

An Inventory of Crop Wild Relatives of the United States

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ABSTRACT

The use of crop wild relatives (CWRs) in breeding is likely to continue to intensify as utilization techniques improve and crop adaptation to climate change becomes more pressing. Significant gaps remain in the conservation of these genetic resources. As a first step toward a national strategy for the conservation of CWRs, we present an inventory of taxa occurring in the United States, with suggested prioritization of species based on potential value in crop improvement. We listed 4600 taxa from 985 genera and 194 plant families, including CWRs of potential value via breeding as well as wild species of direct use for food, forage, medicine, herb, ornamental, and/or environmental restoration purposes. United States CWRs are related to a broad range of important food, forage and feed, medicinal, ornamental, and industrial crops. Some potentially valuable species are threatened in the wild, including relatives of sunflower (*Helianthus annuus* L.), walnut (*Juglans regia* L.), pepo squash (*Cucurbita pepo* L.), wild rice (*Zizania* L.), raspberry (*Rubus idaeus* L.), and plum (*Prunus salicina* Lindl.), and few accessions of such taxa are currently conserved ex situ. We prioritize 821 taxa from 69 genera primarily related to major food crops, particularly the approximately 285 native taxa from 30 genera that are most closely related to such crops. Both the urgent collection for ex situ conservation and the management of such taxa in protected areas are warranted, necessitating partnerships between concerned organizations, aligned with regional and global initiatives to conserve and provide access to CWR diversity.

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Abbreviations: CWR, crop wild relative; FAOSTAT, Food and Agriculture Organization of the United Nations statistical database; GP, gene pool; GRIN, Germplasm Resources Information Network; ITPGR, International Treaty on Plant Genetic Resources for Food and Agriculture; NPGS, National Plant Germplasm System; TG, taxon group; USFS, U.S. Forest Service; WUS, wild utilized species.

NEARLY 40 yr ago Jack Harlan outlined the major factors explaining the extent of use of crop wild relatives (CWRs) in plant breeding. His list included the degree of domestication of the crop, the perceived genetic vulnerability of the crop, the availability of CWRs for use, the degree of difficulty in using CWRs in breeding, and the economic conditions and disposition of breeders toward their use (Harlan, 1976).

Use of CWRs has steadily increased over the past decades, providing improved pest and disease resistance, tolerance to abiotic

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stresses, increased yield, novel cytoplasm, and quality traits to banana (*Musa acuminata* Colla), barley (*Hordeum vulgare* L.), bean (*Phaseolus vulgaris* L.), cassava (*Manihot esculenta* Crantz), chickpea (*Cicer arietinum* L.), corn (*Zea mays* L.), lettuce (*Lactuca sativa* L.), oat (*Avena sativa* L.), millet [*Pennisetum glaucum* (L.) R. Br.], potato (*Solanum tuberosum* L.), rice (*Oryza sativa* L.), sugarcane (*Saccharum officinarum* L.), sunflower, tomato (*Solanum lycopersicum* L.), and wheat (*Triticum aestivum* L.), among others (Gur and Zamir, 2004; Hajjar and Hodgkin, 2007; Iltis, 1988; Maxted et al., 2012a; McCouch et al., 2007; Xiao et al., 1996). Advancements in breeding, particularly through novel molecular approaches, have increased the efficiency of the use of wild germplasm substantially (Ford-Lloyd et al., 2011; Tanksley and McCouch, 1997; Volk and Richards, 2011; Zamir, 2001). Research for adaptation to future climates is likely to increase the exploitation of the variation represented in CWRs (Guarino and Lobell, 2011; Ortiz et al., 2008).

Despite substantial efforts over these years, the most significant bottleneck in use identified by Harlan—the availability of CWRs for research and breeding—continues to be of concern, with substantial genetic variation yet to be conserved and financial and political constraints still to be resolved (FAO, 2010; Fowler and Hodgkin, 2004).

An estimated one out of five plant species is threatened worldwide by habitat loss or modification, agricultural modernization, pollution, overexploitation, invasive species, and/or climate change (Brummitt and Bachman, 2010), and nearly 30% of the native flora of the United States is of conservation concern (CPC, 2012). Crop wild relatives are not exempt from these pressures (Bilz et al., 2011; Jarvis et al., 2008; Ureta et al., 2011; Wilkes, 2007).

The urgent collection and subsequent storage in ex situ facilities where these genetic resources can be made available for research and breeding is therefore warranted. The complementary protection of CWRs in situ is necessary to support the ongoing evolution of CWR populations (Heywood, 2008; Maxted and Kell, 2009; Maxted et al., 1997; Meilleur and Hodgkin, 2004), in both wild areas and traditional agricultural systems (GSPC, 2002; Rawal, 1975; Zizumbo-Villarreal et al., 2005).

It is becoming increasingly feasible to formulate comprehensive strategies for the conservation of CWR diversity due to advancements in understanding the taxonomic relationships between crops and their wild relatives (Andersson and de Vicente, 2010; Wiersema et al., 2012), improved availability of data on the distribution of these taxa (e.g., FNA, 2008a; GBIF, 2012), and increased power of distribution modeling and conservation analysis (Hijmans and Spooner, 2001; Jarvis et al., 2005; Parra-Quijano et al., 2011; Ramírez-Villegas et al., 2010).

The starting point for CWR conservation planning typically involves the creation of a checklist of included CWR taxon names, to which ancillary data (e.g.,

ecogeographic information, conservation status, use potential, etc.) is added to generate an inventory for the target area of research (Maxted et al., 2008). National inventories of CWRs have been published for a growing list of nations, particularly in Europe (Magos Brehm et al., 2007; Maxted et al., 2012b), and targeted subsequent conservation efforts have been made in over 40 countries worldwide (Meilleur and Hodgkin, 2004). On the global level, a specialist group is active in listing CWRs of conservation concern (International Union for Conservation of Nature, Species Survival Commission, 2008), an initiative is underway to document, collect, conserve ex situ, and prebreed the CWRs of major food and forage crops (Guarino and Lobell, 2011), and progress is being made in planning for an integrated system of genetic reserves for the CWRs of highest priority worldwide (Maxted and Kell, 2009).

