3 Botanical Context for Domestication in North America

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Abstract

Pitseed goosefoot, *Chenopodium berlandieri* Moq., is a widespread allotetraploid weed having $2n = 4x = 36$ (AABB subgenomes) found throughout North America from Mexico to Alaska. It is a critical genetic resource for adaptive improvement of its South American cousin and descendant, quinoa (*C. quinoa* Willd.). It has also been important in its own right at various times throughout history and prehistory, having been domesticated at least twice in the Americas north of the Isthmus of Panama. Botanically, *C. berlandieri* belongs to Section *Chenopodium* Subsection *Cellulata* along with its allotetraploid allies *C. quinoa*, weedy South American *C. hircinum* Schrad., and a complex of putative A-genome diploids concentrated in the semiarid southwestern region of North America. This chapter reviews the botanical and ecological context of *C. berlandieri* and its potential as a genetic resource for improving quinoa.

3.1 Introduction

Pitseed goosefoot, *Chenopodium berlandieri* Moq., is an allotetraploid with $2n = 4x = 36$ (AABB sub-genomes). It is the North American free-living member of a New World allotetraploid goosefoot complex that includes cultivated North American *C. berlandieri* subsp. *nuttaliae* (Safford) Wilson & Heiser; South American cultivated *C. quinoa* Willd.; and free-living South American ecotypes *C. hircinum* Schrad. and *C. quinoa* subsp. *milleanum* (Aellen) Aellen or var. *melanospermum* Hunziker (Wilson 1990; Wilson and Manhart 1993). The distinguishing taxonomic characteristic of this species complex is the fruit, consisting of an achene with rounded margins, adhering alveolate pericarp with a honeycombed pattern, and underlying pitted testa. The thick black testa differentiates pitseed goosefoot from its domesticated relatives, which possess a thinner testa that is usually of lighter color. The thick testa in the free-living chenopods inhibits water uptake, thus providing for a reservoir of dormant seed in the soil and accounting for their germination in the wake of human and natural influences that disturb the soil sufficiently to scarify them.

Pitseed goosefoot is of increasing interest as a genetic resource for improving quinoa's adaptation to low-elevation production environments (Jellen et al. 2019). Quinoa was selected under domestication in high-elevation environments

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S. M. Schmöckel (ed.), *The Quinoa Genome*, Compendium of Plant Genomes,
https://doi.org/10.1007/978-3-030-65237-1_3

(>3000 masl) in the absence of heat stress and with pressure from a narrow spectrum of pests and pathogens due to the extreme altitude. Coastal quinoa, though selected and produced near sea level in a Mediterranean climate zone, was nonetheless relatively isolated from pathogens and pests of the outside world by the extreme aridity of the Atacama Desert to the north, by the Andean Cordillera and Patagonian Desert to the east, and fronted by the vast expanse of the South Pacific to the west. In contrast, pitseed goosefoot evolved throughout North America, with diverse ecotypes adapted to lowland, highland, subtropical, temperate, and desert environments.

3.1.1 Ecological Context of *C. berlandieri*

The free-living forms of tetraploid *C. berlandieri* have been subdivided into five North American botanical varieties, ignoring uncharacterized natural variation south of the Rio Grande River, in the online Flora of North America (1993+). Of these varieties or ecotypes, var. *zschackei* (Murr) Murr ex Graebner is widespread throughout North America; var. *sinuatum* (Murr) Wahl is found in the semi-arid Southwest; var. *boscianum* (Moq.) Wahl is native to the northern Gulf of Mexico Coast; var. *macrocalycium* (Aellen) Cronquist is from the Atlantic Coast; and var. *berlandieri* is found in interior South Texas. Although Flora of North America (1993+) classified a sixth botanical variety, *bushianum* (Aellen) Cronquist, mounting evidence indicates that this is a separate biological entity, *C. bushianum* Aellen, having a distinct genome composition and hexaploid chromosome number (Bhargava et al. 2005, 2007).

All of the free-living forms of *C. berlandieri* are found in disturbed environments, sometimes in association with the aggressive Eurasian hexaploid weed *C. album* L. (lambsquarters). The surest method of discriminating between the two entities is by examining the pericarps, which are typically adhering and alveolate in the former and adhering or non-adhering but always non-alveolate in the latter. Gentle rubbing of the fruits typically exposes the shiny and, generally, non-pitted testas in a sample of lambsquarters.

3.1.2 Molecular Studies of *C. berlandieri*

There is mounting molecular evidence for the interrelatedness of members of the ATGC and, from targeted and whole-genome DNA sequencing studies, that *C. berlandieri* is most likely the basal or ancestral member of the complex. Five earlier studies by Wilson (1981, 1988a, b, c) and Wilson and Manhart (1993) demonstrated using biochemical marker analyses that the South American ATGC members are closely related to each other and to North American *C. berlandieri* and will spontaneously cross-hybridize to produce varying degrees of fertile progeny.

