms showing the distribution of answers regarding the percentage of the accessions of wild *Helianthus* with different categories of characterization and evaluation data. Responses in the survey were binned in four, two, three and four categories, respectively (n = 27). Source: 2021 survey.

uated the accessions to a greater degree. So, while accession level information is available for sunflower genetic resources in the global system, the availability of this data to users and its comprehensiveness need to be considered as areas for improvement in the future.

### Genebank management systems

All genebanks face challenges in the effective and efficient management of their germplasm collections. To address these challenges, genebanks typically employ some type of management system to govern their operations and ensure policy and technical standards are met. Written policies and procedures may be developed to cover all aspects of genebank operations, from the acquisition of new accessions to the maintenance of germplasm health, and the distribution of accessions to users.

In the sunflower conservation strategy questionnaire, respondents (n = 27) were asked to describe their genebank management system and/or written protocols. Almost all respondents had established procedures in place for the conservation and regeneration of accessions (Figure 5.5). Roughly three-quarters of respondents had established procedures for: the acquisition of accessions; their characterization and distribution; and accession information management. Meanwhile,

procedures to safety duplicate accessions (at an offsite location) and maintain germplasm health were relatively lacking, with fewer than half of respondents reporting established protocols.

In terms of the specific written procedures and/or protocols used to direct genebank activities, most institutes (68%) used a combination of resources. These included:

- FAO/IPGRI 1994. Genebank Standards. (n = 14 institutes)
- Written and verified Standard Operating Procedures (SOPs) for key processes (n = 11)
- Rao et al. 2006. Handbooks for Genebanks No. 8: Manual of Seed Handling in Genebanks. Bioversity International. (n = 9)
- Organization’s own “Operational Genebank Manual” (n = 8)
- Hanson 1985. Practical Manuals for Genebanks No. 1: Procedures for Handling Seeds in Genebanks. IBPGR. (n = 7)
- A Quality Management System (n = 4)
- Other (n = 2)

“Other” resources included a country-specific genebank operation manual for Ecuador (Monteros-Altamirano et al. 2018) and an unspecified manual of seed handling in genebanks. Two institutes reported not using any written procedures and/or protocols.

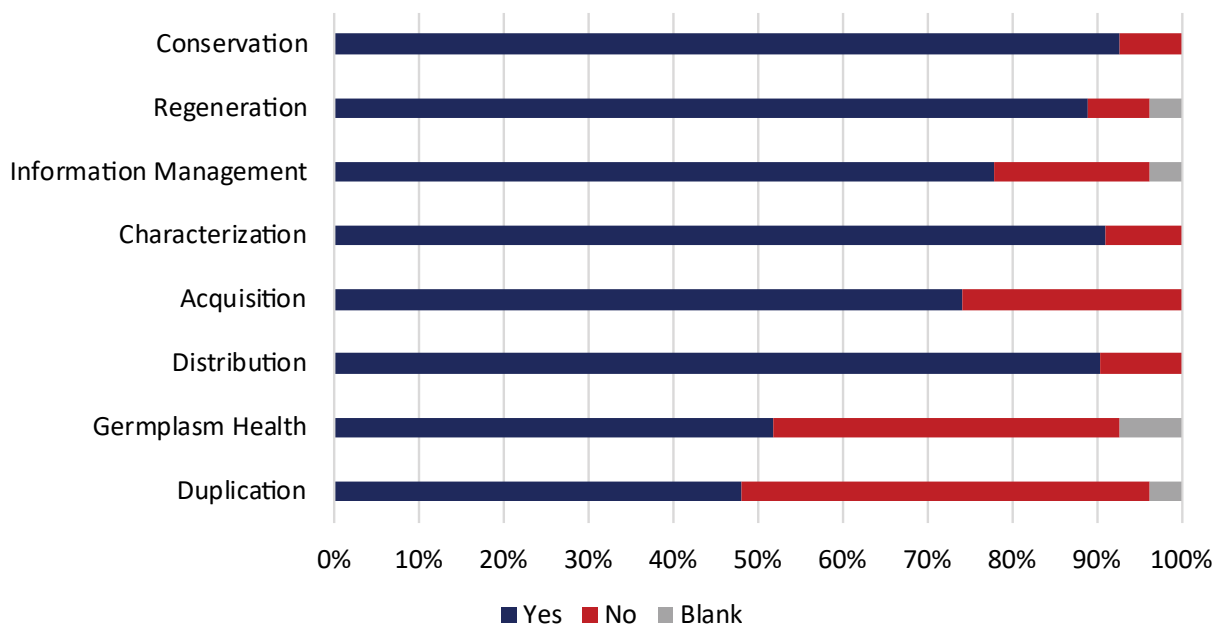


Figure 5.5 Percentage of respondents that have a genebank management system in place and/or written protocols for the specified genebank activity (source sunflower conservation strategy questionnaire 2021, n = 27). Source: 2021 survey.



## 6 EX SITU CONSERVATION IN THE GLOBAL SYSTEM: USE

### Distribution

Seventy-four percent of surveyed institutes distribute germplasm and keep records of the distributions made. A few institutes that do not distribute sunflower accessions cited a lack of requests and limited seed stocks as key limiting factors; in one case (BRA003), the collection is used for long-term storage only (safety duplication).

Of the 20 collections that distribute accessions, most ( $n = 15$ , or 75%) distribute to users internationally, to any country. The remaining five collections distribute only to users within their own country ( $n = 3$ , 15%) or to certain countries ( $n = 1$ , 5%). A Standard Material Transfer Agreement (SMTA, required for germplasm distributions under the Multilateral System of the ITPGRFA;  $n = 13$ ) or other Material Transfer Agreement (MTA;  $n = 11$ ) is normal practice for distribution in almost all cases. Only USDA currently freely distributes materials without terms or conditions (although an MTA or SMTA does apply in some cases). Distributions are typically free to the user: only one institute charges a processing fee for “providing and shipping the samples” and two institutes charge occasionally for the cost of shipping (if the user is able). Distribution-related procedures for phytosanitary certification,

order packaging, and shipping are generally felt to be adequate, with only one institute reporting challenges with phytosanitary certification.

While many institutes could distribute germplasm, in practice distributions are fairly limited for most collections. Only 14 collections report non-zero average annual distributions based on the last three years and, of these, six institutes (CAN004, DEU146, FRA015, IND041, RUS001 and USA020) make more than 100 distributions annually, where a distribution is single sample (i.e., a seed packet for a single accession). USDA is the primary distributor of *Helianthus* germplasm globally, dispensing an order of magnitude more samples annually than any other collection. USDA distributes cultivated accessions more frequently than wild ones (5,265 vs. 2,900 distributions), and more accessions internationally than nationally (5,621 vs. 2,544). For all institutes combined, average annual distributions mirror the USDA patterns.

When asked about how distributions have changed over time (last 5–10 years), most respondents reported that they had roughly stayed the same or had decreased (Figure 6.1). Most of the respondents predicted that average distributions would stay the same in the next five to 10 years.

Despite keeping distribution records, collections found it difficult to quantify the types of users receiving germplasm. Also, many collections made very few annual distributions; therefore, quantification of the types of users receiving germplasm was made for only the five top distributors (100+ samples annually; excluding DEU146, as they did not submit user data).

The institutes distributed very different numbers of samples, so two measures of the proportion of distributions to the various types of users were assessed: 1) The percentage of samples distributed to each type of user was calculated for each of the five distributors, and then averaged over institutes to avoid the bias from the large difference in the total distributions. The overall distribution of the samples using this measure (blue bars in Figure 6.2) indicated that, for the respondents, the highest percentage of distributions went to public sector breeding programs, and academia/universities; 2) The actual sample numbers, aggregated across the five distributors, were used to

determine the percentage distributed to each type of users, 46% of the samples distributed globally were distributed to academia/universities, with 27% being sent to private sector breeding programs. This estimate is heavily influenced by USA020, so it mainly reflects USDA users.

Twelve collections that have made distributions also solicit feedback from germplasm users. When feedback is requested, it is most often about the overall usefulness of the accessions, any resultant reports or publications, the timeliness of distributions, and sample quality. More broadly, 10 institutes described how users can influence genebank priorities, with “providing feedback on available materials and distributions” the most important avenue. The main approaches used by twelve respondents to promote their collections were through institute websites, Genesys, posters/presentations at conferences, publications, and field days

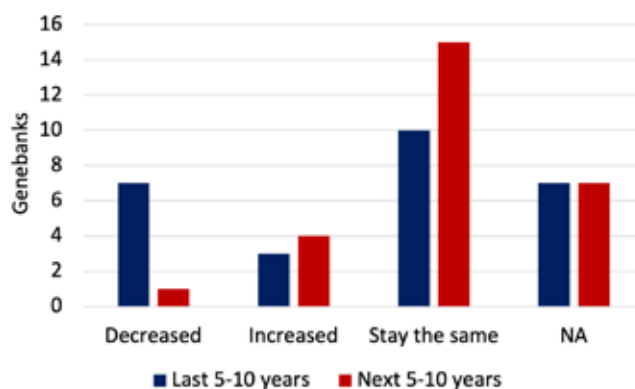


Figure 6.1 Historical changes to distribution patterns and predictions for the next 5-10 years (n = 27). Source: 2021 survey.

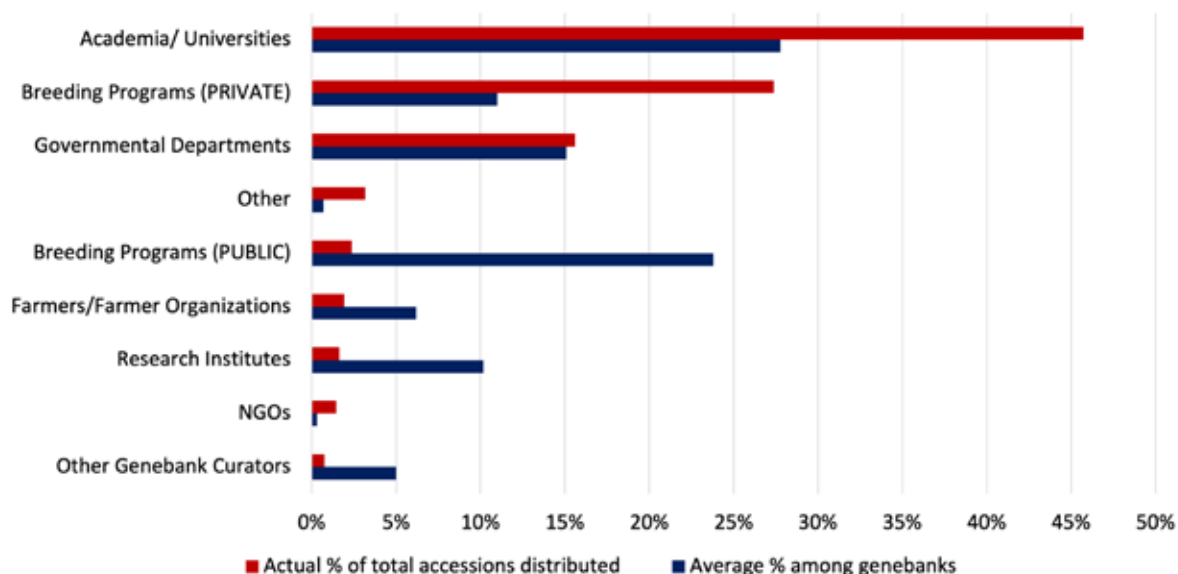


Figure 6.2 The proportion of the total (aggregated across genebanks) number of accessions distributed to various types of users based upon the actual number of accessions distributed versus the average percentage of accessions distributed to each type of users (sample included only genebanks distributing more than 100 accessions per year, n = 5, Source: 2021 survey).



*H. hirsutus*, Rondeau provincial park in Ontario, Canada. Photo: G. Baute

## 7 EX SITU CONSERVATION IN THE GLOBAL SYSTEM: VULNERABILITY

### Collaborations

Collaboration among institutes may mitigate risks, for example by enabling more efficient and secure safety duplication, and foster gains for individual institutes when knowledge and resources are shared. Collaboration of *ex situ* collection holders with other local conservers, such as *in situ* conservation sites, on farm activities or community seedbanks, is also an important way for *ex situ* collections to mitigate risk. The survey respondents were asked to assess the degree of collaboration with the various types of other conservers and to assess the types of joint activities. Ten respondents had no collaboration with other conservers. Sixteen of the respondents had collaboration with other national *ex situ* collections, while fifteen had collaboration with other regional and international *ex situ* collections. With regards to local conservers, five respondents had collaboration with *in situ* conservation sites, six had collaboration with on

farm conservation efforts, four had collaboration with community seedbanks, and seven had collaboration with protected sites that included CWRs. Thus, the most frequent collaboration was with other *ex situ* collection holders.

For each type of collaboration that a respondent participated in, the activities were indicated. The activities included collecting, repatriation, research, safety duplication, training, and others (not specified). Figure 7.1 shows the level of activity by the respondents for that collaboration based upon the number of mentions by the survey respondents. The most common joint activity was collecting. Training was the most frequent joint activity for collaboration with other *ex situ* collection holders and community seedbanks. There was no collaboration for repatriation or the restoration of lost genetic resources to communities or to protected areas. There was no joint research or training with *in situ* conservation sites. Thus, the

majority of the respondents had some degree of collaboration with other genebanks but collaboration was much less with the local conservers, which could be a risk for the genetic resources still conserved *in situ* in protected sites, by farmers, or in community seedbanks.

The survey respondents were also asked to indicate their participation in plant genetic resources networks, working groups, or other opportunities to collaborate with other conservers in the global system. Twelve of the respondents did not participate in any network. Of those that indicated they did participate in a collaborative platform, the most common (n=9) were national or regional networks, three indicated an international forum and only one indicated this was the International Sunflower Association.

### Funding and human resource trends

Most institutes (81%) are funded by their parent organization, which provides an annual budget for recurrent costs. Those that indicated they had no recurrent funds, did have funds to cover some of their

operations from projects or from other government agencies. On the whole, budgets have been stable or increasing over the last five years for a majority of *Helianthus* collections (67%), although 33% of collections have experienced budget cutbacks.

While levels of expertise needed for genebank activities are generally felt to be adequate, many institutes are struggling with inadequate numbers of staff for routine operations, meeting distribution requests, and fulfilling user information needs. For example, 37% of genebanks do not have adequate human resources for their routine operations, leading to regeneration backlogs (as discussed earlier), among other challenges. Potentially compounding these challenges, some collections anticipate expanding (i.e., adding new accessions) in the next 10 years (Figure 7.2).