As a primary step in the process toward a national strategy for the conservation of CWRs, we report on an inventory of the CWR flora occurring in the United States and a prioritization of these taxa based on their potential value in agricultural crop research.

The United States Context

More than 20,000 species of plants, or about 7% of the world's flora, are native or naturalized in North America north of Mexico (FNA, 2008b), but the region has not been considered a major center of crop plant diversity (Vavilov, 1926). Those indigenous species that were domesticated before European contact in eastern North America include pepo squash, sunflower, marsh-elder (*Iva annua* L.), and chenopod (*Chenopodium berlandieri* Moq.) (Smith, 2006) and in the arid southwestern United States include Sonoran panic (*Panicum hirticaule* J. Presl var. *hirticaule*) (Nabhan, 1985) and devil's-claw [*Proboscidea parviflora* (Wootton) Wootton and Standl. subsp. *parviflora*] (Bretting and Nabhan, 1986). Blueberry (*Vaccinium* section *Cyanococcus*) and cranberry (*Vaccinium* section *Oxycoccus*) (Ballington, 2001), blackberry (*Rubus fruticosus* L., sensu lato and hybrids) (Finn, 2001), and pecan [*Carya illinoensis* (Wangenh.) K. Koch] (Flack, 1970) may be counted as more recent domestications. The number of CWRs native to the United States may therefore at first glance be estimated to be fairly small.

Three factors significantly increase the number of potentially valuable CWRs. The relatives of a complex of Mesoamerican crop species, including corn, a number of bean (*Phaseolus* L.) and squash species, chili pepper (*Capsicum* L.), American cotton (*Gossypium hirsutum* L.), and tobacco (*Nicotiana rustica* L.) (Nabhan, 1985; Zizumbo-Villarreal and Colunga-GarcíaMarín, 2010), are distributed in the southern regions of the United States (USDA-ARS National Genetic Resources Program, 2012). Second, a number of crops domesticated in other temperate regions of the world are congeneric with species occurring in the United States, for example, strawberry (*Fragaria* L.)

(Hummer et al., 2011) and hops (*Humulus* L.) (Peredo et al., 2010). Finally, approximately 4000 plant species have been introduced to the region since the Colombian Exchange (Guo et al., 2009), including weedy relatives of crop plants.

Several well-documented examples of use of native CWRs in breeding exist. North American wild grape (*Vitis* L.) germplasm proved critical in providing resistance to phylloxera (*Phylloxera vitifoliae* Fitch) as a rootstock in European grape (*Vitis vinifera* L.) production in the late 1800s, and these stocks continue to provide the basis for protection worldwide (Gale, 2003). Genes for resistance to a range of diseases and pests, including rust (*Puccinia helianthi* Schwein.), downy mildew [*Plasmopara halstedii* (Farl.) Berl. & De Toni], powdery mildew [*Golovinomyces cichoracearum* (DC.) V.P. Heluta], broomrape (*Orobanche cumana* Wallr.), sclerotinia head and stalk rot [*Sclerotinia sclerotiorum* (Lib.) de Bary], and sunflower moth (*Homoeosoma electellum* Hulst), have been identified in native sunflowers and successfully transferred into cultivars (Seiler and Gulya, 2004).

Several U.S. government entities support activities focused on CWR conservation. The USDA-ARS National Plant Germplasm System (NPGS) published in situ conservation guidelines for U.S. CWRs (Plant Germplasm Operations Committee, 1999) and recently formed a subcommittee on CWRs within the Plant Germplasm Operations Committee (Plant Germplasm Operations Committee, 2010). The NPGS Germplasm Resources Information Network (GRIN) Taxonomy Section is preparing a database of crop gene pools listing CWRs based on an evaluation of breeding and crossability studies (Wiersema et al., 2012).

Over the past decade the NPGS has supported 61 explorations for the U.S. CWRs of food, forage, woody landscape, and ornamental crop plants (K. Williams, personal communication, 2012). Genetic reserves for the wild relatives of grape (Pavek et al., 2001), chili pepper (Nabhan, 1990), and cranberry (K. Hummer, personal communication, 2010) have been established. Explorations regarding possible locations and feasibility of protected areas for CWRs of pecan, potato, sweet pea (*Lathyrus* L.), and edible alliums (*Allium* L.) were also completed (Plant Germplasm Operations Committee, 1999).

The U.S. Forest Service (USFS) actively maintains a number of CWR populations in National Forests (USFS, 2010) and CWRs are informally conserved across the United States on these and other public lands. The Bureau of Land Management, in partnership with the Millennium Seed Bank of the Royal Botanic Gardens, Kew, and local organizations across the country, has collected CWR accessions within the “Seeds of Success” Program (Bureau of Land Management, 2012). Building on a partnership between ARS and USFS to collaborate on the establishment of in situ reserves for U.S. CWRs, the agencies are in the process of developing a coordinated strategy for CWR management (L. Stritch, personal communication, 2012).

MATERIALS AND METHODS

National Inventory of Crop Wild Relatives

To broadly cover the wild plant species occurring in the United States that have potential value in crop research, we compiled an inventory of CWRs that may be used in crop breeding as well as wild utilized species (WUS) directly used for food, forage, medicine, herb, ornamental, and/or environmental restoration purposes. Very few WUS are the central focus of plant breeding programs although some taxa may be semidomesticated, and WUS may have a high potential for crop development.