Storchova et al. (2015) provided strong evidence for common ancestry of ATGC members through Bayesian and Maximum Parsimony phylogenetic analyses of DNA sequences from two *flowering locus T-like* (*FTL*) introns. Moreover, they were able to discriminate between *FTL* versions of the two sub-genomes and reported for the first time that each locus showed affinity to diploid species from different hemispheres. Walsh et al. (2015) sequenced introns 16 and 17 of the *salt overly sensitive 1* (*SOS1*) gene and found similar results. Brown et al. (2015) repeated these findings a third time by comparing sequences from the amylose-synthesis gene *granule bound starch synthase 1* (*GBSS1* or *waxy*). Kolano et al. (2016) compared nuclear ITS sequences and found that all seven *C. berlandieri* genotypes were basally situated relative to the six quinoa genotypes in their study.

Jarvis et al. (2017) compared whole-genome nuclear resequencing data from five *C. berlandieri*, two *C. hircinum*, and 16 *C. quinoa* genotypes in a bootstrapped phylogenetic analysis and showed that *C. berlandieri* was basal to the South American free-living and domesticated genotypes. An additional comparison of whole mtDNA- and cpDNA-based phylogenies in these same genotype sets has reaffirmed these relationships (D Jarvis, personal communication).

3.1.3 Potential Diploid Progenitor Gene Pools of the ATGC in North America

Recent DNA sequencing-based studies of ATGC members and *Chenopodium* diploids (Storchova et al. 2015; Walsh et al. 2015; Brown et al. 2015; Jarvis et al. 2017) have instituted a nomenclature system for the two sub-genomes, with 'A' representing the sub-genome most similar to a large group of New World-native diploids and 'B' representing the sub-genome closest to Eurasian diploids *C. ficifolium* Smith and *C. suecicum* Murr. Kolano et al. (2011) previously reported a minisatellite DNA sequence, 18–24 J, that hybridized abundantly to chromosomes of the B genome in *Chenopodium* diploids, tetraploids, and hexaploids.

Jarvis et al. (2017) demonstrated through comparison of the QQ74 quinoa deep-sequenced reference genome and shallow-sequenced diploids *C. pallidicaule* Aellen (A sub-genome, Andean) and *C. suecicum* (B sub-genome, Central European) that there is abundant synteny and even collinearity of scaffolded sequence contigs between each diploid and distinct sets of orthologous quinoa chromosomes. The three aforementioned single-gene sequencing studies (Storchova et al. 2015; Walsh et al. 2015; Brown et al. 2015) found that A-genome diploids were positioned basally to a clade containing ATGC members, while B-genome diploids were positioned basally to a clade containing ATGC members along with sequenced taxa from the Eurasian *C. album*-complex. Kolano et al. (2016) reported that nuclear ITS sequence in most of the ATGC members is more similar to B-genome diploids *C. ficifolium* and *C. suecicum* than to the A-genome diploids—a predictable result, since only one nucleolar organizer region (NOR) locus has been retained in most ATGC members and it is on a chromosome carrying the 18–24 J B-genome-abundant minisatellite (Kolano et al. 2011).

The question of which New World A-genome is, or is closest to, the original donor of the A genome in the ATGC members is elusive, although studies of cytoplasmic DNA have confirmed that the A-genome diploid was the female parent in the hybridization event that occurred roughly 3.3–6.3 Mya (Kolano et al. 2016; Jarvis et al. 2017). Table 3.1 contains a comprehensive list of known North American- and incomplete list of South American-native diploids presumed to carry variants of the A genome. Kolano et al. (2016) reported that whole-genome DNA of *C. watsonii* A. Nels. was more effective in hybridizing to A-genome chromosomes of *C. berlandieri* and *C. quinoa* than 12 other putative A-genome diploids in genomic in situ hybridization (GISH) experiments. Among their other 12 diploids were South American *C. pallidicaule* and *C. petiolare* Kunth and North American *C. atrovirens* Rydb., *C. desiccatum* A. Nels., *C. fremontii* S. Wats., *C. hians* Standl. (probably not *C. hians* but more likely *C. desiccatum*), *C. incanum* (S. Wats.) A. A. Heller, *C. leptophyllum* (Moq.-Tand.) Nutt. ex S. Wats., *C. neomexicanum* Standl. (collected at a site more typical of *C. arizonicum* Standl. or *C. sonorense* Benet-Pierce & M. G. Simpson), *C. nevadense* Standl., *C. pratericola* Rydb., and *C. standleyanum* Aellen. Morphologically, *C. berlandieri* most closely matches the North American-native diploid members of *Chenopodium* subsect. *Cellulata*, among which are included the seven species of the *C. neomexicanum* complex (Benet-Pierce and Simpson 2017) and *C. watsonii*. Another diploid complex, that of *C. hians*, has tremendous diversity in California and specimens from that state were recently subdivided into twelve taxa by Benet-Pierce and Simpson (2019). Of additional interest is the observation that most of these diploids and several free-living taxa of the ATGC possess the fishy trimethylamine-odor phenotype—a trait that has not been observed in the B-genome diploids *C. ficifolium* and *C. suecicum*.