Systematic risk assessments are an essential planning tool that help genebanks meet their long-term conservation goals. By quantifying the risks a collection faces, an action plan can be developed to both mitigate existing risks and put contingency measures in place for unanticipated risks. Despite the importance

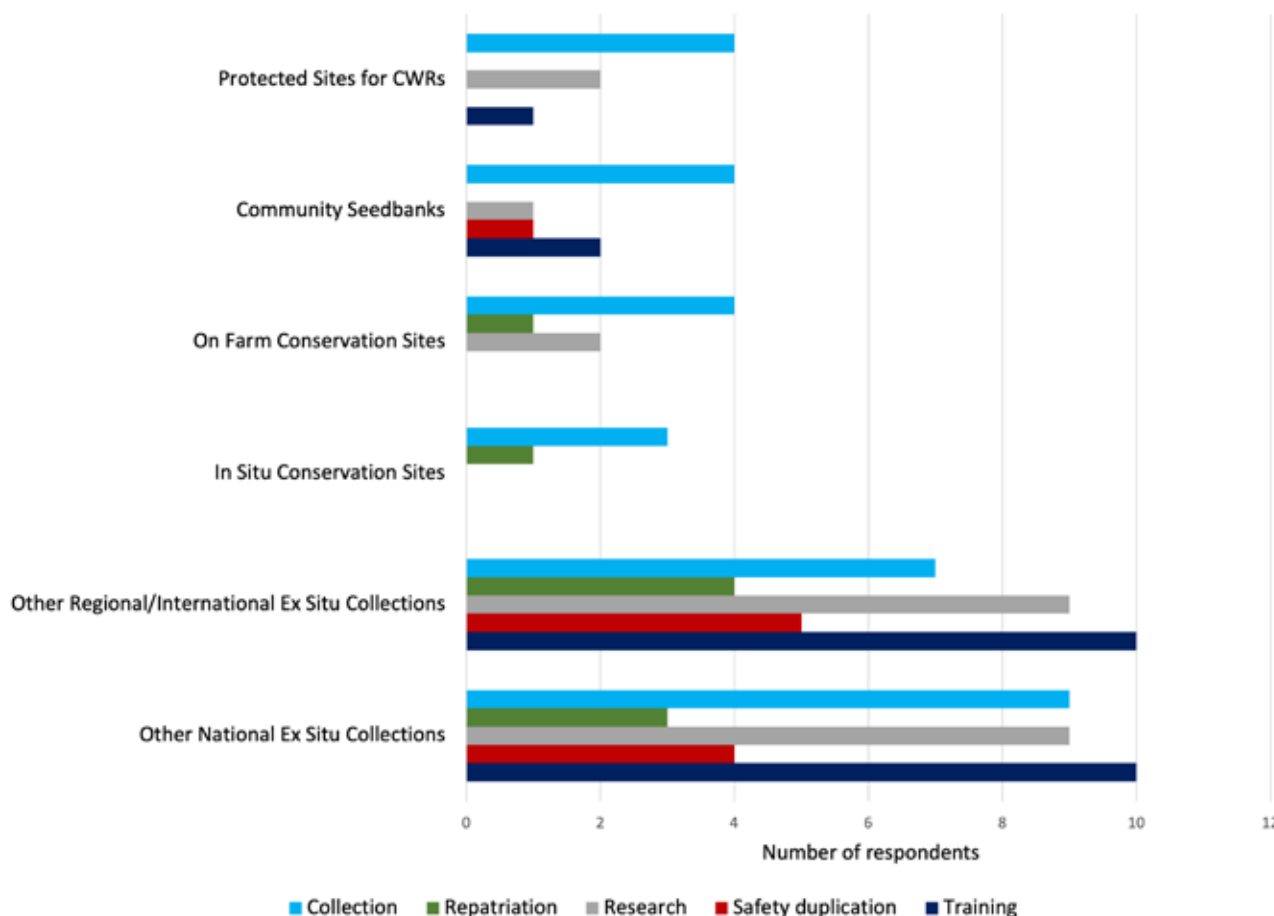


Figure 7.1 Number of reports for the various collaborations that included collecting, repatriation, research, safety duplication, and training (n = 27), Source: 2021 survey.

of formal risk assessment, only 26% of responding institutes have completed such assessments and/or developed management plans for their *Helianthus* collections. When respondents were asked about the top three threats to their *Helianthus* collections, common answers included: insufficient funding, human resources, and infrastructure; declining requests for conserved materials (i.e., collection underuse and reduced relevance); challenges with multiplication and regeneration (owing to allogamy); regeneration backlogs; and emerging pests and diseases under climate change. Specifically, some of the key threats identified by the respondents were:

#### Inadequate resources for routine genebank operations

- Lack of stable and adequate annual funding for genebank operations
- Lack of funding from outside government programs.
- Lack of qualified trained staff
- Lack of additional financial resources for maintenance and storage of the samples in the genebank.
- Old and poorly operating equipment as well as lack of basic equipment used in the genebank and for regeneration.
- Inadequate long term storage capacity
- Poor electrical supply

#### Low priority for crop collection amongst farmers and users

- Low priority of *Helianthus* compared to other such as common bean or maize or others
- Limited opportunities for interactions with other *Helianthus ex situ* collections
- Decreased requests for the cultivation of local varieties
- Increased request for cultivars introduced from abroad
- Underutilization of the accession in the collection

- Sunflowers are suffering from genetic erosion and this could result in extinction since it is being neglected by most farmers.
- Lack of use of germplasm by research/breeding.
- Low interest of breeders in accessing the genebank's collection.
- Decreasing interest of small scale farmers and gardeners to access local landraces maintained in genebank's collection.
- Relevance of the collection with limited modern breeding materials (cultivated) being donated; and we are not a breeding organization, nor are we funded to lead crop-wide evaluations
- Changing climate and evolving and emerging pests affecting crop success.

#### Constraints for collection management

- Mixed/mis-labelled accessions
- Allogamy system for multiplication and regeneration requires cultivation in spatial insulation to prevent cross-pollination, so regeneration slow process
- Risk due to uncertainty in isolation time (before flowering), reliability of isolation, and quality of the materials used for isolation
- Germplasm that will not mature under local growing conditions
- Maintaining specific germplasm such as CMS lines
- Insufficient capacity to regenerate or re-collect, if longevity of collection is unacceptably short
- Plant diseases or storage conditions
- High proportion of germplasm requiring regeneration
- Risk that some germplasm has been lost due to its age and low quantity of stock
- Seed loss during multiplication/regeneration activities
- Changing climate and evolving and emerging pests affecting regeneration and crop success
- Only field management of *H. tuberosus* collection is possible

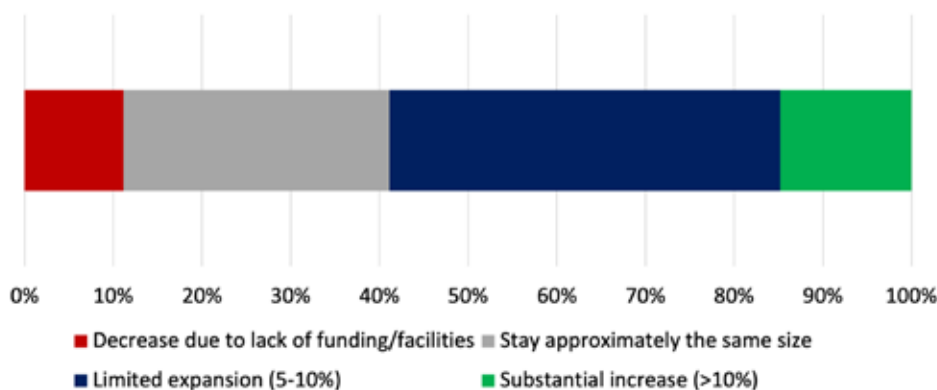


Figure 7.2 Predicted collection dynamics over the next 10 years. Source: 2021 survey.

For several risk factors, most respondents ranked their current situation as insufficient (Figure 7.3). Only about half of respondents have sufficient funding for routine operations, while a majority struggle with insufficient retention of trained staff, low interest in PGR conservation by donors, inadequate genetic variability in the collection, poor access to germplasm information, low feedback from users, and low use by breeders and/or researchers. The expected situation is, however, predicted to improve for most of the

risk factors, except for the retention of trained staff. Thus, there is a degree of optimism amongst these collection holders that the conservation and use of their collection will improve in the future. Generally, the survey respondents concluded that there was a need for an international effort to expand collaboration, raise awareness on sunflower genetic resources conservation, secure the conservation of these genetic resources and ensure that these are used for the sustainable production of sunflowers for the future.

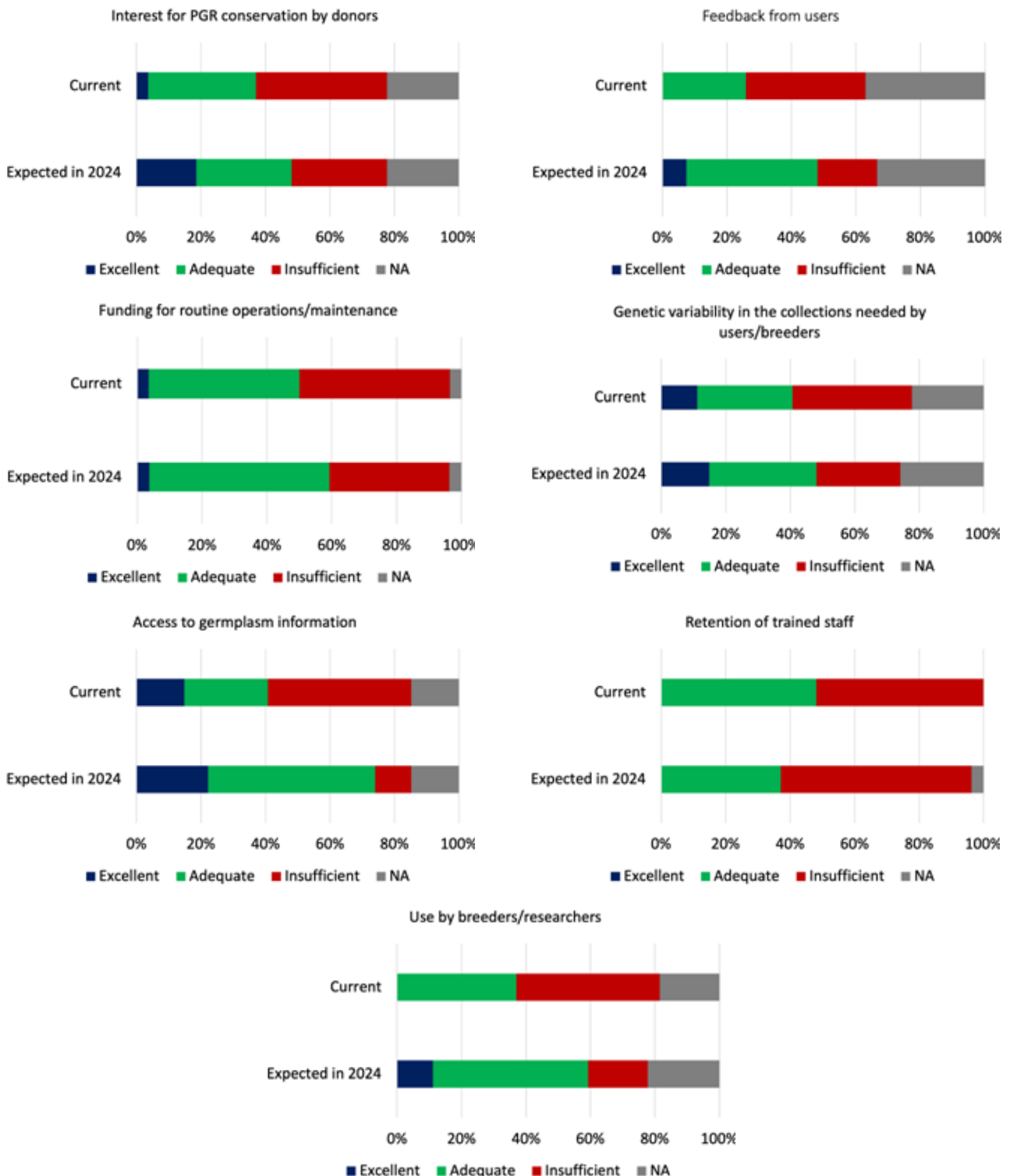


Figure 7.3 Current status and the expected status by 2024 for key risk factors for the conservation and use of the sunflower collections (n = 27). Source: 2021 survey.





## 8 SUNFLOWER CURATOR CONSULTATION SERIES

A consultation workshop with two sessions was held to discuss three key questions related to the composition and conservation of sunflower genetic resources. The attendees for the two sessions are listed in Appendix 7. The summary of the responses to the three questions for each consultation is given separately below.

### 8.1 Consultation Session A

#### Discussion Topic 1: what are we conserving? (or not conserving?)

There was extensive discussion of whether the relative lack of CWR holdings (outside of the USA) constituted a problematic “collection gap” for other geographic regions. While the Australian and some European collections maintain several CWR species, not all species in the genepool are represented. Many *Helianthus* species are not maintained outside of their native range owing to poor performance in these novel environments (due to unsuitable soils, climate, etc.). Owing to the outcrossing nature of *Helianthus* species, regeneration can also be costly and time-consuming.

It was generally felt that, while all CWRs should be conserved, this should be prioritized only by major regional collections and/or those in the native range.

#### Discussion Topic 2: How well are we conserving *Helianthus* genetic resources?

Collections vary in terms of the major challenges they face; for example, while some had stable funding, others struggled with severe resource shortages. Approaches for prioritizing among accessions were discussed for cases where funding is limited or unstable. The importance of safety duplication was also stressed, with many collections noting limitations on backing up accessions (e.g., financial or regulatory constraints). As discussed above, regeneration also represents an important bottleneck for all collections, both limiting collection size and leading to genetic erosion over time in collections. For relatively secure collections with stable funding, an important goal is to increase the amount of characterization and evaluation data available for accessions; evaluation efforts will require coordination among institutions and supplementary funding.

### Discussion Topic 3: How can we better conserve *Helianthus* genetic resources?

Top priorities that emerged from the discussion were the need to upgrade documentation systems, standardize passport data (across institutions), and facilitate data sharing. The key theme of generating more evaluation data, and then digitizing and sharing said data, was also reiterated. Transnational collaborations will be critical for the sunflower genetic resource conservation community. Sharing accession information, expertise, germplasm, and relevant data (e.g., protocols, evaluation data, and research results) will result in net gains for the community. Avenues for further connection and collaboration were discussed.

#### Overall meeting summary:

The first meeting of the Global Sunflower Conservation Strategy was well attended, with curators from eleven different countries providing important feedback on progress to date and guidance in the development of the Strategy. Curators highlighted the need for balance in conserving CWRs: while higher representation of CWRs in major genebanks is desirable, this needs to be well justified on a case-by-case basis given the challenges associated with their conservation. Regeneration is the most problematic step due to environmental mismatches outside the native range, the cross-pollinating nature of *Helianthus* species, and the time and costs involved. While all *Helianthus* species should be conserved globally, these might be divided among genebanks (with adequate resources) on the basis of where species grow well; well-funded genebanks in countries where sunflower is a valuable crop and/or those in the native range might have a comparative advantage for CWR conservation. Curators also discussed the current challenges they face in managing their collections, with a dichotomy emerging between those collections with adequate and stable funding versus those without. Apart from insufficient funding, problems with regeneration and barriers to the exchange of accessions across national boundaries were other key limitations; germplasm exchanges help to build collections, support research, and allow adequate safety duplication. To better use existing collections, the generation of meaningful evaluation data is needed; this will require coordination among institutions, as well as with academics and/or other sunflower researchers and breeders, in addition to supplementary funding. Fostering collaboration will be crucial to better conserve sunflower genetic resources in the future. Upgrades to documentation systems, the standardization of passport data, and greater digitization of relevant data will all facilitate cooperation and sharing. Other avenues for collaboration, such as via existing networks, were explored.

## 8.2 Consultation Session B

### Discussion Topic 1: What are we conserving? (or not conserving?)

Curators highlighted the importance of maintaining diverse collections of *Helianthus* genetic resources, including CWRs, landraces, and open-pollinated varieties. The genetic diversity held in these collections supports breeding and improvement work for sunflower and is particularly necessary in the face of climate change and emerging diseases. The USDA sunflower collection was highlighted for holding an impressive (and complete) array of CWRs, with good genetic representation of the diversity found in wild populations across the US. While there are challenges with conserving CWRs (especially perennials), the theme of the discussion revolved around the need to mine existing collections for desirable genes more efficiently. As wild species are not easy to work with, breeders (both private and public sector) typically do not work with wild germplasm for practical reasons. For now, breeders still have access to a high level of diversity within cultivated materials, but crucial pre-breeding work must be performed by others invested in bridging this gap for the future.

### Discussion Topic 2: How well are we conserving *Helianthus* genetic resources?

Given the costly nature of *ex situ* conservation of plant genetic resources, many curators described challenges with inadequate resources (funding and/or labour). Globally, the sunflower community is also experiencing a critical erosion of expertise, owing to the retirement of key personnel. Given these shortages, the suggestion was made to prioritize the conservation of older cultivated materials (landraces, open-pollinated varieties, etc.) that are most useful for breeding programs, and to prioritize the conservation of CWRs that are threatened *in situ*. The curator of the USDA collection noted that they can accept donations of such materials, when useful to other collections (to have a secure back-up) and/or when collections are facing resource shortages and probable accession loss. The possibility of *in situ* conservation was also discussed for some CWRs; however, habitat loss, altered disturbance regimes, and rapid climate change all threaten wild populations. As such, holding separate *ex situ* collections is essential for certain species.

### Discussion Topic 3: How can we better conserve *Helianthus* genetic resources?

The connection between genebank curators, the genetic resources they conserve, and genebank users and/or breeders was viewed as essential. Yet, owing to time and/or resource limitations, many curators do

not regularly reach out to users. Creating stronger bridges between collectors, curators, and breeders will have many benefits, enabling better use of current collections. The Crop Germplasm Committees of the US National Plant Germplasm System were highlighted as an effective system to facilitate interactions among stakeholders of different types (federal, industry, academia, etc.). Another theme that emerged from the discussion included the global decline of expertise in the sunflower community, which affects many collections, and the resultant increased need for collaboration among genebanks. Collaboration among stakeholders (including public-private cooperation) was felt to be crucial for addressing the challenges currently facing individual genebanks.

