# Chapter 2
# North American Wild Relatives of Grain Crops

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

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

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

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## 2.1 Introduction

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

## 2.2 Amaranth (*Amaranthus* L.)

### 2.2.1 Introduction

#### 2.2.1.1 Origin of the Crop and Brief History of Use

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

#### 2.2.1.2 Cultivation

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

## 2.2.2   Crop Wild Relatives in North America

### 2.2.2.1   Gene Pools

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

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

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

**Table 2.1**  (continued)

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

**Table 2.1** (continued)

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

(continued)

**Table 2.1** (continued)

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

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

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

#### 2.2.2.2    Useful Crop Wild Relative Traits

The grain amaranth CWR are potential sources of useful herbicide tolerance, increased seed size, non-shattering seed, high-protein foliage, squalene seed oil, wider geographic adaptation, and improved harvest index. The INDEAR company in Argentina is preparing to release a new grain amaranth cultivar, INDEAR-9, that has resistance to ALS inhibitor herbicides provided by an *A. hybridus* allele (personal communication, Gerónimo Watson). The largest seeds in the genus are

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

### 2.2.3   Wild Economic Species

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

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

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

### 2.2.4    Conservation Status of North American Wild Relatives

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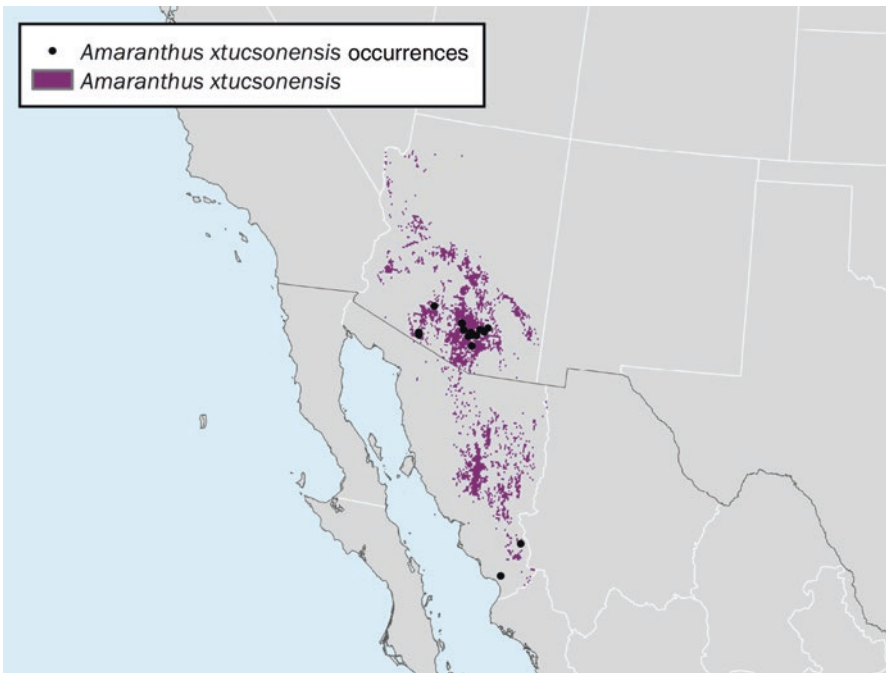


**Fig. 2.1** Species distribution map of modeled potential distribution of *Amaranthus ×tucsonensis* Henrickson based on climatic and edaphic similarities with herbarium and gene bank reference localities. Full methods for generation of map and data providers are given in Appendix 1
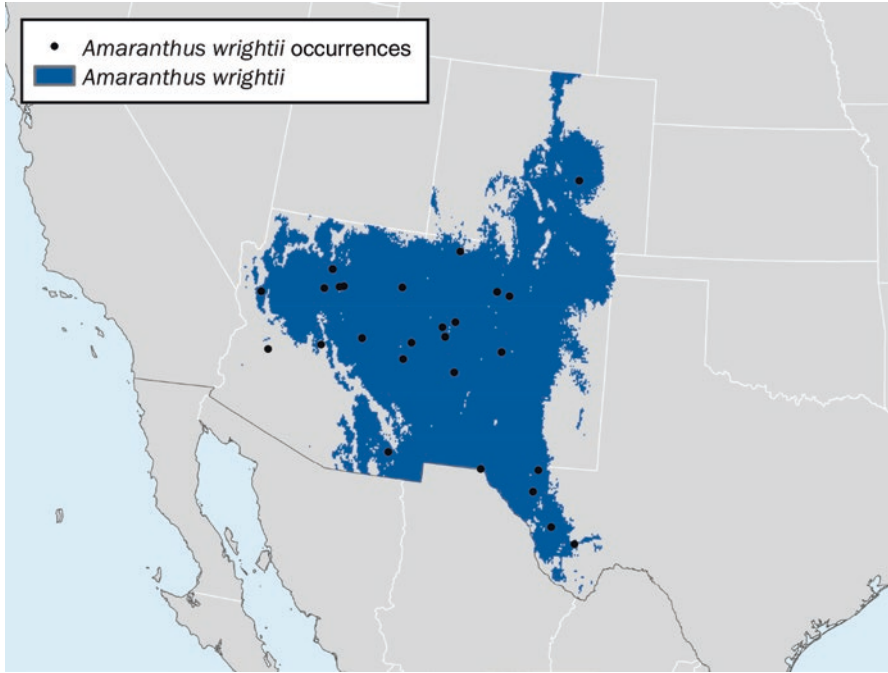
**Fig. 2.2** Species distribution map of modeled potential distribution of *Amaranthus wrightii* S. Watson based on climatic and edaphic similarities with herbarium and gene bank reference localities. Full methods for generation of map and data providers are given in Appendix 1