Table 3.1 Comprehensive list of North American and partial list of South American putative A-genome diploid *Chenopodium* species

Chenopodium L. Species	Habitat
albescens Small	S Texas mesquite woodlands
arizonicum Standl.	Upper Sonoran scrub lands
atrovirens Rydb.	W USA, montane
aureum Benet-Pierce	W USA, montane
brandegeeae Benet-Pierce	S California, montane
cycloides A. Nels.	W Great Plains, sandy soils
desiccatum A. Nels.	W USA, deserts and plains
eastwoodiae Benet-Pierce	Sierra Nevada Mountains
flabellifolium Standl.	San Martin Island, BC, Mexico
foggii Wahl	New England, granitic forest soils
fremontii S. Wats.	W USA, montane woodlands
hians Standl.	W USA, montane woodlands
howellii Benet-Pierce	NE California, Sierra Nevada Mountains
incanum (S. Wats.) A. A. Heller	W USA, deserts
incognitum Wahl	W USA, montane chaparral
lenticulare Aellen	Upper Chihuahuan scrub lands
leptophyllum (Moq.-Tand.) Nutt. ex S. Wats.	W USA, deserts
lineatum Benet-Pierce	Sierra Nevada Mountains
littoreum Benet-Pierce & M. G. Simpson	C California, coastal dunes
luteum Benet-Pierce	Sierra Nevada Mountains
neomexicanum Standl.	Mogollon Plateau, igneous soils
nevadense Standl.	W Great Basin, sodic clay pans
nitens Benet-Pierce and Simpson	W USA, deserts and plains
pallescens Standl.	E Great Plains
pallidicaule Aellen	Andean seed crop (*canahua*)
palmeri Standl.	Upper Sonoran scrub lands
parryi Standl.	Upper Chihuahuan scrub lands
petiolare Kunth[a]	Andean Puna zone
philippianum Aellen	S Andes
pratericola Rydb.	USA, sandy soils
sandersii Benet-Pierce	S California, montane
simpsonii Benet-Pierce	S California, montane
sonorense Benet-Pierce & M. G. Simpson	Sonoran Desert
standleyanum Aellen	C USA, woodlands
subglabrum (S. Wats.) A. Nels.	W Great Plains, sandy soils
twisselmannii Benet-Pierce	Sierra Nevada Mountains
wahlii Benet-Pierce	S California, montane
watsonii A. Nels.	W USA, plains, corrals

[a] Fits taxonomic description of *C. paniculatum* Hook. (Reiche 1911)

3.2 Descriptions of *C. berlandieri* Subspecies and Botanical Varieties

3.2.1 *C. berlandieri* subsp. *berlandieri* var. *boscianum*

Variety *boscianum* is a locally common weed on rock jetties, sand and gravel piles, roadsides, and other disturbed areas where the root zone experiences cyclic tidal drainage on barrier islands and estuaries along the northwestern Gulf of Mexico coast from Laguna Madre to Mobile Bay (Fig. 3.1). This taxon is noteworthy for its production of fishy-smelling trimethylamine throughout the plant (Cromwell 1950), a trait that is dominantly inherited in hybrids with quinoa (personal observations). Variation for timing of flowering and seed set, ranging from spring to very late fall, is a characteristic of var. *boscianum* populations. Occurrence of tropical cyclones is instrumental in seed dispersal of this taxon; Jellen and Maughan (unpublished) encountered populations still bearing substantial quantities of seed in early December 2014—an exceptional year due to the absence of landfalling tropical cyclonic systems in the northern Gulf of Mexico. Many of these populations contained plants that flowered in mid-late summer, presumably in response to shortening daylengths. On the other hand, populations observed on Padre Island, in extreme southeastern Texas, in April exhibited day-neutrality and possessed only faint trimethylamine odor.

Phenotypic variation for var. *boscianum* fruits and typical habitats are shown in Fig. 3.1. Hybrids between the *boscianum* ecotype and cultivated quinoa are >90% fertile in the F_2 generation (Fig. 3.2). At BYU, lines with large and light-colored seeds, heat tolerance, and close resemblance to quinoa panicles have been selfed to the F_9 generation. These plants have consistently produced ample seed in multiple field environments including Bolivia, coastal Peru, northern Guyana, Morocco, the Pacific Northwest, and Great Basin of the USA.

3.2.2 *C. berlandieri* subsp. *berlandieri* var. *berlandieri*

Variety *berlandieri* is found in locally common populations along crop fields in sandy soils of the lower Rio Grande Valley. It also inhabits disturbed roadsides intersected by arroyos, especially on saline or expanding clay substrates, sometimes in the shade of locust trees, and often in association with putative diploid *C. albescens*. Figure 3.3 shows phenotypic variation for fruit morphology and typical habitats of this ecotype.

In the spring of 2018 Jellen, Maughan, and Jarvis (personal communication) collected 30 populations of var. *berlandieri* across South Texas from San Antonio to Brownsville. These plants had a very strong trimethylamine odor, like the northern Gulf Coast populations of var. *boscianum*; few to no bracts in their large inflorescences; and leaves that most often had two prominent basal lobes. In addition, the pericarps were usually black and lacked the yellow-orange area at the stylar base typical of var. *zschackei*.