### **Overall meeting summary:**

The second meeting of the Global Sunflower Conservation Strategy was well attended, with curators present from nine different countries, and particularly strong representation from the Americas. A lively discussion provided important feedback on progress with the Strategy to date, as well as guidance on the development of the action plan. Curators highlighted the importance of conserving CWRs (particularly those threatened in the wild or with restricted ranges), and additionally open-pollinated varieties and landraces.

These older, yet genetically diverse, cultivated materials are extremely useful for breeding programs, given the challenges and inefficiencies with mining wild germplasm for desirable genes using traditional breeding. Ultimately, building stronger bridges between breeders and collectors/curators will enable greater use of wild germplasm in current collections. To this end, genebanks should seek outside collaborations to support the acquisition of further evaluation data for their collections (tailored to the needs of genebank users), and pre-breeding work should be fostered and encouraged wherever possible. However, these efforts may be hampered by a global decline in expertise in the sunflower conservation community, as identified by curators. As leading experts on the crop retire (and are not replaced) and public breeding programs close down, the long-term security and use of many collections is being negatively impacted. These losses are particularly dire in the face of climate change and emerging pests/diseases, when it is crucial that we more fully use the genetic diversity in existing collections. The need to work together and develop collaborations among genebanks was emphasized, as well as public-private partnerships. Collaborations will facilitate the sharing of both practical expertise and materials, with many curators noting this may be crucial for overcoming current challenges.



Sunflower evaluation nursery, Chirundu, southern Zambia. Photo: Neil Palmer for the Crop Trust.

## 9 GLOBAL STRATEGY FOR THE CONSERVATION AND USE OF SUNFLOWER GENETIC RESOURCE

In sunflower, domestication, dispersal, and intensive breeding have led to genetic bottlenecks despite relatively high phenotypic diversity. The cultivated germplasm is estimated to contain only about two-thirds (50–67%) of the genetic diversity present in wild *H. annuus*, with higher levels of genetic diversity observed in landraces versus elite cultivars. The bulk of cultivar diversity is present in wild sunflower populations from the east-central US, the region where domestication occurred. Thus, wild *H. annuus*, the landraces developed by early native American farmers, and the other species in the primary and secondary genepool are very important genetic resources for the future of the crop and need to be a key focus for the global crop diversity conservation system.

Globally, there are 40,501 accessions of *Helianthus* species conserved at 107 institutes, but 19 institutions conserve about 90% of the total *Helianthus* accessions held globally and 89% of the accessions of *Helianthus* wild species held globally. Thus, the current global system is characterized by a small number of institutions that hold nearly all the accessions that are conserved globally. A sunflower conservation strategy

questionnaire was circulated and a total of 27 collections returned questionnaires (47% return rate). Overall, the survey respondents conserved about 77% of the estimated total number of accessions globally and were a very good sample of global collections.

Overall, according to the survey, *H. annuus* is the most conserved species, but two institutes hold only *H. tuberosus* accessions. Regionally, very few accessions of species other than *H. annuus* are conserved outside America and Europe. The products of research and breeding programs accounted for more than half of all the accessions of *H. annuus* conserved, but this is not unexpected given the history of breeding and germplasm exchange for the cultivated sunflower. The obsolete and/or traditional cultivars and landraces only represent 13% of the total number of accessions conserved globally. Sixteen of the survey respondents held 92% of the accessions of *Helianthus* species that are conserved globally. The USDA collection at USA020 has the largest and most diverse collection of these other *Helianthus* species. This is not surprising given the distribution of most of these taxa in the US. There has been a high degree of germplasm exchange

for sunflower in the past, and this history of sharing accessions (both of cultivated and wild materials) between institutes means there are likely substantial overlaps among *Helianthus* collections. Landraces from North America (Canada, USA, Mexico) and OPVs farmer varieties of the cultivated sunflower and some of the wild *Helianthus* species have gaps in their *ex situ* conservation and this is a significant risk for the long term improvement of the cultivated *Helianthus* species. This gap needs to be addressed within the global system with an increased focus on collection, *ex situ* conservation, and safety duplication, or with a greater focus on securing diversity in protected areas. Both approaches in conjunction would be best.

The status of *ex situ* conservation and use within the global system was assessed through the survey. Most accessions were found to be conserved under long-term storage conditions. In general, most of the institutes were well-equipped with facilities for multiplying and regenerating seed, whether field sites or greenhouse/glasshouse space. Proper facilities for seed packaging and viability testing were available to most, but provisions for seed health testing were less common. There were significant issues for routine operations that constituted risks that could lead to backlogs for the respondents. The number of respondents reporting that they performed regular seed viability monitoring was low. Health testing was generally performed only as needed or was required for new materials entering the collection or to fulfill legal requirements for distribution. Regenerating accessions at adequate intervals to maintain viability is a challenge for many institutes, owing to limited funds and/or staffing shortages, but currently there are significant regenerations backlogs for only a few institutes. Only two institutions used monitoring of viability and seed quantity to identify accessions in need of regeneration. This approach is more secure and reduces the need to regenerate to avoid loss of viability, and should be much more widely adopted. The proportion of collections secured with safety duplication was low. In general, the respondents faced constraints for routine operations for conservation that will risk significant backlogs for viability testing, health testing, regeneration, and safety duplication. This is a risk for the maintenance of the accessions being conserved in the global system.

A majority, but not all, of responding institutes use a database to manage accession information and more than half make their accession data publicly accessible, at least in part, but not always online outside of the institute in a searchable format. Collection data for a significant number of institutes are also included in other national, regional, and/or international databases, but may not always be up to date. By far the most commonly available accession data are passport

and taxonomy information, while characterization and evaluation data are available for half of the respondents, although incomplete. So, while accession level information is available for sunflower genetic resources in the global system, the availability of these data to users and its comprehensiveness need to be considered as urgent areas for improvement.

Almost all respondents had established procedures in place for routine operations, except for safety duplication and maintenance of germplasm health, but these were not part of a formal quality management system for most of the collections.

While many institutes could distribute germplasm, in practice distributions are very limited for most collections. USDA is the primary distributor of *Helianthus* accessions globally. The highest proportion of samples went to public sector breeding programs, academia/universities, and farmers/farmer organizations. When feedback is requested, it is most often for the overall usefulness of the accessions, any resultant reports or publications, the timeliness of distributions, and sample quality. Most of the respondents predicted that average distributions would stay the same in the next five to ten years despite being relatively low for many of the institutes.

The survey respondents were asked to assess the degree of collaboration with various types of other conservers and to assess the types of joint activities. The most frequent collaboration was with other *ex situ* collection holders. The most common joint activity was collecting and training with other *ex situ* collection holders and community seedbanks. There was no collaboration for repatriation or the restoration of lost genetic resources to communities or to protected areas. There was no joint research or training with *in situ* conservation sites. This is not surprising given the limited distribution of the wild species to North America, but there is a need to consider greater collaboration in the region, including with institutions in Mexico. The survey respondents were also asked to indicate their participation in plant genetic resources networks, working groups, or other opportunities to collaborate with other conservers in the global system. Most of the respondents did not participate in any national, regional or international network. Only one respondent indicated that this was the International Sunflower Association. This indicates the low level of collaborative opportunities amongst conservers and users in the current global system for sunflower.

When asked about top threats to their *Helianthus* collections, common answers included: insufficient funding, human resources, and infrastructure; declining requests for conserved materials (*i.e.*, collection underutilization and reduced relevance); chal-

allenges with multiplication and regeneration (owing to allogamy); regeneration backlogs; and emerging pests and diseases under climate change. Only about half of respondents have sufficient funding for routine operations, while a majority struggle with insufficient retention of trained staff, low interest in PGR conservation by donors, inadequate genetic variability in the collection, poor access to germplasm information, low feedback from users, and inadequate use by breeders and/or researchers. Overall, there is a degree of optimism amongst these collection holders that the conservation and use of their collection will improve in the future, though the rationale for this is obscure. Generally, the survey respondents concluded that there was a need for an international effort to expand collaboration, raise awareness on sunflower genetic resources conservation, secure the conservation of these genetic resources and ensure that these are used for the sustainable production of sunflowers for the future.

The current global conservation system for sunflower is described in Table 9.1. Currently there are a limited number of active key conservers *in situ* and *ex situ*, but there are few links between them. This is a significant risk to the future conservation of these resources, especially in North America. The level of the diversity conserved *in situ* and the degree of the representation in *ex situ* collection is not known. There are very few studies on the population level diversity of the wild species, or the diversity among the more primitive landraces or farmers varieties in North America, nor of the diversity among farmers varieties and heritage varieties in areas of Europe where sunflower production is 100–300 years old. With seed saving by these farmers and selection for adaptation, these may be important sources of diversity that could be at risk of loss. Thus, this is a gap in the current *ex situ* conservation system that needs to be addressed.

The global *ex situ* system for the conservation of sunflower genetic resources consists of four elements.

1. The first is the largest national collection, USA020, that is in effect playing both a national and an international role for the global system. The current system lacks an international genebank with a mandate for sunflower, but USA020 is formally in the MLS, has a long history of international exchange and has the most diverse collection today, with opportunities to expand into the future. USDA's global leadership in conservation and in use is critical for the future of the global system for the conservation of sunflower genetic resources. The expansion of this global leadership to include collection holders in Canada and Mexico should be encouraged since all three countries host very significant species level diversity. This role for USDA was recognized by the participants in the two global consultations in relation to conservation of wild relatives and safety duplication for cultivated accessions, but this could be expanded given USDA's expertise in conservation and links to users.
2. There are other genebanks that have a significant collection that captures both cultivated and wild diversity, based upon the details reported on the composition of collections in the survey. They also are recognized leaders in the global conservation system but in many cases their links to users are only national and perhaps regional.
3. The third group of genebanks of significance to the global system are those that hold collections of mainly the products of local research and breeding programs. Sometimes, these cannot be shared outside the institute or country. In some cases, the breeding programs are no longer of importance to the institute, so the future of the collection is not secure. This group of genebanks would be classified as user or breeding collections. The value of discontinued breeding program material should be first assessed, and then a selection of this material should be maintained by collections in elements (1) and (2).
4. Another type of user collections are those held by public or private sector breeding programs

**Table 9.1** Current participants in the Global System for the Conservation of *Helianthus* genetic resources

	Description of conserver
<i>In situ</i>	Natural areas where the wild species are maintained, with or without protection
	Farmers that conserve cultivated diversity on farm, both primitive landraces and obsolete varieties that have been selected for local adaptation
<i>Ex situ</i>	USA020 is the largest and most diverse collection. It has also been the most accessible to users globally. It also has access to most of the localities for the wild species
	FRA015, RUS001, ROM002, DEU146, UKR001, UKR012, ESP195, GBR004, SRB002, AUS165, ARG1348, POL003, BRA014, and IND001 hold collections that conserve a diversity of landrace, obsolete or farmers varieties and/or wild populations
	Nationally based institutions that conserve mainly products of research and breeding programs that have been or are linked to users in breeding programs in the past or currently
	Public and private sector users that also conserve sunflower genetic resources for their own use

or seed companies. They conserve genetic resources that are important for their research or breeding effort, but these are not shared in the global system at all. A path should be created to allow this type of germplasm to become part of the global system and collections should be made aware of the existence of this possibility.

In elements (2)-(4) there are few links between the various genebanks and few opportunities for partnerships globally. The USDA collection is mainly a source of germplasm for these genebanks.

The current global system of conservation and use of sunflower diversity is generally insecure, with a number of poorly resourced operations, limited availability of seed to all users, limited online sharing of accession-level information, and limited engagement of conservers and users globally, nationally, and locally. Some of these weaknesses are due to the fluctuating priority given to sunflower by international donors, national governments, public and private researchers, local authorities, farmers, urban markets, and consumers. Any decline in priority is a risk not only to *ex situ* conservation but also to the continued conservation of diversity in farmers' fields. If and when the priority of the crop rises again, there may not be the diversity available to take advantage of the opportunity of the increased demand.

However, the current global system for the conservation of sunflower genetic resources does have some advantages that can be built upon. There are at least 12 genebanks with experience and expertise that other conservers can turn to for help and guidance, in their efforts to meet international standards. These genebanks, especially that of USDA, can also serve as conveners in global efforts to increase the security of conservation, adopt new technology and methods, enhance capacity and expertise on sunflower and collectively address some of the major constraints to a more effective and sustainable global system. These genebanks can also take on leadership in advocacy and communication on the importance of conservation and use of sunflower diversity. Another strength of the current system is the considerable national and local capacity for conservation in North America, where the largest national collection is located, which increases the opportunities for expanding the secure conservation of landraces and most of the wild species.

The main disadvantages of the current system are the lack of committed annual support for conservation of sunflower in many national genebanks, the general lack of knowledge on the diversity that is conserved, the current low level of support for research into sunflower, and the vulnerability of much of the

diversity to loss, both *ex situ* in genebanks as well as in farmers' fields and in natural areas. The purpose of this strategy is to recommend priority actions to shift from the current disorganized arrangements to a truly global system of conservation and use that is more secure, rational, cost-effective and engaged with users. These recommended actions will be used by the Crop Trust and others to identify and obtain the key investments needed to secure conservation and use for the long term.

A global strategy must identify the key priority actions that need to be taken, who should be involved and what kind of resources will be required. For conservation, this has been done with the two consultations held as part of the strategy development. Overall, there are two strategic objectives identified based on the survey and the consultation, with the following key activities:

1. Secure conservation of sunflower genetic resources for the long term:
  - a. Address insecurity in *ex situ* conservation due to suboptimal routine operations, facilities, and safety duplication that are leading to backlogs.
  - b. Address risks to unique diversity still being conserved in farmers' fields and in natural areas through *ex situ* (i.e. new collecting) and *in situ* conservation, including on farm conservation of old cultivars/landraces.
  - c. Address constraints to global engagement among conservers, and between conservers and users.
  - d. Carry out advocacy and communication on the importance of sunflower and its conservation to the public, local governments and communities, policymakers and other research communities to increase awareness and financial support and reduce the decline in production, research and conservation.
2. Increase the use of conserved genetic diversity.
  - a. Increase access to accession level information, preferably by making it readily available online to all users.
  - b. Address constraints to distribution due to insufficient seed quantity, quality, viability and phytosanitary constraints.
  - c. Address policy bottlenecks to distribution. Increase the use of the SMTA and the number of *Helianthus* accessions in the MLS.
  - d. Increase phenotypic evaluation and genotyping, with results openly shared with users.
  - e. Use genomics to characterize diversity globally.
  - f. Establish and make available core collections or other key subsets to facilitate use.
  - g. Facilitate the use of the CWR with more focus on public-private partnerships in pre-breeding.
  - h. Increase genebanks' engagement with researchers.

Addressing the key activities in these strategic objectives will facilitate the development of a more sustainable, longer-term, and more rational global system for conservation and use of sunflower genetic resources. The first steps in addressing these global objectives will be to build a global collaboration with committed leadership to facilitate the use of dedicated financial resources to implement both collective and individual activities to enhance the secure, efficient, and sustained conservation of sunflower genetic resources.

**Priority Action: Establish a global international advisory group for the engagement of key collection holders and main users of sunflower genetic resources, and to lead the implementation of agreed priority activities.**

An international advisory group (IAG) for the conservation and use of sunflower PGR is needed that enables conservers and users of sunflower genetic resources to communicate and collaborate more effectively. The international advisory group could be mainly operated virtually, with in-person meetings when funds are available.

We recommend that the IAG should:

- Implement recommendations in this strategy document.
- Monitor the progress in implementing recommendations in this strategy document and other priority activities as they arise.
- Facilitate *ex situ* collection holders and users to: share experiences; collectively improve conservation practices; establish quality management system protocols, processes and standards; offer each other capacity-building opportunities; and address the needs for safety duplication.
- Address the challenges individual genebanks are facing through collaboration.
- Address the declining support for specific user collections, landrace diversity in farmers' field and diversity of CWRs in natural areas that are at risk of loss due to natural disasters, and declining perceived importance of the crop.
- Increase the availability, and comprehensiveness, of accession level information for sunflower genetic resources in the global system.
- Discuss the future needs for conservation and use with key representatives of the user community, and make plans for addressing future needs.
- Serve as a source of experts when needed, as in the targeting of key gaps in diversity for collecting or re-collecting, or facilitating collaborative research to enhance production and use.
- Periodically review priorities to improve the global system for the conservation and use of sunflower genetic resources.