For listed CWRs we aimed to include the full range of taxa with the potential to contribute to crop improvement, including both those species where gene exchange with the crop is relatively straightforward and more distant relatives requiring advanced techniques to produce viable hybrid progeny. Our starting point for defining CWRs followed Maxted et al. (2006, p. 2680): “A crop wild relative is a wild plant taxon that has an indirect use derived from its relatively close genetic relationship to a crop; this relationship is defined in terms of the CWR belonging to Gene Pools (GPs) 1 or 2, or taxon groups (TGs) 1 to 4 of the crop.” The definition classifies taxa based on whether they occur in Harlan and de Wet’s (1971) crop GPs 1 or 2, encompassing closely related taxa that are relatively easy to cross using conventional methods in breeding programs. If data from interspecific hybridization or genetic relatedness studies are unavailable, Maxted et al. (2006) proposed a classification system based on taxonomic groups equating to rank in relation to the crop species. Data on gene pool and taxon group concepts for available crops was gathered from GRIN taxonomy (Wiersema et al., 2012) and from the “Harlan and de Wet Crop Wild Relative Inventory” (Vincent et al., 2012).

A growing number of crops have benefited from traits introgressed from distant gene pools (Abberton, 2007; Ballington, 2001; Bradshaw et al., 2006; Chuda and Adamus, 2009; Frese et al., 2001; Mallikarjuna et al., 2006; Mii, 2009; Rygulla et al., 2007), and as breeding techniques improve, taxa from such gene pools are increasingly likely to be of interest to crop improvement programs. Such species are additionally useful for taxonomic and evolutionary research. We therefore broadened our CWR definition to include species in the tertiary gene pool. In some crops these may include taxa from related genera (e.g., *Tripsacum* L. for maize, *Aegilops* L. and *Amblyopyrum* Eig for wheat [Wiersema et al., 2012]).

Crop wild relatives and WUS taxa occurring in the United States were compiled from the GRIN World Economic Plants database (USDA-ARS National Genetic Resources Program, 2011), based on Wiersema and León (1999), completed volumes of the *Flora of North America* (FNA, 2008a), McGuffin (2000), and the Native Seed Network Database (Native Seed Network, 2010). Both native and introduced taxa were included. In addition to listing taxa to the infraspecific level, information on origin status, number of accessions (available plus unavailable) in GRIN, noxious weed status, associated crop, crop gene pool, and associated crop use was obtained. Taxa with multiple uses were listed first by their primary use and thereafter by subsequent uses. For taxa with uses both as CWRs and WUS, use as a genetic resource was prioritized over direct uses. Additional data on occurrence and weed status was gathered from the

PLANTS Database (USDA-NRCS, 2010). The threat status of taxa was recorded from NatureServe (NatureServe, 2009) and the International Union for Conservation of Nature Red List of Threatened Species (IUCN, 2012).

Taxonomic verification was performed via the “Taxonomic Name Resolution Service” (Boyle et al., 2013) and GRIN taxonomy (USDA-ARS National Genetic Resources Program, 2012), the latter of which served as the final authority. The Inventory was reviewed by NPGS curators, members of the NPGS Crop Germplasm Committees, and USDA-ARS crop experts, who submitted revisions and proposed additional taxa.

Prioritization of the Crop Wild Relatives of Agricultural Crops

When using an inclusive definition for crops together with a broad definition of CWRs, national and regional studies have resulted in the majority of flora being listed as CWRs. Approximately 80% of the species in the European and Mediterranean floras were listed as CWRs in an inventory for that region (Kell et al., 2008), and 77% of the flora of Portugal similarly listed as CWRs or WUS (Magos Brehm et al., 2007). Given the extent of potentially useful plant taxa in the United States and general resource constraints in conservation and research funding, we further prioritized taxa within the Inventory to focus subsequent conservation efforts on species with the greatest potential impact on crop research.

We first compiled and prioritized crop species based on their contribution to global agricultural production and food security, with the assumption that important crops are the focus of the most active breeding programs with experience in the use of exotic germplasm. The crop list was collated from the Food and Agriculture Organization of the United Nations statistical database (FAOSTAT) production and food supply data (FAO, 2011), Annex 1 of the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGR) (FAO, 2002), Appendix 2 (“Important Food Crops”) of Groombridge and Jenkins (2002), and Prescott-Allen and Prescott-Allen (1990). These sources emphasize food crops but some include fiber, forage, and industrial crops.

Listed crops were further prioritized based on the number of sources and importance attributed within the sources: (i) major crops (Priority 1) were assigned to crops listed in more than one source, among the specific crop commodities listed in FAOSTAT and in Prescott-Allen and Prescott-Allen (1990), and all crops in Annex 1 of the ITPGR and in Groombridge and Jenkins (2002) and (ii) minor and nonfood crops (Priority 2) were assigned to crops listed in only one source, plus crops recorded in FAOSTAT general commodities as well as Annex 1 forages and the “*Brassica* complex” crops other than those in the genus *Brassica* L. itself. The resulting compilation of the world’s major crops included 242 crops and 268 genera (101 crops and 119 genera in Priority 1 and 141 crops and 149 genera in Priority 2) (Supplemental Table S1). The list included all agricultural crops recorded in FAOSTAT as important to production or to food supply in the United States (FAO, 2011).

The National Inventory was compared to the world’s major crops list and crosschecked with GRIN taxonomy to derive a list of CWR taxa occurring in the United States that are within the gene pools of priority crops. The resulting list of priority CWRs was reviewed by NPGS curators, members of the NPGS Crop Germplasm Committees, and ARS crop experts.

Priority 1 CWR taxa were further categorized based on perceived value and ease of use in breeding programs. Native plant species were assigned a higher priority, as they have a long history of adaptation in contrast to naturalized species, which may have limited variation due to the founder effect (Amsellem et al., 2001). Closely related (defined here as within GPs 1–2 or TGs 1–3) native taxa, plus any additional taxa recorded in the literature or identified by researchers as potentially useful in crop breeding, were assigned the highest priority (Priority 1A). Distantly related and/or nonnative taxa that were not specifically identified by the research community as a target for use were listed as Priority 1B. The few gene pools (notably blackberry and raspberry in *Rubus* L.) for which relatedness information was not available were categorized based on occurrence status.