3.2.3 *C. berlandieri* subsp. *berlandieri* var. *macrocalycium*

Variety *macrocalycium* is an eastern North American seashore (/lakeshore?) plant often found in competition with *C. album*, mostly along the Middle Atlantic and New England Coasts up through the Canadian Maritime provinces. Its phenotype is characterized by its relatively large (to 2 mm diameter) fruits and large calyces that typically spread away from the fruit, exposing it at maturity. It is therefore an intriguing genetic resource for potentially improving quinoa seed size, provided that *macrocalycium* carries complementary alleles contributing to this trait. Figure 3.4 shows variation for fruit type in a small collection of var. *macrocalycium* and also typical habitats where it is found.

In 2008, an experimental population was generated at BYU by crossing Ames 29207 from the beach at Saco, Maine, with the quinoa variety

Fig. 3.1 **a** Fruit morphology of 18 accessions of *C. berlandieri* var. *boscianum* from populations collected along the northern Gulf of Mexico Coast, from west to east. (top row, l to r) BYU 1470, Matagorda, Texas; BYU 1474, Freeport, Texas; BYU 1475, San Luis Pass, Texas; BYU 1301, San Leon, Texas; BYU 1476, Jamaica Beach, Texas; (second row) BYU 1469, Bolivar Peninsula, Texas; BYU 1466, Port Arthur, Texas; BYU 1465, Little Florida Beach, Louisiana; BYU 1455, Cypremort Point, Louisiana; BYU 1458, Golden Meadow, Louisiana; (third row) BYU 1460, Grand Isle, Louisiana; BYU 17131, Metairie, Louisiana; BYU 17134, Yscloskey, Louisiana; BYU 14112, Long Beach, Mississippi; BYU 14113, Gulfport, Mississippi; (bottom row) dispersal unit of BYU 1470; BYU 14114, Biloxi, Mississippi; BYU 14115, Pascagoula, Mississippi; BYU 14111, Mobile Bay, Alabama; dispersal unit of BYU 14111. **b** Photographs of typical *C. berlandieri* var. *boscianum* habitats. (l to r) Rockport, TX; Yscloskey, LA; Coden, AL

Fig. 3.2 Fruit morphology in an F_2 population derived from an interspecific quinoa cv. 'Real-1' X *C. berlandieri* var. *boscianum* (BYU 937 from Galveston Bay, Texas) cross. Top row (l to r): 'Real-1', BYU 937, F_1 hybrid. Rows two, three, and bottom show fruits from random F_2 plants in the population. (Jellen et al. 2019)

'Ingapirca'. The F_1 plant was large, fertile, and vigorous; however, well over half of the F_2 generation plants failed to set seeds under heat-stress conditions in the greenhouse (25C + temperatures) and those that did possessed black seeds and wild-type (highly lax) panicle morphologies. Consequently, var. *macrocalycium* may not be an advantageous taxon for improving quinoa's heat tolerance.

3.2.4 *C. berlandieri* subsp. *berlandieri* var. *sinuatum*

Variety *sinuatum* (Fig. 3.5) is present in locally common populations along roadsides, disturbed (including recently burned) fields, semi-desert scrub and chaparral, and open grasslands throughout southwestern North America (Flora of North America 1993+). Within relatively undisturbed grasslands *sinuatum* can comprise fairly extensive stands, with variation for branching pattern and plant color. In Arizona-New Mexico, it is often found in association with the diploid taxa *C. arizonicum*, *C. neomexicanum*, *C. palmeri*, and *C. sonorense* and in the Davis Mountains of West Texas, with *C. lenticulare*. *Sinuatum* is primarily a summer-fall fruiting ecotype; its flowering is timed to coincide with the mid-summer arrival of the Sonoran-Chihuahuan Monsoon in Arizona-New Mexico-West Texas, although the presence of spring-