- Work closely with the USDA Crop Germplasm Committee for Sunflower.

USDA has the largest and most diverse collection of sunflower and its CWRs, and it is the primary distributor of *Helianthus* germplasm globally. Further, most of the native range of sunflower CWRs is within the USA. Given this, and that USDA leadership in the conservation of sunflower is already widely acknowledged at the international level, we suggest that the members of the existing USDA Crop Germplasm Committee for Sunflower could take the lead in creating the proposed IAG by expanding their group and including the other key collection holders. The IAG should aim to include representatives from FRA015, RUS001, ROM002, DEU146, UKR001, UKR012, ESP195, GBR004, SRB002, AUS165, ARG1348, POL003, BRA014, IND001, CAN004, and the National Genetic Resources Center (CNRG) of INIFAP in Mexico. [NORGEN](#), which coordinates collaboration among the national genetic resources systems of Canada, Mexico and the USA, should also be involved in the work of the IAG.

The [International Sunflower Association](#) (ISA) should also be involved as a partner in this endeavor, and could potentially also take the lead in forming the IAG.

**Priority Action: Establish a partnership among North American countries and address collection gaps for cultivated landraces and CWR**

While USDA holds an extensive, and very comprehensive, collection of US populations of wild sunflowers, Mexican diversity has not been adequately documented, collected, or preserved. Yet the range of several *Helianthus* species extends southwards into Mexico, and populations there probably hold unique diversity. Alleles for heat and drought tolerance, for example, may be particularly relevant in the context of climate change. Therefore, more field research and extensive collecting are needed to fully document the *Helianthus* species in Mexico, including: their abundance and distribution; genetic diversity and population structure; and morphological variation. Similarly, little recent effort has gone into surveying and collecting the northern end of the range for *H. annuus* in Canada, and this is also a priority activity. A relatively modest investment would go a long way towards collecting and conserving Mexican and Canadian genetic resources for sunflower. One practical way forward may entail partnerships between Mexican academics and/or conservationists and those in Canada and the USA, under the aegis of the regional PGR network. Ideally, the germplasm collected should be conserved *ex situ* in-country and duplicated at the USDA as fully integrated accessions, or under a "black box" arrange-



ment if an agreement for fully integrated duplication cannot be reached. In Mexico, CNRG of INIFAP and the [FESI-UNAM seedbank](#) could collect and conserve *Helianthus* germplasm. FESI-UNAM genebank has a focus on wild species and has a long-standing collaboration with the RBG Kew Millennium Seed Bank and safety duplicates of sunflower CWR could also be stored there. Access to *Helianthus* genetic resources in Mexico will be under the terms of the CDB and its Nagoya protocol, as Mexico is not currently a contracting party of the ITPGRFA. However, discussions with the Mexican authorities should take place to explore the inclusion of sunflower genetic resources in the MLS of the ITPGRFA.

The other priority gaps in *ex situ* conservation are the wild species that have a small number of accessions conserved in genebanks, have a small distribution or/and an alarming (or unknown) *in situ* conservation status, such as: *Helianthus inexpectatus* D. J. , *H. carnosus* Small, *H. × multiflorus* L., *H. arizonensis* R. C. Jacks, *H. verticillatus* Small, and *H. × doricoides* Lam., *H. agrestis* Pollard, and *H. glaucophyllus* D. M. Sm. A comprehensive collecting, multiplication and safety duplication plan should be developed and put in place for these CWR.

**Priority Action: Safety backup of cultivated and CWR accessions**

The low level of safety duplication among the genebanks holding sunflower germplasm is a risk for the global system that needs to be addressed urgently. It is recommended that all CWR accessions that are not safety duplicated should be sent to the USDA for regeneration and safety backup. Preferably, the safety duplicates should be fully integrated into the USDA collection; if this is not possible, then a “black box” approach can be used. Additionally, if possible, a safety duplicate should also be deposited at Svalbard Global Seed Vault.

**Priority Action: Rationalize the global sunflower collection and increase the accessibility of genetic diversity from CWR, landraces, and open-pollinated varieties.**

While tremendous diversity is available outside of the elite genepool, accessing this diversity can be challenging for practical reasons. During the consultation sessions, curators highlighted the importance of maintaining diverse collections of *Helianthus* genetic resources, including CWRs, landraces, and open-pollinated varieties. The genetic diversity held in these col-

lections supports breeding and improvement work for sunflower, particularly necessary in the face of climate change and emerging diseases.

The USDA sunflower collection was highlighted for holding an impressive (and comprehensive) array of CWRs, with good genetic representation of the diversity found in wild populations across the USA. While there are challenges with conserving CWRs, a need was recognized to mine existing collections for desirable genes more efficiently. As wild species are not easy to work with, breeders (both private and public sector) typically avoid wild germplasm for practical reasons. USDA, the Riesberg Lab and others have conducted extensive pre-breeding and therefore some CWR diversity can be now found in pre-bred lines. However, more can be done to facilitate the rationalization and use of the diversity that is conserved in *ex situ* collections (including pre-breeding lines) through: (a) increasing accession-level data that is accessible on international PGRFA portals and its completeness, and using digital object identifiers (DOIs); (b) phenotyping and genotyping together with screening for abiotic/biotic stress resistance to get detailed information about the genebank accessions; (c) increased data availability; and (d) the development of a minimum descriptor list to stimulate the generation of more data. Priority for conducting these activities should be given to the largest sunflower collections identified in this strategy.

**Priority action: Hold a consultation to discuss the future needs for conservation and use with key representatives of the users.**

The development of this strategy involved several key collection holders of sunflower genetic resources, but a very limited number of users. Thus, one of the next steps in the implementation of the global strategy should be to hold a consultation to discuss the future needs for conservation and use with key representatives of the users of sunflower diversity. This should include public and private researchers/breeders as well as other key stakeholders, such as representatives of the commercial users of sunflower diversity, policy makers, NGO, and others who have an interest in the long-term potential for the commodity. This consultation should focus on what users need from any collaborative platform, and how it could operate. Leadership for this consultation should come from both the key genebanks as well as important users. This consultation would then further develop the priorities for the global systems with a roadmap to facilitate the actions needed.



Sonnen Blume.

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# APPENDICES

## Appendix 1. The Global Sunflower Conservation Strategy questionnaire

### ORGANIZATION INFORMATION

#### 1. Organization holding/maintaining the *Helianthus* collection:

Name of Organization

Address

City/Town

State/Province

ZIP/Postal Code

Country

Website

#### 2. Curator in charge of the *Helianthus* collection:

Name

Job Title

Telephone

Email

#### 3. Name of respondent to this questionnaire (if not as above):

Name

Function/Job Title

Telephone

Email

#### 4. Additional key contact person for the *Helianthus* collection (if applicable):

Name

Function/Job Title

Telephone

Email

#### 5. Is the organization in charge of the *Helianthus* collection the legal owner of the collection? (Y/N) If not, who is the owner?

#### 6. Describe the organization (select one):

Governmental organization

University

Private organization

NGO or charity

Other (please specify)

#### 7. Does the genebank or collection operate under a national conservation strategy, policy, or plan? (Y/N) If yes, please specify.

**8. Who has the most influence on genebank priorities (e.g., objectives, species focus, activities)? (Select one).**

The curator(s) of the collection

The organization/department management

A governing committee

A stakeholder committee

Other (please specify)

## THE *HELIANTHUS* COLLECTION

**9. Basic information on the *Helianthus* collection:**

Year of establishment

Total number of *Helianthus* accessions (today)

Total number of *Helianthus* species (today)

Total number of *Helianthus* accessions currently available for distribution

**10. The main objectives of the collection include (select all that apply):**

Long-term conservation

Working collection for public breeding/research program

Working collection for private breeding/research program

Academic or educational use

Reference collection

Other (please specify)

**11. For the cultivated species, *Helianthus annuus*, indicate the number of accessions by germplasm type:**

Total number of accessions

Landraces

Obsolete/traditional cultivars

Advanced/improved cultivars

Breeding/research materials

Specialist genetic stocks

Wild or weedy populations

Unknown

Other

**12. Please indicate the total number of accessions of other *Helianthus* species (NOT *Helianthus annuus*) in your collection:**

**13. If you hold accessions of other *Helianthus* species, as indicated in Q12, please complete the additional document "Sunflower Crop Wild Relatives (Q13)" to detail your collection holdings by species. Please return via email with the questionnaire.**

**14. If you hold cultivated accessions of *Helianthus tuberosus* (Jerusalem artichoke or sunchoke), please complete the additional document "Jerusalem Artichoke (Q14)" to detail your collection holdings. Please return via email with the questionnaire.**

**15. To what extent do you consider the *Helianthus* accessions in your collection to be unique and not duplicated elsewhere (excluding safety duplication)?**

	100% unique	More than 50% unique	Less than 50% unique	Fully duplicated elsewhere
Cultivated <i>Helianthus annuus</i>				
Wild <i>Helianthus annuus</i>				
Crop wild relatives (i.e., other <i>Helianthus</i> spp.)				

**16. Please describe the current importance of your *Helianthus* collection, as well as any aspects that you consider to be particularly unique or of special value.**

17. Across the entire *Helianthus* collection, how many countries of origin are represented?

18. Describe the geographic origins of the collection by indicating the proportion (%) of cultivated *Helianthus annuus* accessions that were collected/obtained (total should sum to 100%):

Nationally

Regionally (excluding own country)

Internationally (excluding own region)

Unknown

19. Are there any known or perceived gaps in your *Helianthus* collection (check all that apply):

Genetic gaps

Taxonomic gaps

Ecogeographic gaps

Other gaps

Please briefly describe any gaps.

20. If there are collection gaps, as indicated in Q19, how and when do you plan to fill these gaps, if at all?

21. To what extent do you consider duplication within your *Helianthus* collection to be a problem?

No duplication within the collection

Low amounts of duplication (< 10%)

Moderate amounts of duplication (10-30%)

Duplication is extensive (> 30%)

Do you have plans to conduct collection rationalization to eliminate duplicates?

22. To characterize collection dynamics, indicate the number of *Helianthus* accessions that have been:

Acquired in the past 10 years?

Lost from the collection in the past 10 years?

Removed as they were identified as duplicates?

## EX SITU CONSERVATION FACILITIES

23. Indicate the proportion (%) of *Helianthus* accessions that are maintained under the following conditions:

(Note: if accessions are maintained under multiple conditions, total may exceed 100%.)

Short-term storage

Medium-term storage

Long-term storage

For the following questions in this section (Q24-Q30), you need answer only for the storage conditions applicable for your collection.

24-26. Please describe the storage facilities:

	Short-term storage (Q24)	Medium-term storage (Q25)	Long-term storage (Q26)
Type of facility (warehouse, cold chamber, freezer, etc.)			
Conservation method (seed, in vitro, etc.)			
Temperature (°C)			
Relative humidity (%)			

**27. The storage facilities may be best understood as:**

	Short-term storage	Medium-term storage	Long-term storage
Cold chambers			
Individual freezers			
Air-conditioned rooms			
Air-conditioned rooms with dehumidifier			
Not climate-controlled			

**28. The temperature and relative humidity are monitored by (check all that apply):**

	Short-term storage	Medium-term storage	Long-term storage
Internal temperature monitors			
Internal relative humidity monitors			
External sounding alarms			
Automated monitoring system			
Daily visit by genebank or security staff			
Others (please specify)			

**29. What type of packaging is used for seed (i.e., achene) conservation?**

	Short-term storage	Medium-term storage	Long-term storage
Sealed aluminum packs			
Sealed, vacuum-packed aluminum packs			
Plastic containers			
Glass containers			
Paper envelopes or bags			
Cloth bags			
Other (please specify)			

**30. Are seeds dried before storage?**

	Short-term storage	Medium-term storage	Long-term storage
Yes			
No			
N/A			

**31. Do the genebank facilities include (check all that apply):**

Separate work areas for 'dirty' and 'clean' seed handling procedures			
Separate work areas for seed packaging for storage and distribution			
Dedicated laboratory and trained staff for seed viability testing			
Dedicated laboratory and trained staff for seed health testing			
Low temperature seed dryer			
Suitable field sites for regeneration and multiplication			
Greenhouse/glasshouse facilities for regeneration and multiplication			
Other (please specify)			

## GERMPLASM MANAGEMENT

**32. Have you established a genebank management system or written procedures/protocols for:**

	Yes	No	N/A
Acquisition			
Conservation (storage, maintenance, etc.)			
Regeneration			
Characterization			
Distribution			
Safety duplication			
Information management			
Germplasm health (viability testing, phytosanitary, etc.)			

**33. The genebank uses written procedures and protocols from (check all that apply):**

No written procedures or protocols
Hanson 1985. Practical Manuals for Genebanks No. 1: Procedures for Handling Seeds in Genebanks. IBPGR.
FAO/IPGRI 1994. Genebank Standards.
Rao et al. 2006. Handbooks for Genebanks No. 8: Manual of Seed Handling in Genebanks. Bioversity International.
Organization's own "Operational Genebank Manual"
Written and verified Standard Operating Procedures (SOPs) for key processes
A Quality Management System (QMS)
Other (please specify)

**34. Please describe your quality control activities for conserved seeds:**

	Frequency	Protocols/Methods
Germination testing		
Viability testing		
Health testing		

**35. What is the normal regeneration interval (in years) to maintain the viability of your *Helianthus* collection?**

**36. What proportion (%) of your *Helianthus* collection requires urgent regeneration (apart from the normal routine regeneration)?**

Cultivated <i>Helianthus annuus</i>
Wild <i>Helianthus annuus</i>
Crop wild relatives (other <i>Helianthus</i> spp.)

**37. Is the collection affected by diseases that may restrict germplasm distribution? (Y/N) If yes, please list the relevant diseases and describe the extent.**

## SAFETY DUPLICATION

**38. Are accessions safety duplicated at another genebank?**

Yes
Partly
No
Don't know

**If you answered Yes or Partly, please complete the following three questions (Q39-Q41). If No, skip these questions.**

**39. Please indicate the proportion (%) of *Helianthus* accessions safety duplicated by arrangement: (Note: if accessions are safety duplicated at more than one location, total may exceed 100%.)**

Svalbard

Black box outside country

Integrated in another collection outside country

Black box within country

Integrated in another collection within country

Other

**40. Please list the institution(s) where your germplasm is safety duplicated.**

**41. Do all safety duplication sites have formal agreements to establish terms and obligations? (Y/N)**

**42. Are there constraints to duplicating the collection outside your country? (Y/N) If yes, please specify.**

**43. Are *Helianthus* accessions from other collections safety duplicated at your facilities? (Y/N) If yes, please provide the name(s) of the original collection holder(s) and the number of accessions?**

## DOCUMENTATION AND INFORMATION MANAGEMENT

**44. Do you use a searchable electronic platform (computerized database) for storing and retrieving accession-level data? (Y/N) If yes, what software is used?**

**45. The accession-level information is (check all that apply):**

Public

Private

Available by written catalogue or by contacting the curator

Available & searchable online within the institute

Available & searchable online outside the institute

**46. If the accession-level information is publicly available on the internet, please provide the URL (web address).**

**47. The accession-level database provides the following information (check all that apply):**

Passport

Taxonomy

Characterization

Evaluation

Genotypes

Images

Distribution

Other (please specify)

**48. What proportion (%) of the *Helianthus* collection has:**

Passport data

Geo-referencing data

**49. If you use a computerized database to manage the collection and share accession data, is it adequate to meet the needs of both the genebank and users? (Y/N) If inadequate, are there plans to upgrade or improve this system?**

**50. Are the accession-level data describing your collection available in other, external databases?**

Yes

Partly

No

If Yes/Partly, specify the database(s):

National

Regional

International



## CHARACTERIZATION AND EVALUATION

51-2. What proportion (%) of cultivated and wild accessions have:

	Cultivated accessions (Q51)	Wild accessions (Q52)
Agro-morphological (phenotypic) characterization data		
Genotypic characterization data (molecular markers, etc.)		
Abiotic stress tolerance data		
Biotic stress tolerance data		

53. If abiotic/biotic stresses have been at least partially assessed, please list the specific stresses that have been evaluated.

54. Indicate the descriptors used for agro-morphological characterization:

FAO/IPGRI multi-crop passport descriptors (MCPD 2015)
IBPGR sunflower descriptors (1985)
Institute-specific descriptors
UPOV descriptors
USDA sunflower descriptors
Other (please specify)

55. Can you describe any core collections or other trait-specific subsets of accessions that have been established for the *Helianthus* collection?