RESULTS AND DISCUSSION

The National Inventory contains 4596 taxa, representing 3912 species from 985 genera and 194 plant families. Crop wild relatives in the inventory are represented by 2495 taxa representing 1905 species from 160 genera and 56 families. Wild utilized species are represented by 2101 taxa from 2007 species from 833 genera and 182 families. Major families are listed in Table 1. The Inventory is available online at <http://www.ars-grin.gov/misc/tax/> (accessed 1 Oct. 2012). Future plans are to fully integrate these data into GRIN so that detailed information is available for each taxon and the Inventory can be queried by taxonomy, priority level, and geographic distribution.

Crop wild relatives identified in the United States are primarily related to food crops (Table 2). These include genetic resources for globally important crops such as strawberry, sunflower, sweet potato [*Ipomoea batatas* (L.) Lam.], bean, stone fruits (*Prunus* L.), and grape as well as regionally important crops such as pecan, yerba maté (*Ilex paraguariensis* A. St.-Hil.), quinoa (*Chenopodium quinoa* Willd.), and cranberry. Forage and feed CWRs are also well represented, particularly legumes (*Trifolium* L., *Lupinus* L., *Lotus* L., and *Astragalus* L.) and grasses (*Agrostis* L., *Bromus* L., *Festuca* L., and *Poa* L.). Significant genetic resources of medicinal crops include Echinacea (*Echinacea* Moench), tobacco (*Nicotiana* L.), St. John’s-wort (*Hypericum* L.), poppy (*Papaver* L.), and artemisia (*Artemisia* L.). Crop wild relatives of ornamental crops include *Rosa* L., *Coreopsis* L., *Lilium* L., *Phlox* L., *Rudbeckia* L., and *Penstemon* Schmidel. Crop wild relatives of material and industrial crops include relatives of flax (*Linum* L.), cotton (*Gossypium* L.), and jatropha (*Jatropha* L.).

The WUS species listed as distributed in the United States are primarily used for ornamental, restoration, and medicinal purposes. A number of food species of cultural and economic significance are also identified, such as wild rice, sugar maple (*Acer saccharum* Marshall), and pawpaw [*Asimina triloba* (L.) Dunal].

Nonnative species make up 12.3% of the Inventory (14.7% of CWRs and 9.6% of WUS), and 212 taxa (4.6% of total) are federal and/or state listed noxious weeds.

Genetic resource priorities for listed taxa should take into account weed regulations and conservation priorities for the species affected by these invasive plants.

Several introduced CWR taxa were identified as containing genetic resources of interest to breeders, including relatives of beet (*Beta vulgaris* L.) (L. Panella, personal communication, 2011), lettuce (B. Hellier, personal communication, 2011), and clover (W. Williams, personal communication, 1997). Recent alfalfa (*Medicago sativa* L.) breeding efforts have used cold-adapted naturalized populations of *Medicago sativa* L. subsp. *falcata* (L.) Arcang. from South Dakota to develop rangeland varieties adapted to the Intermountain West (Peel et al., 2009). These examples demonstrate the potential value of novel variation in naturalized species (Bossdorf et al., 2005), which should not be neglected in inventories of useful plant species.

The threat status of 3512 (76.4%) taxa in the Inventory has been recorded in NatureServe. Eight (0.2%) taxa were assessed as known or presumed extinct in the wild, 115 (2.5%) as globally critically imperiled and 111 (2.4%) as imperiled, 337 (7.3%) vulnerable, 798 (17.4%) apparently secure, and 2143 (46.6%) globally secure. Of the included taxa, the International Union for Conservation of Nature Red List of Threatened Species assessed 16 taxa as extinct, endangered, or vulnerable (IUCN, 2012). Sixty-two taxa are listed as endangered under the U.S. Endangered Species Act (Endangered Species Act of 1973, 16 U.S.C. Sec 1531), 10 taxa as threatened, and 11 taxa as candidates for listing (NatureServe, 2009). Among the taxonomic groups with the largest number of threatened taxa are members of the family Fabaceae, particularly within

Table 1. Major families of U.S. crop wild relatives (CWRs) and wild utilized species (WUS).

Families	CWRs		WUS		
	No. of genera	No. of taxa	Families	No. of genera	No. of taxa
Fabaceae	19	693	Asteraceae	97	216
Poaceae	31	448	Poaceae	71	156
Asteraceae	12	182	Rosaceae	29	135
Rosaceae	6	163	Fabaceae	52	106
Amaranthaceae	6	137	Ericaceae	23	79
Brassicaceae	11	67	Pinaceae	6	71
Grossulariaceae	1	67	Cyperaceae	6	55
Solanaceae	4	63	Salicaceae	2	48
Cyperaceae	1	48	Ranunculaceae	14	45
Amaryllidaceae	1	47	Boraginaceae	17	43
Other (46)	68	580	Other (172)	516	1147

the genera *Astragalus*, *Lotus*, *Lupinus*, and *Trifolium* (see Supplemental Table S2 for a full listing of extinct, imperiled, endangered, and threatened taxa).

Threatened species with known or high potential value in crop breeding include the wild walnut *Juglans hindsii* (Jeps.) R. E. Sm., which is used as a primary rootstock for English walnut worldwide and is critically imperiled in its native California habitat (Phillips and Meilleur, 1998), and close relatives of sunflower, squash, cotton, gooseberry (*Ribes uva-crispa* L.), raspberry, onion (*Allium cepa* L.), wild rice, and plum (Table 3). The conservation of these genetic resources should be prioritized urgently.

Over 96,000 gene bank accessions of 2800 taxa listed in the Inventory are recorded in GRIN, but a large proportion

Table 2. Uses of U.S. crop wild relatives (CWRs) and wild utilized species (WUS).