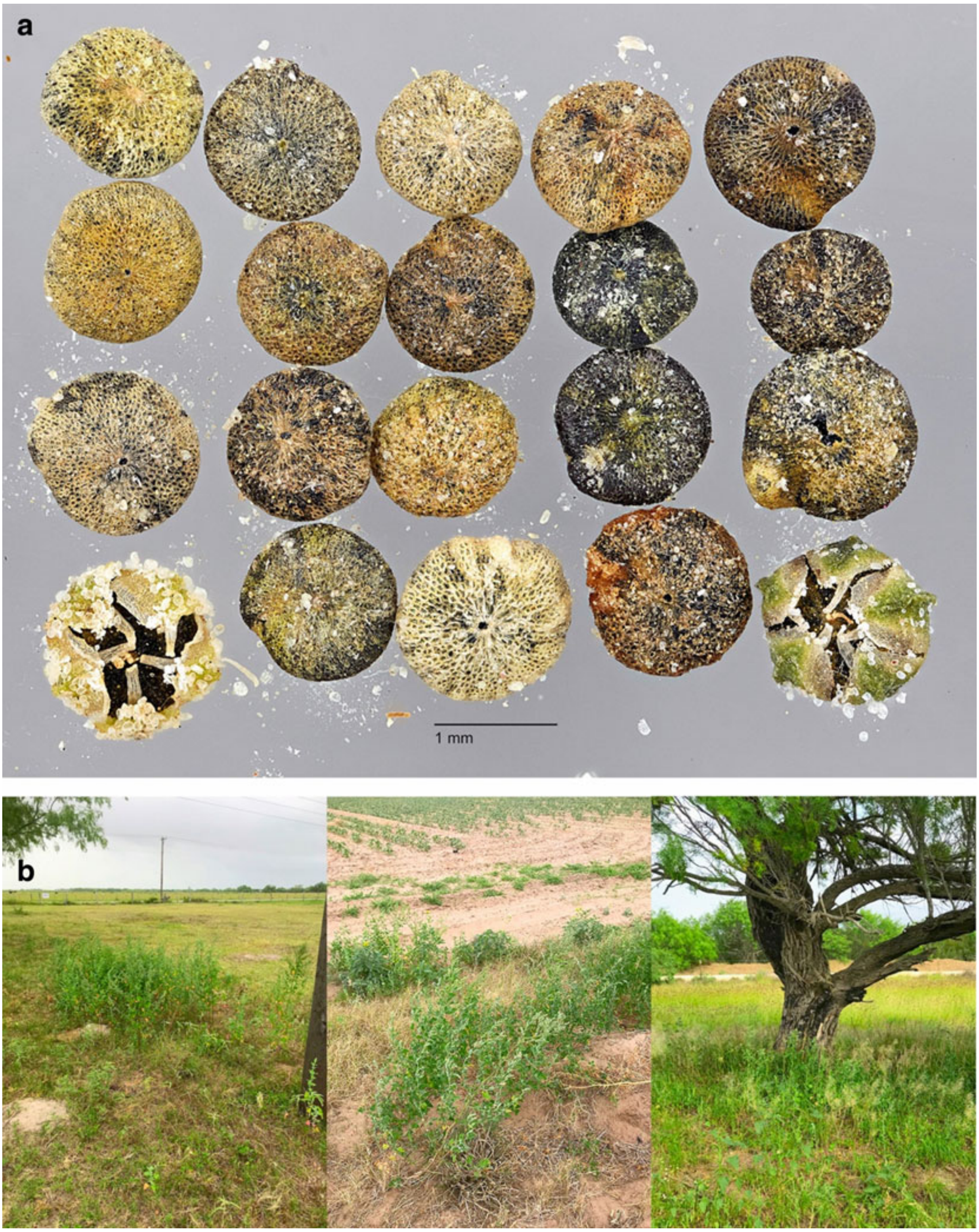

Fig. 3.3 **a** Fruit morphology of 18 accessions of *C. berlandieri* var. *berlandieri* from populations collected in South Texas. (top row, l to r) BYU 1801, Cotulla, La Salle Co.; BYU 1804, Catarina, Dimmit Co.; BYU 1806, Webb Co.; BYU 1807, Webb Co.; BYU 1809, San Diego, Duval Co.; (second row) BYU 1814, Falfurrias, Brooks Co.; BYU 1817, Brooks Co.; BYU 1818, Linn, Hidalgo Co.; BYU 1819, Lasara, Willacy Co.; BYU 1820, Del Mar Heights, Cameron Co.; (third row) BYU 1822, Rio Hondo, Cameron Co.; BYU 1823, Riviera, Kleberg Co.; BYU 1824, Corpus Christi, Nueces Co.; BYU 1830, Beeville, Bee Co.; BYU 1832, Mustang Hollow, Live Oak Co.; (bottom row) dispersal unit of BYU 1802, Artesia Springs, Cotulla Co.; BYU 1833, George West, Live Oak Co.; BYU 1834, Three Rivers, Live Oak Co.; BYU 1836, Hidden Acres, San Patricio Co.; dispersal unit of BYU 1836. **b** Photographs of typical *C. berlandieri* var. *berlandieri* habitats. (l to r) Horse pasture, Kleberg Co., Texas; edge of cotton field, Hidalgo Co., Texas; roadside under locust tree, Bee Co., Texas

Fig. 3.4 **a** Fruit morphology of six accessions of *C. berlandieri* var. *macrocalycium*. (top row, l to r): calyces of BYU 1488 and BYU 1489; (second row): calyx of BYU 803; BYU 803, Ames 29207 from Saco, Maine; BYU 1488 from Slaughter Beach, Delaware; BYU 1489 from Sea Isle City, New Jersey; (third row): BYU 1490 from Ocean Grove, New Jersey; BYU 14110 from Navarre Beach, Florida; BYU 17129 from Rye Beach, New Hampshire; (bottom row): calyces of BYU 1490, BYU 14110, and BYU 17129. **b** Typical habitats of var. *macrocalycium*: Slaughter Beach, Delaware (left) and Sea Isle City, New Jersey (right, with *C. album*)