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

### 2.3.1 Introduction

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

### 2.3.2 Crop Wild Relatives in North America

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

### 2.3.3   Wild Economic Species

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

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

### 2.3.4   Conservation Status of North American Wild Relatives

#### 2.3.4.1   In Situ

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

#### 2.3.4.2   Ex Situ

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

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

### 2.4.1   Introduction

#### 2.4.1.1   Origin of the Crop and Brief History of Use

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

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

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

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

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

### 2.4.1.2 Cultivation

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

## *2.4.2 Crop Wild Relatives in North America*

### 2.4.2.1 Gene Pools

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

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

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

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

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

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

### 2.4.2.2   Useful Crop Wild Relative Traits

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

## 2.4.3   Wild Economic Species

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

## 2.4.4   Conservation Status of North American Wild Relatives

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

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

## 2.5   Buckwheat (*Fagopyrum* Mill.)

### 2.5.1   *Crop Wild Relatives in North America*

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

## 2.6  Oat (*Avena sativa* L.)

### 2.6.1  Introduction

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

### 2.6.2  Crop Wild Relatives in North America

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

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

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

### 2.6.3  Wild Economic Species

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

### 2.6.4  Conservation Status of North American Wild Relatives

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

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

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

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

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

### 2.7.1 Introduction

#### 2.7.1.1 Origin of the Crop and Brief History of Use

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

#### 2.7.1.2 Cultivation

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

### 2.7.2 Crop Wild Relatives in North America

#### 2.7.2.1 Gene Pools

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

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

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

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

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

#### 2.7.2.2   Useful Crop Wild Relative Traits

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

### 2.7.3   Wild Economic Species

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

### 2.7.4   Conservation Status of North American Wild Relatives

The genus *Panicum* has about 100 species in the modern strict sense after reduction from about 450 species in recent revisions (Aliscioni et al. 2003). Within *Panicum*, reticulate allopolyploid evolution makes relationships between the species

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

## 2.8  Quinoa (*Chenopodium quinoa* Willd.)

### 2.8.1  Introduction

#### 2.8.1.1  Origin of the Crop and Brief History of Use

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

#### 2.8.1.2  Cultivation

Entrepreneurial farmers are rapidly changing the map of quinoa production. Much of the higher-quality Andean-origin quinoa is intolerant of temperate summer conditions during pollination, which is an impediment to wider adoption as a crop, especially in

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

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

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

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

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

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

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

## 2.8.2  Crop Wild Relatives in North America

### 2.8.2.1  Gene Pools

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

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

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

(continued)

**Table 2.7** (continued)

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

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

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

*Chenopodium quinoa* is an allotetraploid composed of two CWR genomes, A and B. Identifying the *C. quinoa* genomes in diploid wild species was a terrific scientific achievement. Two wild species have the same two genomes as quinoa and are closely related: *C. hircinum* Schrad. in South America and *C. berlandieri* in North America. These two allotetraploid wild species with genomes A and B are of greatest interest for crop improvement because of genetic similarity and crossing fertility with *C. quinoa* (Matanguihan 2015), placing them in the GP-1. Crosses between quinoa cultivars and various wild *C. berlandieri* accessions have produced consistently fertile $F_1$s and $F_2$ populations with 70–90% fertility (E. Jellen, personal

communication). The two constituent genomes correspond best to diploid genomes in either *C. neomexicanum* or *C. standleyanum* Aellen (genome A) and *C. ficifolium* Sm. (genome B) (Storchova et al. 2015; Walsh et al. 2015). These diploid A and B genome species are wild in North America: *C. neomexicanum* occurs in the southwestern United States and northern Mexico; *C. standleyanum* is a widespread eastern temperate native species; and *C. ficifolium* is an infrequent adventive species. The constituent species are in GP-2 since they may be used someday to make a synthetic allotetraploid that is cross-fertile with quinoa.

### 2.8.2.2  Useful Crop Wild Relative Traits

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

## 2.8.3  Wild Economic Species

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

## 2.8.4   Conservation Status of North American Wild Relatives

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

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

### 2.9.1   Introduction

#### 2.9.1.1   Origin of the Crop and Brief History of Use

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

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

### 2.9.1.2 Cultivation

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

## 2.9.2 Crop Wild Relatives in North America

### 2.9.2.1 Gene Pools

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

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

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

(continued)

**Table 2.8** (continued)

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

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

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

#### 2.9.2.2   Useful Crop Wild Relative Traits

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

### 2.9.3   Wild Economic Species

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

### 2.9.4   Conservation Status of North American Wild Relatives

The widespread temperate weedy *Setaria* species naturalized in North America are generally already represented in the NPGS (USDA, ARS 2017) (Table 2.8) and some of the other gene banks represented in GENESYS (Global Crop Diversity Trust 2017), and their genomes have been analyzed (Layton and Kellogg 2014). However, many of the wild non-weedy species lack representation in germplasm collections and should be accessioned. For example, germplasm of *Setaria corrugata* (Elliott) Schult., an annual wild species in Florida that closely resembles *S. viridis* (Rominger 2003), is absent from germplasm collections. Similarly, *Setaria*

*arizonica* Rominger, which has a vulnerable conservation status (Natureserve 2017) because of its limited distribution in Arizona and adjacent Sonora, is not represented in these collections. There is no information available on the crossing ability or genomes of either of these species.

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