## DISTRIBUTION

56. Do you distribute accessions from your *Helianthus* collection? (Y/N) If no, why not?

If you answered Yes to the previous question (Q56), please complete the remaining questions in this section (Q57-Q69). If you answered No, you may skip to the next section.

57. Are you able to distribute:

Only to users in your own country
Only to users in certain countries (i.e., regionally)
Internationally, to any country

58. What best describes the conditions that must be met for distribution:

Freely distributed without terms or conditions
Institutional material transfer agreement (MTA) or other bi-lateral agreement
The Nagoya Protocol for the CBD
The International Treaty on PGR for Food and Agriculture (ITPGRFA)
Other (please specify)

59. For the following categories, how many accessions are typically distributed annually (average of last 3 years)? Answer where applicable.

(Note: wild materials include wild *Helianthus annuus* as well as other *Helianthus* species.)

	Nationally	Internationally
Cultivated accessions		
Wild accessions		

60. How have your distributions changed over the last 5-10 years?

Increased
Stayed the same
Decreased

**61. How do you expect your distributions to change over the next 5–10 years?**

Increase

Stay the same

Decrease

**62. Are there factors that currently limit, or may limit in future, the distribution and use of materials maintained in your collection?**

**63. Do you keep records of the germplasm distributed? (Y/N)**

**64. Of your annual distributions, what kind of users have received germplasm from your collection? Please estimate the proportion (%) of total distribution over the last 5 years (total should sum to 100%):**

Farmers or farmer organizations

Governmental departments

Other genebank curators

Academic researchers and students (universities)

Research institutes

Breeding programs: public sector

Breeding programs: private sector

Non-governmental organizations (NGOs)

Other

**65. Do you charge fees for the following services? (Y/N)**

The cost of accessions

The cost of shipping

**66. Do you have adequate procedures in place for: (Y/N)**

Phytosanitary certification

Packaging

Shipping

**67. Do you routinely solicit feedback from recipients on the following aspects (check all that apply):**

Timeliness of the distribution

Helpfulness of genebank staff in selection of accessions

Quality of samples sent

Quality and usefulness of accession-level information received

Usefulness of the accessions received

Reports/publications resulting from the evaluation or use of the accessions received

Resultant characterization/evaluation data sets

Varietal releases

Other (please specify)

**68. How do germplasm users influence the management of the collection (check all that apply)?**

Through feedback on available materials/distributions

Through formal consultations

Through participation in the governing body of the genebank

Other (please specify)

**69. How are the accessions available for distribution publicized?**

## LONG-TERM COLLECTION VULNERABILITY

**70. Does your organization provide most or all of the recurrent costs for maintaining the *Helianthus* collection? (Y/N) If not, who are your other significant funders?**

**71. How has the budget for conservation of the collection changed over the last 5 years?**

Increased

Stable

Decreased

**If it has decreased, please describe any other funds sourced to make up the shortfall?**

**72. Do you have adequate staff, training, and expertise for: (Y/N)**

	Number of staff	Level of expertise	Training
Managing routine annual genebank operations			
Meeting annual distribution requests			
Addressing the needs of users for accession-level information			

**73. Has there been a formal risk assessment performed and management plan developed for the genebank? (Y/N) If yes, how recently?**

**73. What do you consider to be the 3 most important vulnerabilities or threats to the *Helianthus* collection?**

1:

2:

3:

**74. What are the primary disease/pathogen or pest concerns for:**

Seed storage

Distribution

Regeneration/multiplication

**75. How do you predict the size of the collection to change in the next 10 years?**

Stay approximately the same size

Limited expansion (5-10%)

Substantial increase (>10%)

Decrease owing to collection rationalization

Decrease due to lack of funding/facilities

**77. Please indicate the current and expected situation of your *Helianthus* collection with respect to the following risk factors, where 1 = excellent, 2 = adequate, 3 = insufficient, N/A = not applicable:**

	Current situation	Expected situation (2024 onwards)
Funding for routine operations/maintenance		
Retention of trained staff		
Interest for PGR conservation by donors		
Genetic variability in the collections needed by users/breeders		
Access to germplasm information (passport data, etc.)		
Feedback from users		
Use by breeders/researchers		

## NETWORKS AND PARTNERSHIPS

**78. Does your genebank collaborate with other collection holders? If yes, please describe the form of your collaborations (check all that apply):**

	Collection	Repatriation	Research	Safety duplication	Training	Other
Other national ex situ collection holders						
Other regional or international ex situ collection holders						
In situ conservation sites						
On farm conservation sites						
Community seedbanks						
Protected sites for wild relatives						
Other (please specify)						

**79. Do you collaborate with an *in situ* conservation programme? (Y/N) If yes (or planned for future), please describe.**

**80. Do you participate (or have you participated in the last 10 years) in a plant genetic resource network (including germplasm holders and/or users)? (Y/N) If yes, please describe the network & provide a URL if applicable.**

## FINAL CONSIDERATIONS

**81. Please add any further comments you may have in regard to your *Helianthus* collection and/or this questionnaire. Recommendations for the sunflower conservation strategy are also welcome.**

## Appendix 2. Surveyed institutes holding *Helianthus* collections

- 1. ALB026:** Institute of Plant Genetic Resources (IRGJB), Agricultural University of Tirana  
*Address:* Rruga "Siri Kodra" 132/1, Tirana, Albania  
*Website:* <http://qrgj.org>
- 2. ARE003:** International Center for Biosaline Agriculture (ICBA)  
*Address:* Al Ruwayyah 2, Academic City, P.O. Box 14660, Dubai, United Arab Emirates  
*Website:* <http://www.biosaline.org/>
- 3. ARG1348:** Banco Activo de Germoplasma de Manfredi (BGMANFREDI), Instituto Nacional de Tecnología Agropecuaria (INTA) Manfredi  
*Address:* Ruta Nacional NRo. 9, Km 636, Manfredi, Córdoba, 5988, Argentina  
*Website:* <https://www.argentina.gob.ar/inta>
- 4. AUS165:** Australian Grains Genebank (AGG)  
*Address:* 110 Natimuk Road, Horsham, Victoria, 3400, Australia
- 5. BGD003:** Bangladesh Agricultural Research Institute (BARI)  
*Address:* BARI Rd., Joydebpur, Gazipur, 1701, Bangladesh  
*Website:* <http://www.bari.gov.bd/>
- 6. BGR001:** Institute for Plant Genetic Resources 'Konstantin Malkov' (IPGR-Sadovo)  
*Address:* 2 Druzhba Str., Sadovo, Plovdiv, 4122, Bulgaria  
*Website:* <http://ipgrbg.com>
- 7. BGR029:** Dobrudzha Agricultural Institute (DAI)  
*Address:* Dobrudzha Agricultural Institute, General Toshevo, Dobrich, 9520, Bulgaria  
*Website:* <http://www.dai-gt.org>
- 8. BLR011:** Republican Unitary Enterprise (RUE) "Research and Practical Center of the National Academy of Sciences of the Republic of Belarus for Arable Farming"  
*Address:* Timiryazev St. 1, Zhodino, Minsk Region, 222160, Belarus  
*Website:* <https://izis.by/by/>
- 9. BRA003:** Embrapa Recursos Genéticos e Biotecnologia (CENARGEN), Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA)  
*Address:* Parque Estação Biológica, PqEB s/n°, Brasília, Distrito Federal, 70770-901, Brazil  
*Website:* <https://www.embrapa.br/recursos-geneticos-e-biotecnologia>
- 10. BRA014:** Embrapa Soja (CNPSo), Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA)  
*Address:* Rodovia Carlos João Strass, s/n° Acesso Orlando Amaral, Londrina, Paraná, 86001-970, Brazil  
*Website:* <https://www.embrapa.br/en/soja>
- 11. CAN004:** Plant Gene Resources of Canada (PGRC), Agriculture & Agri-Food Canada  
*Address:* 107 Science Place, Saskatoon, Saskatchewan, S7N 0X2, Canada  
*Website:* <http://pgrc.agr.gc.ca/>
- 12. CZE122:** Výzkumný Ústav Rostlinné Výroby (VURV), Crop Research Institute (CRI)  
*Address:* Drnovská 507/73, Ruzyně, Prague 6, 161 06, Czech Republic  
*Website:* <http://www.vurv.cz>
- 13. DEU146:** Leibniz Institute of Plant Genetics and Crop Plant Research (IPK)  
*Address:* Corrensstrasse 3, Seeland, OT Gatersleben, 6466, Germany  
*Website:* <https://www.ipk-gatersleben.de/>

- 14. DNK059:** Department of Bioscience, University of Aarhus (AAU)  
*Address:* Ole Worms Alle, Building 135, Aarhus C, 8000, Denmark  
*Website:* <https://bio.au.dk/en/>
- 15. ECU023:** Departamento Nacional de Recursos Fitogenéticos (DENAREF), Instituto Nacional de Investigaciones Agropecuarias (INIAP)  
*Address:* Panamericana Sur Km. 1 vía Tambillo, Mejía, Pichincha, 171107, Ecuador  
*Website:* <http://www.iniap.gob.ec/pruebav3/recursos-fitogeneticos/>
- 16. ESP004:** Centro Nacional de Recursos Fitogenéticos (CRF), Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria (INIA-CSIC)  
*Address:* Autovía A-2, Km. 36 Apdo. 1045, Alcalá de Henares, Madrid, 28805, Spain  
*Website:* [http://webx.inia.es/web\\_coleccionescrf/PasaporteCRFeng.asp](http://webx.inia.es/web_coleccionescrf/PasaporteCRFeng.asp)
- 17. ETH085:** Ethiopian Biodiversity Institute (EBI)  
*Address:* P.O. Box 30726, Addis Ababa, Ethiopia  
*Website:* <http://www.ebi.gov.et>
- 18. FRA015:** Institut National de la Recherche Agronomique (INRAE), Occitanie-Toulouse  
*Address:* Chemin de Bordes Rouge, Castanet-Tolosan, Occitanie, 31326, France  
*Website:* <https://www6.toulouse.inrae.fr/lipm/Recherche/Genetique-et-Genomique-du-Tournesol/CRB-Tournesol>
- 19. GBR004:** Millennium Seed Bank (MSBP), Royal Botanic Gardens Kew  
*Address:* Wakehurst Place, Ardingly, West Sussex, RH17 6TN, United Kingdom  
*Website:* <http://brahmsonline.kew.org/msbp>
- 20. HUN003:** Növényi Diverzitás Központ (NÖDIK)  
*Address:* Külsőmező 15, Tápiószéle, 2766, Hungary  
*Website:* <http://www.nodik.org/>
- 21. IND001:** National Bureau of Plant Genetic Resources (NBPGR), Indian Council of Agricultural Research (ICAR)  
*Address:* Pusa Campus, New Delhi, 110012, India  
*Website:* <http://www.nbpgr.ernet.in>
- 22. IND041:** Indian Institute of Oilseeds Research (IIOR), Indian Council of Agricultural Research (ICAR)  
*Address:* Rajendranagar, Hyderabad, 500030, India  
*Website:* <https://icar-iior.org.in/>
- 23. ITA368:** Banca del Germoplasma Autoctono Vegetale (BaGAV), University of Udine  
*Address:* Via delle Scienze 206, Udine, 33100, Italy  
*Website:* <https://bagav.uniud.it/>
- 24. ITA395:** Consiglio per la Ricerca in Agricoltura e L'Analisi dell'Economia Agraria, Centro di Ricerca Cerealicoltura e Colture Industriali, Sede di Bologna (CREA-CI-BO)  
*Address:* Via di Corticella 133, Bologna, 40128, Italy  
*Website:* <https://www.crea.gov.it/en/web/cerealicoltura-e-colture-industriali>
- 25. JPN183:** National Agriculture and Food Research Organization (NARO) Genebank  
*Address:* 2-1-2 Kannondai, Tsukuba-shi, Ibaraki-ken, 305-8602, Japan  
*Website:* [http://www.gene.affrc.go.jp/about\\_en.php](http://www.gene.affrc.go.jp/about_en.php)
- 26. KEN212:** Genetic Resources Research Institute (GeRRI), Kenya Agricultural & Livestock Research Organization  
*Address:* P.O. Box 781, Kikuyu, Kiambu, 902, Kenya  
*Website:* [https://www.kalro.org/Genetic\\_Resources\\_Research\\_Institute](https://www.kalro.org/Genetic_Resources_Research_Institute)

- 27. LKA036:** Plant Genetic Resources Centre (PGRC), Department of Agriculture  
*Address:* P.O. Box 59, Gannoruwa Agricultural Complex, Peradeniya, Kandy, Sri Lanka  
*Website:* <https://www.doa.gov.lk/SCPPC/index.php/en/institute/35-pgrc-2>
- 28. LSO015:** Lesotho National Plant Genetic Resources Centre (LNPGR), Department of Agricultural Research  
*Address:* P.O. Box 829, Maseru, 100, Lesotho  
*Website:* <http://www.agricresearch.gov.ls/index.html>
- 29. MAR088:** Centre Régional de la Recherche Agronomique de Settat (CRRAS), Institut National de la Recherche Agronomique (INRA)  
*Address:* Route Tertiaire 1406, A 5 km de Settat Maroc, Settat, 26000, Morocco  
*Website:* <https://www.inra.org.ma/fr/content/crra-de-settat>
- 30. MEX006:** Banco Nacional de Germoplasma Vegetal (BANGEV), Universidad Autónoma Chapingo (UACH)  
*Address:* Carretera Mexico-Texcoco Km 38.5, Chapingo, Texcoco, México, 56230, Mexico  
*Website:* <http://www.conabio.gob.mx/remib/doctos/bangev-uach.html>
- 31. MEX069:** Centro de Conservación de Semillas Ortodoxas (CC-SO), Región Norte, Universidad Autónoma Agraria Antonio Narro (UAAAN)  
*Address:* Calzada Antonio Narro 1923, Buenavista, Saltillo, Coahuila, 25315, Mexico  
*Website:* <https://www.uaaan.edu.mx/>
- 32. MEX131:** Centro Universitario de Ciencias Biológicas y Agropecuarias (CUCBA), Universidad de Guadalajara (UDG)  
*Address:* Camino Ramón Padilla Sánchez 2100, Nextipac, Zapopan, Jalisco, 45200, Mexico  
*Website:* <http://www.cucba.udg.mx/>
- 33. MEX194:** Instituto de Investigación y Capacitación Agropecuaria, Acuícola y Forestal del Estado de México (ICAMEX)  
*Address:* Conjunto Sedagro s/n, Rancho San Lorenzo, Metepec, México, 52140, Mexico  
*Website:* <https://icamex.edomex.gob.mx/>
- 34. MEX201:** Centro Regional Universitario Sur (CRUS), Universidad Autónoma Chapingo (UACH)  
*Address:* Cristóbal Colón, Esquina con Camino Cosechero, Zimatlán de Álvarez, Oaxaca, 71200, Mexico  
*Website:* <http://scru.chapingo.mx/crus/>
- 35. MEX208:** Centro Nacional de Recursos Genéticos (CNRG), Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias (INIFAP)  
*Address:* Boulevard de la Biodiversidad 400, Rancho las Cruces, Tepatitlán de Morelos, Jalisco, 47600, Mexico  
*Website:* [https://vun.inifap.gob.mx/portalweb/\\_Centros?C=007](https://vun.inifap.gob.mx/portalweb/_Centros?C=007)
- 36. MEX263:** Depositario Nacional de Referencia de Semillas (DNRS), Servicio Nacional de Inspección y Certificación de Semillas (SNICS)  
*Address:* Av. Presidente Juárez Número 13, Colonia El Cortijo, Tlalnepantla de Baz, México, 54000, Mexico  
*Website:* <https://www.gob.mx/snics>
- 37. MMR015:** Myanmar SeedBank (MSB), Department of Agricultural Research (DAR)  
*Address:* Yezin, Zayarthiri Township, Nay Pyi Taw, 15013, Myanmar  
*Website:* <https://www.moali.gov.mm/en/content/department-agricultural-research>
- 38. MNG030:** Institute of Plant and Agricultural Science (IPAS), Mongolian State University of Life Sciences  
*Address:* Darkhan - 15 bag, Darkhan Uul, 45047, Mongolia  
*Website:* <http://www.ipas.edu.mn/>
- 39. MWI041:** Malawi Plant Genetic Resources Centre (MPGRC)  
*Address:* Chitedze Research Station, P.O. Box 158, Lilongwe, Malawi  
*Website:* <https://www.spgrc.org.zm/malawi-mainmenu-29>