Use	Major families (and number of taxa)	No. of families	No. of genera	No. of taxa
<u>CWRs (genetic resource of)</u>				
Food	Poaceae (304), Fabaceae (168), Rosaceae (136), Amaranthaceae (95), Asteraceae (90), Grossulariaceae (67), Brassicaceae (61), Solanaceae (54), Cyperaceae (48), Amaryllidaceae (47), Convolvulaceae (40), Ericaceae (39), and Asparagaceae (35)	47	103	1472
Forage and feed	Fabaceae (521), Poaceae (142), and Amaranthaceae (42)	5	29	709
Medicinal	Asteraceae (63), Hypericaceae (44), and Euphorbiaceae (17)	7	10	150
Ornamental	Plantaginaceae (39), Rosaceae (27), and Asteraceae (19)	5	6	99
Material and industrial	Linaceae (21), Malvaceae (13), and Asteraceae (8)	10	15	57
Herb	Lamiaceae (5)	1	2	5
Soil conservation	Fabaceae (3)	1	1	3
<u>WUS (direct use for)</u>				
Ornamental	Ericaceae (65), Asteraceae (49), Fabaceae (43), Rosaceae (41), Salicaceae (30), Oleaceae (22), Poaceae (20), Papaveraceae (17), and Ranunculaceae (16)	149	440	812
Restoration	Asteraceae (151), Poaceae (53), Cyperaceae (48), Fabaceae (31), Boraginaceae (29), Ranunculaceae (26), Rhamnaceae (26), Apiaceae (23), Onagraceae (22), Liliaceae (22), Polygonaceae (18), and Rosaceae (17)	83	336	755
Medicinal	Asteraceae (12), Lamiaceae (11), and Fabaceae (9)	82	139	180
Food	Rosaceae (72), Poaceae (6), and Sapindaceae (5)	17	26	112
Forage and feed	Poaceae (72), Fabaceae (11), and Araceae (5)	9	61	99
Forestry	Pinaceae (49), Cupressaceae (7), and Betulaceae (7)	16	28	87
Material and industrial	Fagaceae (9) and Cupressaceae (6)	26	37	52
Soil conservation	Fabaceae (3)	1	3	3
Turf	Poaceae (1)	1	1	1

Table 3. Threatened U.S. crop wild relatives of major crops.

Taxon	Priority category [†]	U.S. ESA [‡]	NatureServe [‡]	No. of accessions [§]
<i>Allium munzii</i> (Ownbey & Aase ex Traub) McNeal	P1B	LE	G1	0
<i>Allium obtusum</i> Lemmon var. <i>conspicuum</i> Mortola & McNeal	P1B		T2 to 3	0
<i>Allium scilloides</i> Douglas ex S. Watson	P1B		G2 to 3	0
<i>Cucurbita okeechobeensis</i> (Small) L. H. Bailey	P1A	LE	G1	0
<i>Fragaria chiloensis</i> (L.) Mill. subsp. <i>sandwicensis</i> (Decne.) Staudt	P1A		T2	2
<i>Gossypium tomentosum</i> Nutt. ex Seem.	P1A		G2 to 3	0
<i>Helianthus carnosus</i> Small	P1B		G1 to 2	2
<i>Helianthus niveus</i> (Benth.) Brandegees subsp. <i>tephrodes</i> (A. Gray) Heiser	P1A		G2 [¶]	10
<i>Helianthus nuttallii</i> Torr. & A. Gray subsp. <i>parishii</i> (A. Gray) Heiser	P1B		GX [¶]	0
<i>Helianthus paradoxus</i> Heiser	P1A		G2	1
<i>Helianthus smithii</i> Heiser	P1B		G2	6
<i>Helianthus verticillatus</i> Small	P1B		G1	2
<i>Hordeum arizonicum</i> Covas	P1B		G2 to 4	0
<i>Ipomoea microdactyla</i> Griseb.	P1B		G2	1
<i>Juglans hindsii</i> (Jeps.) R. E. Sm.	P1A		G1	16
<i>Lathyrus grimesii</i> Barneby	P1B		G2	3
<i>Lathyrus holochlorus</i> (Piper) C. L. Hitchc.	P1B		G2	1
<i>Leymus pacificus</i> (Gould) D. R. Dewey	P1B		G2 to 3	0
<i>Manihot walkerae</i> Croizat	P1B	LE	G1	0
<i>Phaseolus texensis</i> A. Delgado & W. R. Carr	P1B		G2	0
<i>Prunus eremophila</i> Prigge	P1B		G1	0
<i>Prunus murrayana</i> E. J. Palmer	P1A		GX	0
<i>Ribes binominatum</i> A. Heller	P1A		G2 to 3	3
<i>Ribes echinellum</i> (Coville) Rehder	P1B	LT	G1	3
<i>Ribes erythrocarpum</i> Coville & Leiberg	P1B		G2	2
<i>Rubus aliceae</i> L. H. Bailey	P1A		GX	0
<i>Rubus hawaiiensis</i> A. Gray	P1A		G2 to 3	13
<i>Rubus macraei</i> A. Gray	P1A		G2	1
<i>Solanum incompletum</i> Dunal	P1B	LE	G1	0
<i>Solanum nelsonii</i> Dunal	P1B	C	G2	0
<i>Solanum sandwicense</i> Hook. & Arn.	P1B	LE	G1	0
<i>Solanum wallacei</i> (A. Gray) Parish	P1B		G2	0
<i>Tripsacum floridanum</i> Porter ex Vasey	P1A		G2	0
<i>Vanilla mexicana</i> Mill.	P1A		G2 to 4	0
<i>Vicia menziesii</i> Spreng.	P1B	LE	G1	0
<i>Vicia ocalensis</i> R. K. Godfrey & Kral	P1B		G1	1
<i>Zizania texana</i> Hitchc.	P1A	LE	G1	0

[†]P1A, native taxa closely related to important crop plants; P1B, nonnative and/or distantly related to important crop plants.

[‡]Taxa listed as endangered (LE), threatened (LT), or as a candidate for listing (C) under the U.S. Endangered Species Act (Endangered Species Act of 1973, 16 U.S.C. Sec 1531) (U.S. ESA), and/or listed as known or presumed extinct in the wild (GX), globally critically imperiled (G1), and globally imperiled (G2) in NatureServe (NatureServe, 2009). Note: G3 is categorized as globally vulnerable and G4 as apparently secure and T denotes global listing at the infraspecific level.