Fig. 3.5 **a** Fruit morphology of 14 accessions of *C. berlandieri* var. *sinuatum*. (top row, l to r): BYU 402 from San Diego, California; BYU 1494 from Cottonwood, Arizona; BYU 870 from Mormon Lake, Arizona; BYU 1452 from Big Tujunga Canyon, California; BYU 1493 from Peeples Valley, Arizona; (second row): BYU 17203 from Cochise Co., Arizona; BYU 14101 from San Juan, New Mexico; BYU 14108 from Cochise Co., Arizona; BYU 1511 from White Pine Co., Nevada; BYU 1653 from the Mojave Desert, California; (third row): BYU 17150 from Wild Rose Pass, Texas; BYU 17158 from the Davis Mountains, Texas; BYU 17212 from Sonoita, Arizona; BYU 17242 from Pima Co., Arizona; (bottom row): calyces of BYU 402, BYU 870, BYU 1494, and BYU 17242. **b** Typical habitats of var. *sinuatum* (l to r): Davis Mountains, Texas; Santa Cruz Co., Arizona; Big Tujunga Canyon, California

fruiting genotypes of similar subtropical varieties *berlandieri* and *boscianum* in Southeast Texas suggest that the existence of *sinuatum* populations capable of exploiting the winter-spring rainfall cycle in relatively frost-free lowland areas of southern Arizona and California should be expected. The presence of populations of fruiting var. *sinuatum* growing in Big Tujunga Canyon (along with diploid *C. incognitum* and *C. album*) and in the Santa Monica Mountains under exceptional drought conditions in August 2014—at a time when many of the chaparral perennials were under drought stress-induced dormancy—indicates that this taxon could be a tremendous breeding resource for improving heat and drought tolerance in quinoa.

Wilson and Heiser (1979) reported low fertility in a small number of crosses between *C. quinoa* and *C. berlandieri* var. *sinuatum*. However, a population at BYU derived from a *C. quinoa* cv. 'Ollague' X var. *sinuatum* (BYU 14108) produced 155/178 (89%) fertile F_2's (Fig. 3.6).

3.2.5 *C. berlandieri* subsp. *berlandieri* var. *zschackei*

Variety *zschackei* is the most common and widespread free-living ecotype of *C. berlandieri* in North America. Its distinguishing characteristic is the orange-yellow pigmentation on the pericarp at the stylar attachment point atop the fruit. This variety is found throughout the continent, especially in interior areas and, in the Southwest, at higher elevations. Within the western USA, in particular, it is a fairly common weed of roadsides, construction sites, and pastures (Fig. 3.7). Variety *zschackei* usually flowers from late summer through fall, presumably as a consequence of spring germination rather than a short-day flowering response.

3.2.6 *C. berlandieri* subsp. *jonesianum*

Subspecies *jonesianum* is an extinct cultivated form of pitseed goosefoot discovered in archeological middens throughout the Oak-Savannah and Oak-Hickory Forest regions of North America (Smith and Funk 1985). A comparison of chloroplast DNA from archeological and modern samples supported the hypothesis that this was a local, rather than an introduced, domesticate (Kistler and Shapiro 2011). Specimens had small (<1.5 mm) seed with thin, dark testas. It was a principal food source for the Hopewell and Early Mississippian mound builders and a key component of the Eastern North America (ENA) Crop Complex (Smith 2006). Two additional *C. berlandieri* forms have been described together from the same archeological sites as subsp. *jonesianum* (Smith and Yarnell 2009): common and similarly small-seeded, but thick-testa specimens representing free-living pitseed goosefoot that was likely a weedy form harvested for greens; and a rare, larger (to 2.4 mm diameter), orange-yellow colored and thin-testa type resembling subsp. *nuttaliae*. The appearance of weedy and cultivated pitseed goosefoot types together indicates they likely formed a crop-weed complex—a situation mirroring modern Andean quinoa-*ajara* and Mesoamerican *huauzontle*-pitseed goosefoot complexes (Gremillion 1993; Wilson and Heiser 1979; Wilson 1990; Wilson and Manhart 1993). Both domesticated seed forms no longer appear in middens that postdate 1000 B.C.E., presumably due to the adoption of the Mesoamerican maize-beans-squash complex (Smith and Yarnell 2009).

3.2.7 *C. berlandieri* subsp. *nuttaliae*

Subspecies *nuttaliae* includes an interesting and phenotypically diverse assemblage of highland Mexican leafy garden greens (*quelites*), inflorescence vegetables (*huauzontle*), and seed crops (*chia roja*), along with a companion a free-living type, proposed *C. pueblense* H. S. Reed, with which it likely has continuously hybridized (Wilson and Heiser 1979). While *huauzontle* and chenopod *quelites* continue to be important food crops in central Mexico, *chia roja* is threatened with extinction as a crop due to shifting patterns of rural cultivation and societal upheaval in its