- 40. NOR017:** The Norwegian Genetic Resource Center (NIBIO)  
*Address:* Reddalsveien 215, Grimstad, 4886, Norway  
*Website:* <https://www.genressurser.no/>
- 41. PAK001:** Plant Genetic Resources Program (PGRP), Pakistan Agricultural Research Council (PARC)  
*Address:* Park Road, Islamabad, 45500, Pakistan  
*Website:* <http://www.parc.gov.pk/index.php/en/pgrp-home>
- 42. POL003:** Plant Breeding and Acclimatization Institute (IHAR)  
*Address:* Radzików, Blonie, 05-870, Poland  
*Website:* <http://www.ihar.edu.pl/>
- 43. PRT001:** Banco Português de Germoplasma Vegetal (BPGV), Instituto Nacional de Investigação Agrária e Veterinária (INIAV)  
*Address:* Quinta de S. José, Sao Pedro de Merelim, Braga, 4700-859, Portugal  
*Website:* <https://www.inia.pt/bpgv>
- 44. ROM002:** National Institute for Agricultural Research-Development (INCDA-Fundulea)  
*Address:* Strada Nicolae Titulescu, Nr.1, Fundulea, 915200, Romania  
*Website:* <http://www.incda-fundulea.ro>
- 45. ROM007:** "Mihai Cristea" Plant Genetic Resources Bank (BRGV Suceava)  
*Address:* B-dul 1 Mai, Nr. 17, Suceava, 720224, Romania  
*Website:* <https://svgenebank.ro/>
- 46. ROM023:** University of Agricultural Sciences and Veterinary Medicine (USAMVB) Timisoara  
*Address:* Calea Aradului, Nr. 119, Timisoara, 300645, Romania  
*Website:* <https://www.usab-tm.ro/>
- 47. RUS001:** N. I. Vavilov Research Institute of Plant Genetic Resources (VIR)  
*Address:* B. Morskaya Str., 42, Saint-Petersburg, 190000, Russia  
*Website:* <http://www.vir.nw.ru>
- 48. SRB002:** Institute of Field and Vegetable Crops (IFVC)  
*Address:* Maksima Gorkog 30, Novi Sad, 21000, Serbia  
*Website:* <https://ifvcns.rs/>
- 49. SWE054:** Nordic Genetic Resource Center (NORDGEN)  
*Address:* P.O. Box 41, Alnarp, 230 53, Sweden  
*Website:* <http://www.nordgen.org>
- 50. SWE089:** The Swedish National Gene Bank for Vegetatively Propagated Horticultural Crops (SLU Alnarp)  
*Address:* Nationella Genbanken, Box 190, Alnarp, 234 22, Sweden  
*Website:* <https://www.slu.se/centrumbildningar-och-projekt/nationellagenbanken/>
- 51. TUN029:** Banque National de Gènes de Tunisie (BNG)  
*Address:* Boulevard du Leader Yasser Arafat, Charguia 1, Tunis, 2035, Tunisia  
*Website:* <http://www.bng.nat.tn/>
- 52. TUR001:** Plant Genetic Resources Department, Aegean Agricultural Research Institute (AARI)  
*Address:* P.O. Box 9, Menemen, İsmir, 35661, Turkey  
*Website:* <https://arastirma.tarimorman.gov.tr/etae/Sayfalar/EN/AnaSayfa.aspx>
- 53. TZA016:** National Plant Genetic Resources Centre (NPGRC)  
*Address:* P.O. Box 3024, Kibaoni, Ilkiushini, Arusha, Tanzania  
*Website:* <https://www.tpri.go.tz/>



- 54. UKR001:** National Center for Plant Genetic Resources of Ukraine (NCPGRU), Institute of Plant Production n.a. V. Y. Yurjev, National Academy of Agrarian Sciences of Ukraine (NAAS)  
*Address:* Moskovsky Prospekt 142, Kharkiv, 61060, Ukraine  
*Website:* <https://yuriev.com.ua/en/>
- 55. UKR012:** Institute of Oilseed Crops (IOK), National Academy of Agrarian Sciences of Ukraine (NAAS)  
*Address:* Institutskaya Str. 1, Zaporizhzhia, Zaporozhye Region, 69093, Ukraine  
*Website:* <http://imk.zp.ua/>
- 56. URY003:** Instituto Nacional de Investigación Agropecuaria (INIA) La Estanzuela  
*Address:* Ruta 50, Km. 11, C. Correo 39173, La Estanzuela, Colonia, 70006, Uruguay  
*Website:* <http://inia.uy/en/experimental-stations/regional-directions/inia-la-estanzuela>
- 57. USA020:** North Central Regional Plant Introduction Station (NCRPIS), United States Department of Agriculture & Agricultural Research Service (USDA-ARS)  
*Address:* 1305 State Ave., Ames, Iowa, 50014, United States of America  
*Website:* <https://www.ars.usda.gov/midwest-area/ames/plant-introduction-research/>
- 58. ZMB030:** Plant Genetic Resources Centre (SPGRC), South African Development Community (SADC) Plant Genetic Resources Network  
*Address:* Private Bag CH6, Lusaka, 15302, Zambia  
*Website:* <https://www.spgrc.org.zm/>
- 59. ZMB048:** National Plant Genetic Resources Centre (NPGRC), Mount Makulu Research Centre  
*Address:* Private Bag 7, Chilanga, 10101, Zambia
- 60. ZWE049:** Genetic Resources and Biotechnology Institute (GRBI)  
*Address:* P.O. Box CY 550, Causeway, Harare, 263, Zimbabwe  
*Website:* <http://www.drss.gov.zw/index.php/library/library-services/genetic-resources>

## Appendix 3. Taxa standardization utilized in database searches

Taxon in Databases	Standardized Taxa
<i>Helianthus agrestis</i>	<i>Helianthus agrestis</i> Pollard
<i>Helianthus angustifolius</i>	<i>Helianthus angustifolius</i> L.
<i>Helianthus annuus</i>	<i>Helianthus annuus</i> L.
<i>Helianthus annus</i>	<i>Helianthus annuus</i> L.
<i>Helianthus annuus</i>	<i>Helianthus annuus</i> L.
<i>Helianthus annuus</i> L.	<i>Helianthus annuus</i> L.
<i>Helianthus annuus</i> L. ssp. <i>Cultus</i> (Wenzl.) Anashcz.	<i>Helianthus annuus</i> L.
<i>Helianthus annuus</i> L. subsp. <i>annuus</i>	<i>Helianthus annuus</i> L.
<i>Helianthus annuus</i> L. var. <i>annuus</i> subsp. — <i>Aultus</i> (Wenzl.) Anashcz.	<i>Helianthus annuus</i> L.
<i>Helianthus annuus</i> L. var. <i>annuus</i> subsp. <i>Cultus</i> (Wenzl.) Anashcz.	<i>Helianthus annuus</i> L.
<i>Helianthus annuus</i> L. var. <i>annuus</i> subsp. <i>Cultus</i> (Wenzl.) Anashcz.	<i>Helianthus annuus</i> L.
<i>Helianthus annuus</i> L. var. <i>annuus</i> Anashcz.	<i>Helianthus annuus</i> L.
<i>Helianthus annuus</i> L. var. <i>pustovojtii</i> Anashcz.	<i>Helianthus annuus</i> L.
<i>Helianthus annuus</i> L. var. <i>annuus</i> Anashcz.	<i>Helianthus annuus</i> L.
<i>Helianthus annuus</i> Lec. ssp. <i>Cultus</i>	<i>Helianthus annuus</i> L.
<i>Helianthus annuus</i> Lec. ssp. <i>Cultus</i>	<i>Helianthus annuus</i> L.
<i>Helianthus annuus</i> subsp. <i>annuus</i>	<i>Helianthus annuus</i> L.
<i>Helianthus annuus</i> subsp. <i>annuus</i> var. <i>pustovojtii</i>	<i>Helianthus annuus</i> L.
<i>Helianthus annuus</i> subsp. <i>lenticularis</i>	<i>Helianthus annuus</i> L.
<i>Helianthus annuus</i> subsp. <i>annuus</i>	<i>Helianthus annuus</i> L.
<i>Helianthus annuus</i> var. <i>albus</i>	<i>Helianthus annuus</i> L.
<i>Helianthus annuus</i> var. <i>californicus</i>	<i>Helianthus annuus</i> L.
<i>Helianthus annuus</i> var. <i>incanus</i>	<i>Helianthus annuus</i> L.
<i>Helianthus annuus</i> var. <i>nuertingen tech</i>	<i>Helianthus annuus</i> L.
<i>Helianthus annuus</i> var. <i>purpureus</i>	<i>Helianthus annuus</i> L.
<i>Helianthus annuus</i> var. <i>pustovojtii</i>	<i>Helianthus annuus</i> L.
<i>Helianthus annuus</i> var. <i>violaceo-nigris</i>	<i>Helianthus annuus</i> L.
<i>Helianthus annuus</i>	<i>Helianthus annuus</i> L.
<i>Helianthus armeniacus</i> subsp. <i>armeniacus</i> , var. <i>vulgaris</i>	<i>Helianthus annuus</i> L.
<i>Helianthus australis</i> subsp. <i>australis</i> , var. <i>purpurens</i>	<i>Helianthus annuus</i> L.
<i>Helianthus australis</i> subsp. <i>intermedius</i> , var. <i>viridis</i>	<i>Helianthus annuus</i> L.
<i>Helianthus pustovojtii</i> subsp. <i>pustovojtii</i>	<i>Helianthus annuus</i> L.
<i>Helianthus annuus</i>	<i>Helianthus annuus</i> L.
<i>Helianthus annuus</i> subsp. <i>texanus</i>	<i>Helianthus annuus</i> subsp. <i>texanus</i> Heiser
<i>Helianthus anomalus</i>	<i>Helianthus anomalus</i> S. F. Blake
<i>Helianthus argophyllus</i>	<i>Helianthus argophyllus</i> Torr. & A. Gray
<i>Helianthus arizonensis</i>	<i>Helianthus arizonensis</i> R. C. Jacks.
<i>Helianthus atrorubens</i>	<i>Helianthus atrorubens</i> L.
<i>Helianthus bolanderi</i>	<i>Helianthus bolanderi</i> A. Gray
<i>Helianthus californicus</i>	<i>Helianthus californicus</i> DC.
<i>Helianthus carnosus</i>	<i>Helianthus carnosus</i> Small
<i>Helianthus ciliaris</i>	<i>Helianthus ciliaris</i> DC.
<i>Helianthus cusickii</i>	<i>Helianthus cusickii</i> A. Gray
<i>Helianthus debilis</i>	<i>Helianthus debilis</i> Nutt.
<i>Helianthus cucumerifolius</i>	<i>Helianthus debilis</i> subsp. <i>cucumerifolius</i> (Torr. & A. Gray) Heiser
<i>Helianthus debilis</i> subsp. <i>cucumerifo</i>	<i>Helianthus debilis</i> subsp. <i>cucumerifolius</i> (Torr. & A. Gray) Heiser

Taxon in Databases	Standardized Taxa
<i>Helianthus debilis</i> subsp. <i>cucumerifolius</i>	<i>Helianthus debilis</i> subsp. <i>cucumerifolius</i> (Torr. & A. Gray) Heiser
<i>Helianthus debilis</i> subsp. <i>debilis</i>	<i>Helianthus debilis</i> subsp. <i>debilis</i> Nutt.
<i>Helianthus debilis</i> subsp. <i>silvestris</i>	<i>Helianthus debilis</i> subsp. <i>silvestris</i> Heiser
<i>Helianthus debilis</i> subsp. <i>tardiflorus</i>	<i>Helianthus debilis</i> subsp. <i>tardiflorus</i> Heiser
<i>Helianthus debilis</i> subsp. <i>vestitus</i>	<i>Helianthus debilis</i> subsp. <i>vestitus</i> (E. Watson) Heiser
<i>Helianthus decapetalus</i>	<i>Helianthus decapetalus</i> L.
<i>Helianthus deserticola</i>	<i>Helianthus deserticola</i> Heiser
<i>Helianthus divaricatus</i>	<i>Helianthus divaricatus</i> L.
<i>Helianthus doronicoides</i>	<i>Helianthus</i> x <i>doronicoides</i> (Lam.) R. C. Jacks
<i>Helianthus eggertii</i>	<i>Helianthus eggertii</i> Small
<i>Helianthus exilis</i>	<i>Helianthus exilis</i> A. Gray
<i>Helianthus floridanus</i>	<i>Helianthus floridanus</i> A. Gray ex Chapm.
<i>Helianthus giganteus</i>	<i>Helianthus giganteus</i> L.
<i>Helianthus subtuberosus</i>	<i>Helianthus giganteus</i> L.
<i>Helianthus glaucophyllus</i>	<i>Helianthus glaucophyllus</i> D. M. Sm.
<i>Helianthus gracilentus</i>	<i>Helianthus gracilentus</i> A. Gray
<i>Helianthus grosseserratus</i>	<i>Helianthus grosseserratus</i> M. Martens
<i>Helianthus grosseserratus</i>	<i>Helianthus grosseserratus</i> M. Martens
<i>Helianthus heterophyllus</i>	<i>Helianthus heterophyllus</i> Nutt.
<i>Helianthus hirsutus</i>	<i>Helianthus hirsutus</i> Raf.
<i>Helianthus</i> hybr.	<i>Helianthus</i> hybr.
<i>Helianthus</i> hybrid	<i>Helianthus</i> hybr.
<i>Helianthus laciniatus</i>	<i>Helianthus laciniatus</i> A. Gray
<i>Helianthus Helianthus</i> x <i>laetiflorus</i> (=scaberrimus)	<i>Helianthus</i> x <i>laetiflorus</i> Pers.
<i>Helianthus laetiflorus</i>	<i>Helianthus</i> x <i>laetiflorus</i> Pers.
<i>Helianthus laetiflorus</i> s	<i>Helianthus</i> x <i>laetiflorus</i> Pers.
<i>Helianthus scaberimus</i>	<i>Helianthus</i> x <i>laetiflorus</i> Pers.
<i>Helianthus</i> x <i>laetiflorus</i>	<i>Helianthus</i> x <i>laetiflorus</i> Pers.
<i>Helianthus laevigatus</i>	<i>Helianthus laevigatus</i> Torr. & A. Gray
<i>Helianthus longifolius</i>	<i>Helianthus longifolius</i> Pursh
<i>Helianthus maximiliani</i>	<i>Helianthus maximiliani</i> Schrad.
<i>Helianthus maximiliani</i>	<i>Helianthus maximiliani</i> Schrad.
<i>Helianthus micricephalus</i>	<i>Helianthus microcephalus</i> Torr. & A. Gray
<i>Helianthus microcephalus</i>	<i>Helianthus microcephalus</i> Torr. & A. Gray
<i>Helianthus mollis</i>	<i>Helianthus mollis</i> Lam.
<i>Helianthus multiflorus</i>	<i>Helianthus</i> x <i>multiflorus</i> L.
<i>Helianthus neglectus</i>	<i>Helianthus neglectus</i> Heiser
<i>Helianthus niveus</i>	<i>Helianthus niveus</i> (Benth.) Brandege
<i>Helianthus niveus</i> subsp. <i>canescens</i>	<i>Helianthus niveus</i> subsp. <i>canescens</i> (A. Gray) Heiser
<i>Helianthus petiolaris</i> var. <i>canescens</i>	<i>Helianthus niveus</i> subsp. <i>canescens</i> (A. Gray) Heiser
<i>Helianthus niveus</i> subsp. <i>tephrodes</i>	<i>Helianthus niveus</i> subsp. <i>tephrodes</i> (A. Gray) Heiser
<i>Helianthus nuttallii</i>	<i>Helianthus nuttallii</i> Torr. & A. Gray
<i>Helianthus nuttallii</i> subsp. <i>nuttallii</i>	<i>Helianthus nuttallii</i> subsp. <i>nuttallii</i> Torr. & A. Gray
<i>Helianthus nuttallii</i> subsp. <i>rydbergii</i>	<i>Helianthus nuttallii</i> subsp. <i>rydbergii</i> (Britton) R. W. Long
<i>Helianthus occidentalis</i>	<i>Helianthus occidentalis</i> Riddell
<i>Helianthus occidentalis</i> subsp. <i>occidentalis</i>	<i>Helianthus occidentalis</i> subsp. <i>occidentalis</i> Riddell
<i>Helianthus occidentalis</i> subsp. <i>plantagineus</i>	<i>Helianthus occidentalis</i> subsp. <i>plantagineus</i> (Torr. & A. Gray) Heiser
<i>Helianthus paradoxus</i>	<i>Helianthus paradoxus</i> Heiser
<i>Helianthus pauciflorus</i>	<i>Helianthus pauciflorus</i> Nutt.
<i>Helianthus laetiflorus</i> var. <i>rigidus</i>	<i>Helianthus pauciflorus</i> subsp. <i>pauciflorus</i> Nutt.