[§]Number of accessions denotes National Plant Germplasm System germplasm listed as wild and collected in the United States.

[¶]Threat assessment at the species level.

of this material is cultivated germplasm conspecific with wild taxa such as American cotton (*G. hirsutum*) and chili pepper (*Capsicum annuum* L.). Germplasm of Inventory taxa listed as wild total 48,780 accessions, and that listed as both wild and from the United States total 20,739 accessions from 2135 taxa. These accessions are distributed unevenly within the Inventory, with 51.8% of accessions comprising 14 genera (*Fraxinus* L., *Helianthus* L., *Pinus* L., *Avena* L., *Elymus* L., *Vaccinium* L., *Rubus* L., *Vitis* L., *Fragaria* L., *Lupinus* L., *Achmatherum* P. Beauv., *Ribes* L., *Solanum* L., and *Trifolium* L.). Of the 232 taxa listed as endangered, threatened, or as a candidate for listing under the

Endangered Species Act (Endangered Species Act of 1973, 16 U.S.C. Sec 1531) as well as taxa listed as known or presumed extinct in the wild, globally critically imperiled, and imperiled in NatureServe (2009), only 157 accessions listed as wild and collected in the United States are conserved in the NPGS.

Priority Crop Wild Relatives of Agricultural Crops

Priority species occurring in the United States total 2256 taxa within 176 genera. These include 821 taxa from 69 genera related to 63 major agricultural crops (Priority 1

Table 4. Priority U.S. crop wild relatives and wild utilized species.

Genus	Associated crop name	Priority (and no. of taxa) [†]	Genus	Associated crop name	Priority (and no. of taxa)
<i>Acer</i>	Sugar maple	P1A (6)	<i>Juglans</i>	Walnut	P1A (7) and P1B (2)
<i>Aegilops</i>	Wheat	P1B (5)	<i>Lactuca</i>	Lettuce	P1A (10) and P1B (1)
<i>Agropyron</i>	Wheat	P1B (2)	<i>Lathyrus</i>	Grasspea	P1B (31)
<i>Allium</i>	Onion, garlic, and leek	P1A (4) and P1B (43)	<i>Leymus</i>	Wheat	P1B (17)
<i>Artocarpus</i>	Breadfruit and jackfruit	P1B (1)	<i>Malus</i>	Apple	P1B (4)
<i>Asparagus</i>	Asparagus	P1B (3)	<i>Manihot</i>	Cassava	P1B (4)
<i>Avena</i>	Oat	P1B (3)	<i>Medicago</i>	Alfalfa	P1B (10)
<i>Beta</i>	Beet, sugar beet, and chard	P1A (4)	<i>Nicotiana</i>	Tobacco	P1B (9)
<i>Brassica</i>	Cabbage, rapeseed, etc.	P1B (5)	<i>Olea</i>	Olive	P1B (1)
<i>Capsicum</i>	Chili pepper and sweet pepper	P1A (2)	<i>Pennisetum</i>	Pearl millet	P1B (10)
<i>Carica</i>	Papaya	P1B (1)	<i>Persea</i>	Avocado	P1B (3)
<i>Carthamus</i>	Safflower	P1B (1)	<i>Phaseolus</i>	Bean	P1A (4) and P1B (15)
<i>Carya</i>	Pecan	P1A (9) and P1B (4)	<i>Piper</i>	Pepper	P1B (1)
<i>Castanea</i>	Chestnut	P1A (3) and P1B (2)	<i>Pistacia</i>	Pistachio	P1A (1)
<i>Cinnamomum</i>	Cinnamon	P1B (1)	<i>Prunus</i>	Stone fruits	P1A (17) and P1B (26)
<i>Cocos</i>	Coconut	P1B (1)	<i>Psathyrostachys</i>	Wheat	P1B (2)
<i>Colocasia</i>	Taro	P1B (1)	<i>Pseudoroegneria</i>	Wheat	P1B (1)
<i>Corylus</i>	Hazelnut	P1A (3)	<i>Psidium</i>	Guava	P1A (1) and P1B (1)
<i>Cucumis</i>	Melon	P1B (4)	<i>Pyrus</i>	Pear	P1B (1)
<i>Cucurbita</i>	Pumpkin and squash	P1A (8) and P1B (2)	<i>Ribes</i>	Currant and gooseberry	P1A (27) and P1B (40)
<i>Cynara</i>	Artichoke	P1B (3)	<i>Rubus</i>	Raspberry and blackberry	P1A (58) and P1B (10)
<i>Daucus</i>	Carrot	P1B (2)	<i>Saccharum</i>	Sugar cane	P1B (9)
<i>Dioscorea</i>	Yam	P1B (3)	<i>Solanum</i>	Potato and tomato	P1A (1) and P1B (38)
<i>Diospyros</i>	Persimmon	P1A (2)	<i>Sorghum</i>	Sorghum	P1B (4)
<i>Diplotaxis</i>	Cabbage, rapeseed, etc.	P1B (2)	<i>Syzygium</i>	Clove	P1B (2)
<i>Elymus</i>	Wheat	P1B (43)	<i>Thinopyrum</i>	Wheat	P1B (2)
<i>Ficus</i>	Fig	P1A (1) and P1B (3)	<i>Tripsacum</i>	Maize	P1A (4)
<i>Foeniculum</i>	Fennel	P1B (1)	<i>Vaccinium</i>	Blueberry and cranberry	P1A (23) and P1B (16)
<i>Fragaria</i>	Strawberry	P1A (11) and P1B (10)	<i>Vanilla</i>	Vanilla	P1A (2)
<i>Gossypium</i>	Cotton	P1A (3)	<i>Vernicia</i>	Tung nut	P1B (1)
<i>Helianthus</i>	Sunflower	P1A (23) and P1B (49)	<i>Vicia</i>	Fava bean and vetch	P1B (14)
<i>Hordeum</i>	Barley	P1B (18)	<i>Vigna</i>	Cowpea, bambara groundnut, etc.	P1B (2)
<i>Ilex</i>	Maté	P1A (6) and P1B (15)	<i>Vitis</i>	Grape	P1A (29)
<i>Illicium</i>	Star-anise	P1A (1)	<i>Zizania</i>	Wild rice	P1A (6)
<i>Ipomoea</i>	Sweet potato	P1A (9) and P1B (31)			