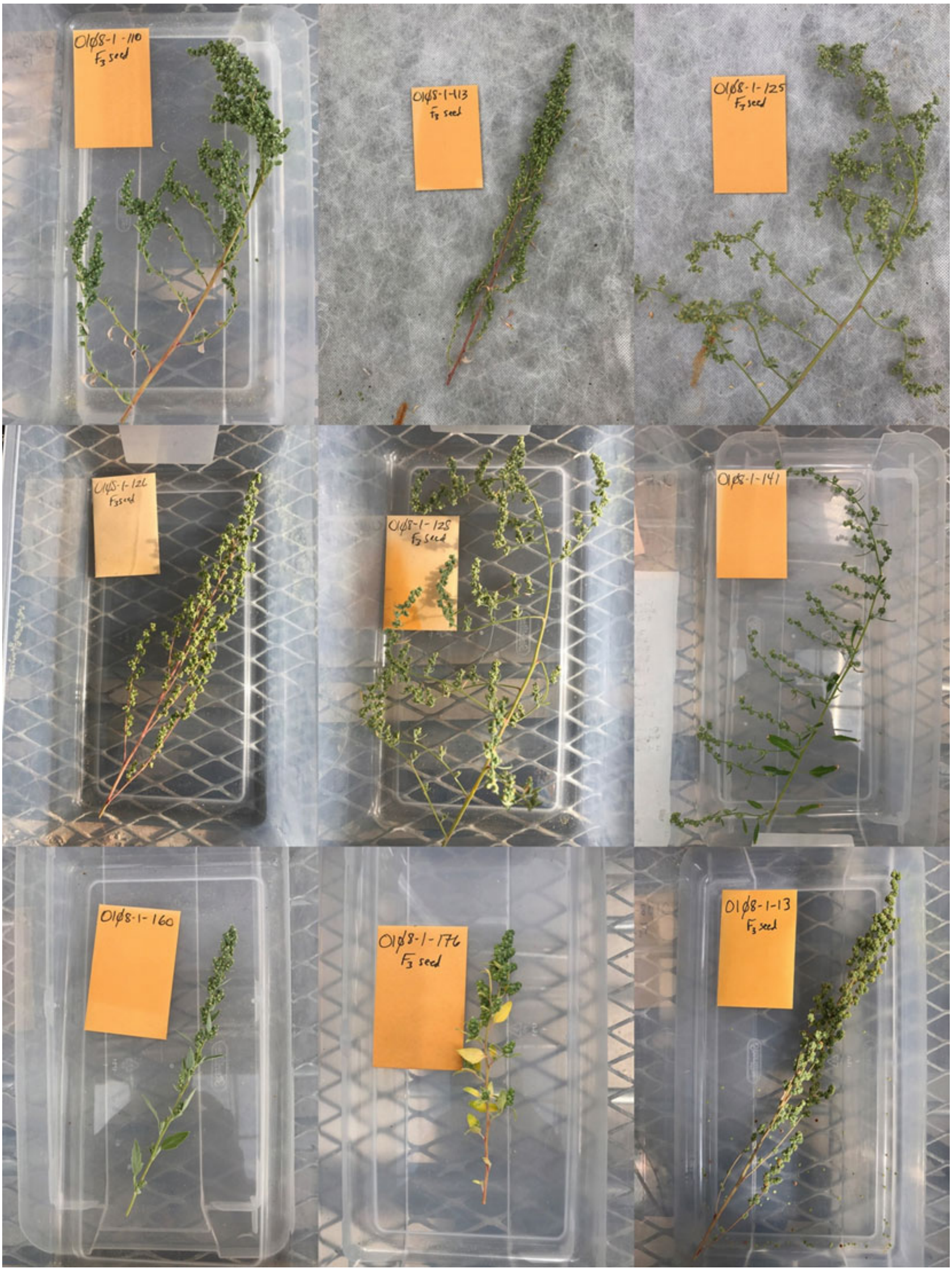

Fig. 3.6 Representative variation for panicle morphology in an F_2 population derived from an interspecific quinoa cv. ‘Ollague’ X *C. berlandieri* var. *sinuatum* (BYU 14108 from the Chiricahua Mountains, Arizona) cross

Fig. 3.7 **a** Fruit morphology of 15 accessions of *C. berlandieri* var. *zschackei*. (top row, l to r): BYU 457 from Duchesne Co., Utah; BYU 555 from Tooele, Utah; BYU 629 from Niobrara Co., Wyoming; BYU 637 from Muddy Pass, Colorado; BYU 641 from Sanpete Co., Utah; (second row): BYU 661 from Thistle, Utah; BYU 718 from Colfax Co., New Mexico; BYU 862 from Fremont Co., Wyoming; BYU 880 from Ramah, New Mexico; BYU 902 from the Laguna Mts., California; (third row): BYU 1007 from Kyle Cyn., Nevada; BYU 1312 from St. Charles, Missouri; BYU 1448 from Sherman Oaks, California; BYU 14118 from Crystalaire, California; BYU 1672 from Burns, Oregon; (bottom row): calyces of BYU 902, BYU 1312, BYU 14118, and BYU 1672. **b** Representative habitats of var. *zschackei* (l to r): La Sal Mountains, Utah; edge of farm field, Shasta Co., California; roadside in pinyon-juniper woodland, Sacramento Pass, Nevada

center of cultivation in Michoacan State (De la Cruz Torres et al. 2010). Figure 3.8 shows fruit variation in subsp. *nuttaliae*.