Taxon in Databases	Standardized Taxa
<i>Helianthus pauciflorus</i> subsp. <i>pauciflorus</i>	<i>Helianthus pauciflorus</i> subsp. <i>pauciflorus</i> Nutt.
<i>Helianthus rigidus</i>	<i>Helianthus pauciflorus</i> subsp. <i>pauciflorus</i> Nutt.
<i>Helianthus rigidus</i> subsp. <i>rigidus</i>	<i>Helianthus pauciflorus</i> subsp. <i>pauciflorus</i> Nutt.
<i>Helianthus rigidus</i> subsp. <i>strumosus</i>	<i>Helianthus pauciflorus</i> subsp. <i>pauciflorus</i> Nutt.
<i>Helianthus pauciflorus</i> subsp. <i>subrhomboideus</i>	<i>Helianthus pauciflorus</i> subsp. <i>subrhomboideus</i> (Rydb.) O. Spring & E. E. Schill.
<i>Helianthus rigidus</i> subsp. <i>subrhombioideus</i>	<i>Helianthus pauciflorus</i> subsp. <i>subrhomboideus</i> (Rydb.) O. Spring & E. E. Schill.
<i>Helianthus petiolaris</i>	<i>Helianthus petiolaris</i> Nutt.
<i>Helianthus petiolaris</i> subsp. <i>fallax</i>	<i>Helianthus petiolaris</i> subsp. <i>fallax</i> Heiser
<i>Helianthus petiolaris</i> var. <i>fallax</i>	<i>Helianthus petiolaris</i> subsp. <i>fallax</i> Heiser
<i>Helianthus petiolaris</i> subsp. <i>petiolaris</i>	<i>Helianthus petiolaris</i> subsp. <i>petiolaris</i> Nutt.
<i>Helianthus porteri</i>	<i>Helianthus porteri</i> (A. Gray) Pruski
<i>Helianthus praecox</i>	<i>Helianthus praecox</i> Engelm. & A. Gray
<i>Helianthus praecox</i> subsp. <i>hirsutus</i>	<i>Helianthus praecox</i> subsp. <i>hirtus</i> (Heiser) Heiser
<i>Helianthus praecox</i> subsp. <i>hirtus</i>	<i>Helianthus praecox</i> subsp. <i>hirtus</i> (Heiser) Heiser
<i>Helianthus praecox</i> subsp. <i>praecox</i>	<i>Helianthus praecox</i> subsp. <i>praecox</i> Engelm. & A. Gray
<i>Helianthus praecox</i> subsp. <i>runyonii</i>	<i>Helianthus praecox</i> subsp. <i>runyonii</i> (Heiser) Heiser
<i>Helianthus pumilus</i>	<i>Helianthus pumilus</i> Nutt.
<i>Helianthus radula</i>	<i>Helianthus radula</i> (Pursh) Torr. & A. Gray
<i>Helianthus resinosus</i>	<i>Helianthus resinosus</i> Small
<i>Helianthus orgialis</i>	<i>Helianthus salicifolius</i> A. Dietr.
<i>Helianthus salicifolius</i>	<i>Helianthus salicifolius</i> A. Dietr.
<i>Helianthus schweinitzii</i>	<i>Helianthus schweinitzii</i> Torr. & A. Gray
<i>Helianthus silphoides</i>	<i>Helianthus silphoides</i> Nutt.
<i>Helianthus silphoides</i>	<i>Helianthus silphoides</i> Nutt.
<i>Helianthus simulans</i>	<i>Helianthus simulans</i> E. Watson
<i>Helianthus smithii</i>	<i>Helianthus smithii</i> Heiser
<i>Helianthus smittii</i>	<i>Helianthus smithii</i> Heiser
<i>Helianthus</i> sp.	<i>Helianthus</i> spp.
<i>Helianthus</i> sp.	<i>Helianthus</i> spp.
<i>Helianthus strumosus</i>	<i>Helianthus strumosus</i> L.
<i>Helianthus strumosus</i> ( <i>macrophyllus</i> )	<i>Helianthus strumosus</i> L.
<i>Helianthus tuberosus</i>	<i>Helianthus tuberosus</i> L.
<i>Helianthus tomentosus</i>	<i>Helianthus tuberosus</i> L.
<i>Helianthus tuberosus</i>	<i>Helianthus tuberosus</i> L.
<i>Helianthus tuberosus</i> L.	<i>Helianthus tuberosus</i> L.
<i>Helianthus tuberosus</i> L. cv. -°-μ-è-Ω-μ-Ü 34	<i>Helianthus tuberosus</i> L.
<i>Helianthus tuberosus</i> L. cv. D19	<i>Helianthus tuberosus</i> L.
<i>Helianthus tuberosus</i> L. cv. Fuseau 60	<i>Helianthus tuberosus</i> L.
<i>Helianthus tuberosus</i> L. cv. K 8	<i>Helianthus tuberosus</i> L.
<i>Helianthus tuberosus</i> L. cv. Сеянец 34	<i>Helianthus tuberosus</i> L.
<i>Helianthus verticillatus</i>	<i>Helianthus verticillatus</i> Small
<i>Helianthus winteri</i>	<i>Helianthus winteri</i> J. C. Stebbins
<i>Helianthus italicum</i>	<i>Helichrysum italicum</i> (Roth) G. Don

## Appendix 4. Overview of the composite dataset for all collection holders

FAO INSTOCDE	Datasource	Region	Accessions all species	<i>Helianthus annuus</i> L.	<i>Helianthus tuberosus</i> L.	<i>Helianthus</i> spp.	<i>Helianthus</i> non specified hybr.	Accessions of CWR	Number of species	CWR and <i>H. tuberosus</i>
USA020	Survey	Americas	5,248	3,710	90	12	10	1,426	53	1,516
BGR029	Survey	Europe	4,890	4,625	70	-	-	195	31	265
IND041	Survey	Asia	3,468	3,444	-	-	-	24	6	24
FRA015	Survey	Europe	3,390	2,870	194	10	-	316	49	510
RUS001	Survey	Europe	2,709	2,608	12	-	8	81	30	93
BRA014	Databases	Americas	2,052	1,834	1	11	8	198	17	199
BRA003	Survey	Americas	1,890	1,620	5	3	3	259	28	264
ROM002	Survey	Europe	1,860	1,828	3	-	-	29	14	32
IND001	Supplementary	Asia	1,596	1,570	2	8	-	16	11	18
AUS165	Survey	Australia	1,434	1,296	1	26	3	108	23	109
POL003	Databases	Europe	1,142	1,113	1	28	-	-	2	1
HUN003	Databases	Europe	1,064	1,056	-	-	-	8	7	8
MAR088	Survey	Africa	1,014	1,014	-	-	-	-	1	-
ARG1348	Survey	Americas	922	922	-	-	-	-	1	-
CAN004	Survey	Americas	2zz781	603	174	-	-	4	4	178
UKR012	Survey	Europe	691	600	16	7	-	68	22	84
DEU146	Survey	Europe	679	468	90	105	-	16	12	106
TUR001	Databases	Europe	666	666	-	-	-	-	1	-
UKR001	Supplementary	Europe	586	510	2	-	-	74	29	76
SRB002	Survey	Europe	524	76	145	-	-	303	28	448
BGR001	Survey	Europe	460	420	-	30	-	10	7	10
TUN029	Survey	Africa	400	400	-	-	-	-	1	-
URY003	Databases	Europe	299	299	-	-	-	-	1	-
ESP004	Survey	Europe	195	195	-	-	-	-	1	-
JPN183	Databases	Asia	187	61	126	-	-	-	2	126
PAK001	Databases	Asia	184	184	-	-	-	-	1	-
MEX006	Databases	Americas	150	150	-	-	-	-	1	-
ECU023	Survey	Americas	122	122	-	-	-	-	1	-
ETH085	Databases	Africa	113	113	-	-	-	-	1	-
BLR011	Databases	Europe	105	105	-	-	-	-	1	-
BLR026	Databases	Europe	101	101	-	-	-	-	1	-
ARE003	Databases	Asia	99	99	-	-	-	-	1	-
CZE122	Survey	Europe	93	93	-	-	-	-	1	-
ITA395	Databases	Europe	78	78	-	-	-	-	1	-
MNG030	Databases	Asia	77	77	-	-	-	-	1	-
ZMB048	Survey	Africa	70	70	-	-	-	-	1	-
ZMB048	Databases	Africa	70	70	-	-	-	-	1	-
UZB006	Databases	Asia	68	66	2	-	-	-	2	2
MEX069	Databases	Americas	66	66	-	-	-	-	1	-
TZA016	Databases	Africa	65	64	-	1	-	-	1	-

FAO INSTOCDE	Datasource	Region	Accessions all species	<i>Helianthus annuus</i> L.	<i>Helianthus tuberosus</i> L.	<i>Helianthus</i> spp.	<i>Helianthus</i> non specified hybr.	Accessions of CWR	Number of species	CWR and <i>H. tuberosus</i>
ZMB030	Databases	Africa	63	63	-	-	-	-	1	-
MEX208	Databases	Americas	57	56	-	-	-	1	2	1
MEX194	Databases	Americas	52	45	1	-	-	6	4	7
GBR004	Survey	Europe	46	11	1	-	-	34	27	35
ZWE049	Survey	Asia	44	44	-	-	-	-	1	-
MEX131	Databases	Americas	42	42	-	-	-	-	1	-
NOR017	Survey	Europe	40	-	40	-	-	-	1	40
LSO015	Survey	Africa	40	40	-	-	-	-	1	-
MWI041	Databases	Africa	40	40	-	-	-	-	1	-
ROM007	Survey	Europe	39	39	-	-	-	-	1	-
LKA036	Databases	Asia	36	36	-	-	-	-	1	-
BLR019	Databases	Europe	30	-	30	-	-	-	1	30
ROM023	Databases	Europe	25	23	2	-	-	-	2	2
BGD003	Databases	Asia	23	23	-	-	-	-	1	-
ALB026	Survey	Europe	22	22	-	-	-	-	1	-
MEX263	Databases	Americas	21	21	-	-	-	-	1	-
MMR015	Survey	Asia	20	20	-	-	-	-	1	-
BLR029	Databases	Europe	20	20	-	-	-	-	1	-
KEN212	Databases	Africa	19	18	-	1	-	-	1	-
ITA368	Survey	Europe	18	2	16	-	-	-	2	16
DNK059	Databases	Europe	18	-	18	-	-	-	1	18
TUR034	Databases	Europe	15	15	-	-	-	-	1	-
LVA014	Databases	Europe	12	-	12	-	-	-	1	12
SWE089	Survey	Europe	11	-	11	-	-	-	1	11
MEX367	Databases	Americas	10	9	-	-	-	1	2	1
PRT001	Databases	Americas	10	10	-	-	-	-	1	-
KGZ040	Databases	Asia	9	9	-	-	-	-	1	-
JOR015	Databases	Asia	8	8	-	-	-	-	1	-
CUB042	Databases	Americas	8	8	-	-	-	-	1	-
JOR105	Databases	Asia	7	7	-	-	-	-	1	-
SDN002	Databases	Africa	6	6	-	-	-	-	1	-
CZE061	Databases	Europe	5	-	5	-	-	-	1	5
TWN001	Databases	Asia	5	5	-	-	-	-	1	-
ISR002	Databases	Europe	5	5	-	-	-	-	1	-
THA300	Databases	Asia	5	5	-	-	-	-	1	-
BLR020	Databases	Europe	4	-	4	-	-	-	1	4
SWZ015	Databases	Europe	4	4	-	-	-	-	1	-
DEU101	Databases	Europe	4	4	-	-	-	-	1	-
BEL002	Databases	Europe	3	-	2	-	-	1	2	3
AUT025	Databases	Europe	3	-	3	-	-	-	1	3
AUT001	Databases	Europe	3	1	2	-	-	-	2	2

FAO INSTOCDE	Datasource	Region	Accessions all species	<i>Helianthus annuus</i> L.	<i>Helianthus tuberosus</i> L.	<i>Helianthus</i> spp.	<i>Helianthus</i> non specified hybr.	Accessions of CWR	Number of species	CWR and <i>H. tuberosus</i>
UGA132	Databases	Africa	3	3	-	-	-	-	1	-
BWA015	Databases	Africa	3	3	-	-	-	-	1	-
ARM059	Databases	Europe	3	-	-	3	-	-	-	-
HRV041	Databases	Europe	3	3	-	-	-	-	1	-
ITA363	Databases	Europe	3	3	-	-	-	-	1	-
PRT102	Databases	Americas	2	-	2	-	-	-	1	2
AZE004	Databases	Europe	2	1	1	-	-	-	2	1
EGY087	Databases	Africa	2	2	-	-	-	-	1	-
CUB014	Databases	Americas	2	2	-	-	-	-	1	-
ERI003	Databases	Africa	2	2	-	-	-	-	1	-
UKR019	Databases	Europe	1	-	1	-	-	-	1	1
MLT001	Databases	Europe	1	-	1	-	-	-	1	1
AZE014	Databases	Europe	1	-	1	-	-	-	1	1
NOR059	Databases	Europe	1	-	1	-	-	-	1	1
NOR073	Databases	Europe	1	-	1	-	-	-	1	1
LTU006	Databases	Europe	1	-	1	-	-	-	1	1
MEX201	Databases	Americas	1	-	-	1	-	-	-	-
ZAF062	Databases	Africa	1	1	-	-	-	-	1	-
NAM006	Databases	Africa	1	1	-	-	-	-	1	-
NGA010	Databases	Africa	1	1	-	-	-	-	1	-
TJK027	Databases	Asia	1	1	-	-	-	-	1	-
NPL069	Databases	Asia	1	1	-	-	-	-	1	-
SWE054	Databases	Europe	1	1	-	-	-	-	1	-
CUB284	Databases	Americas	1	1	-	-	-	-	1	-
PHL129	Databases	Asia	1	1	-	-	-	-	1	-
LBN002	Databases	Europe	1	1	-	-	-	-	1	-
<b>Total</b>			<b>40,501</b>	<b>35,955</b>	<b>1,090</b>	<b>246</b>	<b>32</b>	<b>3,178</b>	<b>498</b>	<b>4,268</b>

## Appendix 5. Total number of accessions for each *Helianthus* taxa conserved *ex situ* and the number of institutions conserving