[†]P1A, native taxa closely related to important crop plants; P1B, nonnative and/or distantly related to important crop plants. Origin status from the Germplasm Resources Information Network (USDA-ARS National Genetic Resources Program, 2012). Contributing gene pool and taxon group concepts from Wiersema et al. (2012) and the "Harlan and de Wet Crop Wild Relative Inventory" (Vincent et al., 2012).

gene pools) (Table 4) and 1435 taxa from 107 genera of minor food crops, forages, and other crops (Priority 2) (Supplemental Table S3). Within Priority 1, 285 closely related, native taxa from 30 genera are listed 1A and 536 distantly related and/or nonnative taxa within 57 genera in 1B.

A number of iconic U.S. edible WUS were given priority for conservation considerations. Within Priority 1, these include sugar maple, wild rice, and American chestnut [*Castanea dentata* (Marshall) Borkh.], plants that have held important stature in traditional regional diets. In addition, 148 food, medicinal, and ornamental WUS from 22 genera were assigned to Priority 2.

At least 17 major crops have benefited from traits contributed by 55 Priority 1 CWR taxa (Table 5). As this count is limited to published references, it is likely an

underestimate of the taxa occurring in the United States that have been successfully used in breeding programs.

The NPGS conserves 8195 accessions of wild native Priority 1 taxa (3952 Priority 1A and 4243 Priority 1B) and 4020 accessions of Priority 2 taxa. Of Priority 1 CWRs, 366 (44.6%) taxa are completely absent from ex situ collections and another 307 (37.4%) are represented by less than 10 germplasm accessions.

Far from possessing few genetic resources, the United States contains a wealth of native and introduced plants related to a broad range of crops. Significant gaps in the ex situ collections of these taxa remain to be filled, and a number of potentially valuable species are threatened in the wild. Meanwhile, new populations of some species are still being discovered (Kraft et al., 2012). Crops that are nationally as well as globally important to food

Table 5. Confirmed use of priority crop wild relatives.