Wilson and Heiser (1979) and Wilson (1990) provided and reviewed evidence supporting the hypothesis that subsp. *nuttaliae* was domesticated independently from *C. quinoa*. Molecular evidence supports this hypothesis, given that Kolano et al. (2012, 2016) and Maughan et al. (2006) found that *C. berlandieri* subsp. *nuttaliae* accessions contained one more 5S rRNA locus (three versus two), and some strains have one more NOR locus than *C. quinoa*.

Brown et al. (2015) and Cepeda-Cornejo et al. (2016) identified *waxy* (high amylopectin) landraces of huauzontle. The *waxy* phenotype is attained only when A- and B-genome orthologs of *GBSS1* are mutated; consequently, these would be expected to be rare phenotypes in the absence of strong selective pressure. These authors hypothesized that the amylose-free phenotypes were selected in Mexico because semi-mature *huauzontle* panicles carrying *waxy* seeds would cook more thoroughly in less time and at lower temperatures than panicles containing seed with insoluble amylose. Brown et al. (2015) found single mutations in each sub-genome that were responsible for all of their *waxy* huauzontles: a *gbss1a-tp* A-genome allele carrying an I54T substitution within the plastid-targeting transit peptide portion of the gene; and a *gbss1b-del* B-genome allele carrying a 78-base deletion. In contrast to vegetable *huauzontle*, Andean quinoa seeds were likely selected to be larger and plumper—traits associated with complete starch—containing amylose. Brown et al. (2015) did not find similar *waxy* phenotypes in the six quinoa strains they examined, though they did identify a nonsense *gbss1b-t* mutant allele in coastal cultivar G-205-95.

3.3 Breeding Potential of *C. berlandieri*

Wilson and Heiser (1979) performed intertaxa ATGC hybridization experiments with results indicating that var. *zschackei* hybrids with *C. quinoa* are highly fertile, while *sinuatum* x *quinoa* hybrids are of low fertility but can be backcrossed by applying *C. quinoa* pollen to F_1 stigmas. In a later study, Wilson and Manhart (1993) documented extensive in-field introgression in the Pacific Northwest of the USA between cultivated quinoa and *C. berlandieri* weeds growing in close proximity. Figure 3.2 illustrates phenotypic variation for fruit morphology in a quinoa var. ‘Real-1’ X var. *boscianum* (BYU 937, Galveston Bay, Texas) segregating F_2 population having 91% self-fertility. Figure 3.6 shows variation for panicle shape in a quinoa var. ‘Ollague’ X var. *sinuatum* (BYU 14108, Chiricahua Mountains, Arizona) segregating F_2 population having 87% self-fertility.

Given the wide range of environments in which *C. berlandieri* is adapted—ranging from subtropical Mediterranean, subtropical Gulf Coastal, subtropical Sonoran Desert, semi-arid temperate, and humid forest zones—this species consequently represents a significant genetic resource for improving quinoa through intertaxa hybridization and selection. This contrasts with *C. quinoa*, which was selectively adapted by human domestication to high-elevation environments in the Andes; to the narrow, geographically isolated coastal strip of central and southern Chile; to humid intermediate-elevation valleys of northwestern Argentina (Curti et al. 2012); and possibly also in antiquity to the high plains of Argentine Patagonia. The importance of pitseed goosefoot germplasm is magnified for quinoa breeders in countries like the USA that are non-participants in the Convention of Biodiversity and Nagoya Protocol, and therefore have limited access to quinoa germplasm.

Fig. 3.8 **a** Fruit morphology of 16 accessions of *C. berlandieri* subsp. *nuttaliae* from Mexico. Top row (l to r): BYU 567 from Opopeo, Michoacan; BYU 668 from Tecoman, Colima; BYU 1669, line H-18 from ININ-Ocoyoacac; BYU 17176 cv. ‘Red Aztec Spinach’; second row: BYU 1670, PI640304; BYU 1668, line H-16 from ININ-Ocoyoacac; BYU 1447, line H-3 from ININ-Ocoyoacac; BYU 1483, PI433230; third row: BYU 1484, *waxy* PI433231; BYU 1485, *waxy* PI568155; BYU 1486, PI568156; BYU 1647, *waxy* line H-4 from ININ-Ocoyoacac; bottom row: BYU 1662, *chia roja* from ININ-Ocoyoacac; BYU 1663, *chia roja* from ININ-Ocoyoacac; BYU 1664, *chia roja* from ININ-Ocoyoacac; BYU 1665, *chia roja* from ININ-Ocoyoacac. *Waxy* phenotyping was reported by Brown et al. (2015) and Cepeda-Cornejo et al. (2016). **b** (l to r) *Chia roja* field near Patzcuaro, Michoacan; green strain of garden *huauzontle* in Toluca, Mexico; pink strain of *huauzontle* in Toluca, Mexico

3.4 Conclusions

Chenopodium berlandieri represents a genetically and ecologically diverse genetic resource for quinoa improvement. It is a species that has been domesticated multiple times as vegetable and seed crops. It also contains a wide variety of interesting genetic mechanisms that allow it to survive and compete in arid, saline, hot, cold, and high-altitude environments. It is also one of a small handful of plants that was domesticated in the Eastern North American Center. As such, pitseed goosefoot should have higher priority in crop genetic resource collection, curation, and maintenance efforts by North American governments.

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