	Total number of accessions globally	Total number of accessions in survey	Number of institutes conserving globally	Number of institutions conserving in survey
<i>Helianthus annuus</i> L.	35,955	27,162	89	27
<i>Helianthus tuberosus</i> L.	1,090	868	39	15
<i>Helianthus petiolaris</i> Nutt.	447	404	13	11
<i>Helianthus debilis</i> Nutt.	256	201	16	11
<i>Helianthus</i> spp.	246	193	14	7
<i>Helianthus maximiliani</i> Schrad.	224	199	16	13
<i>Helianthus praecox</i> Engelm. & A. Gray	194	152	15	12
<i>Helianthus argophyllus</i> Torr. & A. Gray	183	166	14	11
<i>Helianthus nuttallii</i> Torr. & A. Gray	156	136	11	9
<i>Helianthus grosseserratus</i> M. Martens	134	122	13	10
<i>Helianthus pauciflorus</i> Nutt.	116	109	11	9
<i>Helianthus neglectus</i> Heiser	105	87	10	7
<i>Helianthus strumosus</i> L.	104	98	11	9
<i>Helianthus decapetalus</i> L.	82	72	12	9
<i>Helianthus giganteus</i> L.	72	69	11	9
<i>Helianthus niveus</i> (Benth.) Brandege	69	55	9	6
<i>Helianthus mollis</i> Lam.	66	65	12	11
<i>Helianthus pumilus</i> Nutt.	66	65	4	3
<i>Helianthus divaricatus</i> L.	58	55	11	9
<i>Helianthus radula</i> (Pursh) Torr. & A. Gray	46	46	3	3
<i>Helianthus angustifolius</i> L.	44	43	8	7
<i>Helianthus bolanderi</i> A. Gray	42	42	8	8
<i>Helianthus ciliaris</i> DC.	40	39	8	7
<i>Helianthus salicifolius</i> A. Dietr.	40	38	10	9
<i>Helianthus exilis</i> A. Gray	39	39	2	2
<i>Helianthus hirsutus</i> Raf.	39	37	10	8
<i>Helianthus occidentalis</i> Riddell	39	34	9	7
<i>Helianthus resinosus</i> Small	34	32	6	5
<i>Helianthus californicus</i> DC.	34	33	9	8
<i>Helianthus x laetiflorus</i> Pers.	33	30	11	8
<i>Helianthus hybr.</i>	32	24	5	4
<i>Helianthus eggertii</i> Small	32	32	7	7
<i>Helianthus deserticola</i> Heiser	31	30	5	4
<i>Helianthus cusickii</i> A. Gray	28	28	2	2
<i>Helianthus anomalus</i> S. F. Blake	27	25	5	4
<i>Helianthus gracilentus</i> A. Gray	25	25	5	5
<i>Helianthus microcephalus</i> Torr. & A. Gray	24	23	7	6
<i>Helianthus laevigatus</i> Torr. & A. Gray	23	22	7	6
<i>Helianthus porteri</i> (A. Gray) Pruski	20	20	3	3
<i>Helianthus atrorubens</i> L.	20	19	5	4
<i>Helianthus heterophyllus</i> Nutt.	19	19	1	1
<i>Helianthus silphoides</i> Nutt.	18	18	3	3
<i>Helianthus paradoxus</i> Heiser	17	17	3	3
<i>Helianthus schweinitzii</i> Torr. & A. Gray	17	17	3	3
<i>Helianthus smithii</i> Heiser	17	16	8	7
<i>Helianthus glaucophyllus</i> D. M. Sm.	16	16	5	5
<i>Helianthus simulans</i> E. Watson	14	13	4	3



	Total number of accessions globally	Total number of accessions in survey	Number of institutes conserving globally	Number of institutions conserving in survey
<i>Helianthus agrestis</i> Pollard	14	14	3	3
<i>Helianthus floridanus</i> A. Gray ex Chapm.	13	12	4	3
<i>Helianthus laciniatus</i> A. Gray	13	12	4	3
<i>Helianthus winteri</i> J. C. Stebbins <sup>1</sup>	6	6	2	2
<i>Helianthus x multiflorus</i> L.	5	4	4	3
<i>Helianthus carnosus</i> Small	5	5	1	1
<i>Helianthus verticillatus</i> Small	4	4	2	2
<i>Helianthus arizonensis</i> R. C. Jacks.	4	4	2	2
<i>Helianthus longifolius</i> Pursh	3	3	1	1
<i>Helianthus x doronicoides</i> (Lam.) R. C. Jacks	1	1	1	1
<b>Total</b>	<b>40,501</b>	<b>31,120</b>	<b>517</b>	<b>361</b>

<sup>1</sup>USDA has samples from all known *winterii* populations and one of the original discoverers has searched extensively for additional populations without success (Marek, personal communication 2023)

## Appendix 6. Conservation status of *Helianthus* wild species

Taxa	Assessment of <i>in situ</i> status
<i>Helianthus annuus</i> subsp. <i>texanus</i> Heiser	Not available
<i>Helianthus armeniacus</i> subsp. <i>armeniacus</i> , var. <i>vulgaris</i>	Not available
<i>Helianthus inexpectatus</i> D. J. Keil & Elvin	Threatened (California Native Plant Society, Rare Plant Program (2022). Rare Plant Inventory (online edition, v9-01 1.5). Retr 16/09/22, 2011)
<i>Helianthus longifolius</i> Pursh	Possibly Threatened (Nature Serve, 2022) assessed in 1999
<i>Helianthus pustovojtii</i> subsp. <i>pustovojtii</i>	Not available
<i>Helianthus x intermedius</i> R. W. Long	Not available
<i>Helianthus x doronicoides</i> (Lam.) R. C. Jacks	Not available
<i>Helianthus occidentalis</i> subsp. <i>occidentalis</i> Riddell	Not threatened (Nature Serve, 2022) assessed in 1996
<i>Helianthus nuttallii</i> subsp. <i>parishii</i>	Extinct (Knapp et al 2020: <a href="https://doi.org/10.5061/dryad.xsj3tx99n">https://doi.org/10.5061/dryad.xsj3tx99n</a> )
<i>Helianthus verticillatus</i> Small	Threatened (NatureServe, 2022) assessment in 2010
<i>Helianthus arizonensis</i> R. C. Jacks.	Data Deficient (IUCN, 2016)
<i>Helianthus carnosus</i> Small	Threatened (Nature Serve, 2022) assessment made in 2005
<i>Helianthus x multiflorus</i> L.	na
<i>Helianthus winteri</i> J. C. Stebbins	Threatened (Nature Serve 2022) assessment made in 2014
<i>Helianthus laciniatus</i> A. Gray	Not Threatened (Nature Serve, 2022) assessment made in 1989
<i>Helianthus niveus</i> subsp. <i>tephrodes</i> (A. Gray) Heiser	Threatened (Nature Serve, 2022) assessment made in 2001
<i>Helianthus floridanus</i> A. Gray ex Chapm.	Possibly Threatened (Nature Serve, 2022) assessment made in 1993
<i>Helianthus agrestis</i> Pollard	Threatened (IUCN, 1997)
<i>Helianthus simulans</i> E. Watson	Not Threatened ( <a href="http://explorer.natureserve.org/servlet/NatureServe?searchName=Helianthus+simulans1996">http://explorer.natureserve.org/servlet/NatureServe?searchName=Helianthus+simulans1996</a> )
<i>Helianthus glaucophyllus</i> D. M. Sm.	Vulnerable (Nature Serve, <a href="http://explorer.natureserve.org/servlet/NatureServe?searchName=Helianthus+glaucophyllus,2008">http://explorer.natureserve.org/servlet/NatureServe?searchName=Helianthus+glaucophyllus,2008</a> )
<i>Helianthus paradoxus</i> Heiser	Least Concern (IUCN, 2016)
<i>Helianthus schweinitzii</i> Torr. & A. Gray	Vulnerable (NatureServe, 2022) assessment made in 2004
<i>Helianthus smithii</i> Heiser	Threatened (NatureServe, 2022) assessment made in 2007
<i>Helianthus occidentalis</i> subsp. <i>plantagineus</i> (Torr. & A. Gray) Heiser	Threatened (NatureServe, 2022) Assessment made in 2014
<i>Helianthus silphioides</i> Nutt.	Least Concern (IUCN, 2016)
<i>Helianthus debilis</i> subsp. <i>vestitus</i> (E. Watson) Heiser	Threatened (IUCN, 1997)
<i>Helianthus heterophyllus</i> Nutt.	Not Threatened (NatureServe, 2022) assessed in 1998
<i>Helianthus atrorubens</i> L.	Least Concern (IUCN, 2016)
<i>Helianthus occidentalis</i> Riddell	Not Threatened (NatureServe, 2022) assessment made in 1986
<i>Helianthus porteri</i> (A. Gray) Pruski	Not Threatened (NatureServe, 2022) assessment made in 1998
<i>Helianthus praecox</i> subsp. <i>hirtus</i> (Heiser) Heiser	Threatened (NatureServe, 2022) assessment made in 2002
<i>Helianthus debilis</i> subsp. <i>tardiflorus</i> Heiser	Possibly Threatened (IUCN, 1997)
<i>Helianthus debilis</i> subsp. <i>debilis</i> Nutt.	Possibly Threatened (NatureServe, 2022) assessment made in 2000
<i>Helianthus laevigatus</i> Torr. & A. Gray	Not Threatened (NatureServe, 2022) assessment made in 1995
<i>Helianthus praecox</i> subsp. <i>praecox</i> Engelm. & A. Gray	Threatened (IUCN, 1997)
<i>Helianthus debilis</i> subsp. <i>cucumerifolius</i> (Torr. & A. Gray) Heiser	Not Threatened (NatureServe, 2022) assessment made in 1996
<i>Helianthus microcephalus</i> Torr. & A. Gray	Not Threatened (NatureServe, 2022) assessment made in 1985
<i>Helianthus nuttallii</i> subsp. <i>rydbergii</i> (Britton) R. W. Long	Not Threatened (NatureServe, 2022) assessment made in 2000
<i>Helianthus niveus</i> (Benth.) Brandege	Not Threatened (NatureServe, 2022) assessment made in 1991
<i>Helianthus pauciflorus</i> subsp. <i>subrhomboideus</i> (Rydb.) O. Spring & E. E. Schill.	Not Threatened (NatureServe, 2022) assessment made in 2012
<i>Helianthus anomalus</i> S. F. Blake	Vulnerable
<i>Helianthus cusickii</i> A. Gray	Not Threatened (NatureServe, 2022) assessment made in 1988
<i>Helianthus gracilentus</i> A. Gray	Not Threatened (NatureServe, 2022) assessment made in 1990
<i>Helianthus deserticola</i> Heiser	Data Deficient (IUCN, 2016)

Taxa	Assessment of <i>in situ</i> status
<i>Helianthus eggertii</i> Small	Possibly Threatened (NatureServe, 2022), assessment made in 2003
<i>Helianthus niveus</i> subsp. <i>canescens</i> (A. Gray) Heiser	Not Threatened (NatureServe, 2022) assessment made in 2012
<i>Helianthus x laetiflorus</i> Pers.	na
<i>Helianthus californicus</i> DC.	Least Concern (IUCN, 2016)
<i>Helianthus resinosus</i> Small	Least Concern (IUCN, 2016)
<i>Helianthus nuttallii</i> subsp. <i>nuttallii</i> Torr. & A. Gray	Not Threatened (NatureServe, 2022) assessment made in 2002
<i>Helianthus pauciflorus</i> Nutt.	Least Concern (IUCN, 2016)
<i>Helianthus exilis</i> A. Gray	Near Threatened (IUCN, 2016)
<i>Helianthus hirsutus</i> Raf.	Least Concern (IUCN, 2016)
<i>Helianthus ciliaris</i> DC.	Not Threatened (NatureServe, 2022) assessment made in 1990
<i>Helianthus salicifolius</i> A. Dietr.	Least Concern (IUCN, 2016)
<i>Helianthus bolanderi</i> A. Gray	Least Concern (IUCN, 2016)
<i>Helianthus radula</i> (Pursh) Torr. & A. Gray	Not Threatened (NatureServe, 2022) assessment made in 1988
<i>Helianthus angustifolius</i> L.	Not Threatened (NatureServe, 2022) assessment made in 1985
<i>Helianthus debilis</i> subsp. <i>silvestris</i> Heiser	Not Threatened (NatureServe, 2022) assessment made in 1994
<i>Helianthus praecox</i> subsp. <i>runyonii</i> (Heiser) Heiser	Not Threatened (NatureServe, 2022) assessment made in 2001
<i>Helianthus pauciflorus</i> subsp. <i>pauciflorus</i> Nutt.	Not Threatened (NatureServe, 2022) assessment made in 1999
<i>Helianthus divaricatus</i> L.	Least Concern (IUCN, 2016)
<i>Helianthus mollis</i> Lam.	Not Threatened (NatureServe, 2022) assessment made in 1984
<i>Helianthus giganteus</i> L.	Least Concern (IUCN, 2016)
<i>Helianthus petiolaris</i> subsp. <i>fallax</i> Heiser	Least Concern (IUCN, 2016)
<i>Helianthus pumilus</i> Nutt.	Not Threatened (NatureServe, 2022) assessment made in 1994
<i>Helianthus decapetalus</i> L.	Least Concern (IUCN, 2016)
<i>Helianthus nuttallii</i> Torr. & A. Gray	Least Concern (IUCN, 2016)
<i>Helianthus praecox</i> Engelm. & A. Gray	Least Concern (IUCN, 2016)
<i>Helianthus strumosus</i> L.	Not Threatened (NatureServe, 2022) assessment made in 2016
<i>Helianthus neglectus</i> Heiser	Data Deficient (IUCN, 2016)
<i>Helianthus debilis</i> Nutt.	Least Concern (IUCN, 2016)
<i>Helianthus grosseserratus</i> M. Martens	Least Concern (IUCN, 2016)
<i>Helianthus argophyllus</i> Torr. & A. Gray	Least Concern (IUCN, 2016)
<i>Helianthus petiolaris</i> subsp. <i>petiolaris</i> Nutt.	Not Threatened (NatureServe, 2022) assessment made in 2016
<i>Helianthus petiolaris</i> Nutt.	Least Concern (IUCN, 2016)
<i>Helianthus maximiliani</i> Schrad.	Least Concern (IUCN, 2016)

## Appendix 7. Attendance to two consultation sessions for sunflower strategy development

### In Attendance to Session A:

- Dr. Emily BM Drummond (Consultant)
- Dr. Sally L. Norton (Australian Grains Genebank [AGG], Horsham AU)
- Dr. Daniela Valkova (Dobrudzha Agricultural Institute [DAI], General Toshevo BG)
- Dr. Ulrike Lohwasser (Leibniz Institute of Plant Genetics and Crop Plant Research [IPK], Gatersleben DE)
- Ms. Claudia Krebes (Leibniz Institute of Plant Genetics and Crop Plant Research [IPK], Gatersleben DE)
- Ms. Ohn Mar Aung (Myanmar Seedbank [MSB], Nay Pyi Taw MM)
- Mr. Dan Sandru ("Mihai Cristea" Plant Genetic Resources Bank [BRGV], Suceava RO)
- Dr. Vera Gavrilova (N. I. Vavilov Research Institute of Plant Genetic Resources [VIR], St. Petersburg RU)
- Ms. Galina Khafizova (N. I. Vavilov Research Institute of Plant Genetic Resources [VIR], St. Petersburg RU)
- Dr. Sreten Terzić (Institute of Field and Vegetable Crops [IFVC], Novi Sad RS)
- Mr. Erik de Vahl (National Genebank Alnarp [NGBALN], Alnarp SE)
- Dr. Maher Medini (Banque National de Gènes de Tunisie [BNG], Tunis TN)
- Dr. Katerina Vedmedeva (Institute of Oilseed Crops [IOK], Zaporizhzhia UA)
- Ms. Seka Davidzo (Genetic Resources and Biotechnology Institute [GRBI], Harare ZW)

### In Attendance to Session B:

- Dr. Emily BM Drummond (Consultant)
- Dr. Peter Giovannini (Global Crop Conservation Strategies Coordinator, The Crop Trust)
- Dr. Aluana Goncalves de Abreu (Embrapa Recursos Genéticos e Biotecnologia [CENARGEN], Brasília BR)
- Dr. Cláudio Guilherme Portela de Carvalho (Embrapa Soja [CNPSo], Londrina BR)
- Dr. Regina Maria Villas Bôas de Campos Leite (Embrapa Soja [CNPSo], Londrina BR)
- Dr. Axel Diederichsen (Plant Gene Resources of Canada [PGRC], Saskatoon CA)
- Mr. Dallas Kessler (Plant Gene Resources of Canada [PGRC], Saskatoon CA)
- Dr. Fabiano Miceli (Banca del Germoplasma Autoctono Vegetale [BaGAV], Udine IT)
- Dr. Froylan Rincón (Centro de Conservación de Semillas Ortodoxas, Región Norte [CC-SO], Saltillo MX)
- Dr. Maria Joița-Păcureanu (National Institute for Agricultural Research-Development [INCD], Fundulea RO)
- Dr. Vera Gavrilova (N. I. Vavilov Research Institute of Plant Genetic Resources [VIR], St. Petersburg RU)
- Ms. Galina Khafizova (N. I. Vavilov Research Institute of Plant Genetic Resources [VIR], St. Petersburg RU)
- Dr. Brent Hulke (United States Department of Agriculture - Agricultural Research Service [USDA-ARS], Fargo ND, US)
- Dr. Laura F Marek (United States Department of Agriculture - Agricultural Research Service [USDA-ARS], Ames IA, US)
- Dr. Gerald Seiler (United States Department of Agriculture - Agricultural Research Service [USDA-ARS], Fargo ND, US)
- Dr. Federico Condón (Instituto Nacional de Investigación Agropecuaria [INIA], La Estanzuela UY)
- Mr. Onismus Chipfunde (Genetic Resources and Biotechnology Institute [GRBI], Harare ZW)



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