Taxon	Trait [†]
<i>Aegilops cylindrica</i> Host	Salt tolerance (Farooq et al., 1995; Wang et al., 2003)
<i>Aegilops geniculata</i> Roth	Hessian fly resistance (El Khlifi et al., 2004)
<i>Aegilops tauschii</i> Coss.	Rust resistance (Cox et al., 1995), wheat soil-borne mosaic virus, wheat spindle-streak mosaic virus (Cox et al., 1995), drought tolerance (Gororo et al., 2002), yellow rust and leaf rust resistance (Ma et al., 1995), glutenins improvement (Pena et al., 1995), agronomic traits, yield improvement (Pestsova et al., 2006), hessian fly resistance (Suszkiv, 2005), karnal bunt (Villareal et al., 1996), water-logging tolerance (Villareal et al., 2001), and sprouting suppression (Xiu-Jin et al., 1997).
<i>Allium fistulosum</i> L.	Disease resistance (Khrustaleva and Kik, 1998)
<i>Avena sterilis</i> L.	Crown rust resistance (Hoffman et al., 2006) and yield improvement (Takeda and Frey, 1976)
<i>Corylus americana</i> Marshall	Eastern filbert blight resistance (Thompson et al., 1996)
<i>Helianthus anomalus</i> S. F. Blake	Fertility restoration (Seiler, 1991a)
<i>Helianthus argophyllus</i> Torr. & A. Gray	Downy mildew resistance (Hulke et al., 2010; Miller and Gulya, 1988), disease resistance (Jan et al., 2004), and fertility restoration (Seiler, 1991a)
<i>Helianthus bolanderi</i> A. Gray	Genetic stock (Jan, 1992) and fertility restoration (Seiler, 1991a)
<i>Helianthus debilis</i> Nutt.	Powdery mildew resistance (Jan and Chandler, 1988) and fertility restoration (Seiler, 1991a)
<i>Helianthus deserticola</i> Heiser	Downy mildew resistance (Seiler, 1991b)
<i>Helianthus divaricatus</i> L.	Broomrape resistance (Jan et al., 2002)
<i>Helianthus giganteus</i> L.	Fertility restoration (Seiler, 2000) and cytoplasmic male sterility (Whelan and Dedio, 1980)
<i>Helianthus grosseserratus</i> M. Martens	Broomrape resistance (Jan et al., 2002)
<i>Helianthus hirsutus</i> Raf.	Fertility restoration (Seiler, 1991c, 2000)
<i>Helianthus maximiliani</i> Schrad.	Broomrape resistance (Jan et al., 2002) and cytoplasmic male sterility (Whelan and Dedio, 1980)
<i>Helianthus neglectus</i> Heiser	Fertility restoration (Seiler, 1991a)
<i>Helianthus paradoxus</i> Heiser	Salt tolerance (Lexer et al., 2004) and fertility restoration (Seiler, 1991a)
<i>Helianthus pauciflorus</i> Nutt.	Cytoplasmic male sterility (Jan et al., 2006) and sclerotinia resistance (Miller and Gulya, 1999)
<i>Helianthus petiolaris</i> Nutt.	Verticillium resistance (Hoes et al., 1973), disease resistance (Jan et al., 2004), cytoplasmic male sterility (Prescott-Allen and Prescott-Allen, 1986), sunflower moth resistance (Rogers et al., 1984), and fertility restoration (Seiler, 1991a)
<i>Helianthus praecox</i> Engelm. & A. Gray	Downy mildew, rust, verticillium wilt and broomrape resistance (Hajjar and Hodgkin, 2007), fertility restoration (Seiler, 1991a), and downy mildew resistance (Seiler, 1991b)
<i>Helianthus resinosus</i> Small	Fertility restoration (Seiler, 1991c)
<i>Helianthus strumosus</i> L.	Fertility restoration (Seiler, 2000)
<i>Helianthus tuberosus</i> L.	Broomrape resistance (Putt, 1978), sunflower moth resistance (Rogers et al., 1984), and fertility restoration (Seiler, 2000)
<i>Hordeum bulbosum</i> L.	Powdery mildew resistance (Pickering and Johnston, 2005), mosaic virus resistance (Ruge-Wehling et al., 2006), septoria resistance (Toubia-Rahme et al., 2003), and leaf rust resistance (Zhang et al., 2001)
<i>Ipomoea trifida</i> (Kunth) G. Don	Root knot nematode and root lesion nematode resistance (Sakamoto, 1976)
<i>Juglans californica</i> S. Watson	Rootstock (USDA-ARS National Genetic Resources Program, 2012)
<i>Juglans hindsii</i> (Jeps.) R. E. Sm.	Rootstock (McGranahan and Leslie, 2009; USDA-ARS National Genetic Resources Program, 2012)
<i>Juglans major</i> (Torr.) A. Heller and <i>Juglans microcarpa</i> Berland.	Rootstock for alkaline soil (McGranahan and Leslie, 2009)
<i>Juglans nigra</i> L.	Anthracnose resistance (McGranahan and Leslie, 2009) and rootstock (USDA-ARS National Genetic Resources Program, 2012)
<i>Lactuca serriola</i> L.	Downy mildew resistance (Hooftman et al., 2007)
<i>Lactuca virosa</i> L.	Leaf aphid resistance (Eenink et al., 1982)
<i>Malus fusca</i> (Raf.) C. K. Schneid.	Rootstock (USDA-ARS National Genetic Resources Program, 2012)
<i>Medicago sativa</i> L. subsp. <i>falcata</i> (L.) Arcang.	Winter hardiness (Barnes et al., 1977)
<i>Pennisetum purpureum</i> Schumach.	Pest resistance, vigor and yield (Hanna, 1997)
<i>Prunus andersonii</i> A. Gray, <i>Prunus pumila</i> L.,	Rootstock (USDA-ARS National Genetic Resources Program, 2012)
<i>Prunus pumila</i> L. var. <i>besseyi</i> (L. H. Bailey)	
Gleason, and <i>Prunus rivularis</i> Scheele	
<i>Pyrus calleryana</i> Decne.	Rootstock (USDA-ARS National Genetic Resources Program, 2012)
<i>Ribes nigrum</i> L.	Pest and disease resistance (Barney and Hummer, 2005)
<i>Ribes uva-crispa</i> L.	Gall mite resistance (Brennan, 2008)
<i>Solanum stoloniferum</i> Schldl. & Bouché	Late blight resistance (Bradshaw et al., 2006) and potato Y virus resistance (Ross, 1979)
<i>Tripsacum dactyloides</i> (L.) L.	Corn leaf blight resistance (Goodman et al., 1987) and yield improvement and top firing resistance (Prescott-Allen and Prescott-Allen, 1986)
<i>Vitis acerifolia</i> Raf., <i>Vitis aestivalis</i> Michx., <i>Vitis cinerea</i> (Engelm.) Engelm. ex Millardet, <i>Vitis cinerea</i> var. <i>helleri</i> (L. H. Bailey) M. O. Moore, <i>Vitis monticola</i> Buckley, <i>Vitis mustangensis</i> Buckley, and <i>Vitis vulpina</i> L.	Rootstock (USDA-ARS National Genetic Resources Program, 2012)
<i>Vitis labrusca</i> L.	Cold tolerance (Reisch and Pratt, 1996)
<i>Vitis riparia</i> Michx. and <i>Vitis rupestris</i> Scheele	Phylloxera vitifoliae resistance (Prescott-Allen and Prescott-Allen, 1986) and rootstock (USDA-ARS National Genetic Resources Program, 2012)

[†]Published trait listing adapted from the “Harlan and de Wet Crop Wild Relative Inventory” (Vincent et al., 2012).

security could benefit significantly from the long-term conservation and exploitation of these taxa. Following the prioritization of such taxa based on their potential use value, planning for conservation will be facilitated through an analysis of the range of distribution of these taxa and the subsequent identification of hotspots of richness of CWRs in the United States as well as geographic and taxonomic gaps in germplasm collections and in situ conservation.

The focus on the gene pools of major agricultural crops during prioritization within the Inventory resulted in a number of minor or locally important crops and WUS, forages, and other nonfood crops holding secondary priority (Supplemental Table S3). Many of these taxa are economically important and their native U.S. genetic resources may have substantial use value. The development and collation of information both on the use of these taxa in breeding programs as well as the value of their associated crops will contribute significantly to their potential for prioritization and subsequent conservation.

Given the considerable development pressures on wild plants in the United States (Stein et al., 2000) and projected increasing impacts from climate change (Loarie et al., 2009), both the urgent collection for ex situ conservation and the management of taxa in conservation areas are warranted. To achieve these goals for the diversity of prioritized taxa, broad partnerships and networks between the federal, state, tribal, and nongovernmental organizations pursuing conservation activities are needed. Because many of the taxa are distributed across national borders and the genetic resources of such species are potentially valuable globally, such efforts should be aligned with neighboring national strategies and with regional and global initiatives to conserve and provide access to CWR diversity.

Supplemental Information Available

Supplemental material is included with this manuscript. This includes a prioritization of agricultural crops worldwide (Supplemental Table S1), an extended list of threatened U.S. crop wild relatives and wild utilized species (Supplemental Table S2), and a listing of additional prioritized U.S. crop wild relatives and wild utilized species (Supplemental Table S3).

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