

Chapter 6

Pumpkins, Squashes, and Gourds (*Cucurbita* L.) of North America



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Abstract Pumpkins and squash (*Cucurbita* L. spp.) include six independently domesticated crop species and subspecies that are grown worldwide for their edible fruits and seeds and for ornamental interest. Because domesticated pumpkins and squashes can be crossed with each other and with diverse primary genepool relatives, contributions from *Cucurbita* crop wild relatives (CWR) have enabled the development of disease-resistant cultivars and represent a vast pool of untapped genetic variability underlying traits including drought tolerance and disease resistance. Even so, thorough evaluations of these wild species for agronomically important traits are limited. The 12 *Cucurbita* crop wild relatives of North America are more narrowly distributed than they were in the past because of the extinction of megafaunal dispersers and because of habitat loss, and the genetic diversity of wild *Cucurbita* species may be decreasing; one North American wild relative, *C. okeechobeensis* (Small) L. H. Bailey ssp. *okeechobeensis*, is nearly extinct, and some others are rare. Ex situ and in situ conservation of these species that includes phenotypic assessments are needed to better utilize the wealth of genetic resources available for pumpkin and squash crop improvement.

Keywords *Cucurbita* · Ex situ conservation · In situ conservation · Genetic resources

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6.1 Introduction

6.1.1 Origin and Historical Use of the Pumpkins, Squashes, and Gourds

Domesticated *Cucurbita* include “vegetables” called pumpkins, summer and winter squash, and gourds and are among the most important vegetable crops native to North America (Small 2014). The incredibly long and rich domestication histories of multiple North American *Cucurbita* species produced pumpkin, squash, and gourd crops that are unrivalled in fruit morphological diversity (Duchesne 1786; Naudin 1856) and wide range of adaptation to cultivation. Three pumpkin and squash crop subspecies are native to North America: the widely cultivated and economically important *Cucurbita pepo* L. ssp. *pepo* (pumpkin, vegetable marrow, cocozelle, zucchini), *C. pepo* ssp. *ovifera* (L.) D. S. Decker (scallop, acorn, crookneck, straightneck), and *C. argyrosperma* C. Huber ssp. *argyrosperma* (silver-seed gourd, green-stripe cushaw, calabaza pipiana), a less widely cultivated crop that is important in traditional Mesoamerican agricultural systems (Montez-Hernandez and Eguiarte 2002). The three pumpkin and squash crop species and subspecies likely domesticated outside of North America are the widely cultivated *C. maxima* Duchesne ssp. *maxima* (giant pumpkin, hubbard squash, buttercup squash, kabocha squash), *C. moschata* Duchesne (butternut squash), and *C. ficifolia* Bouché (figleaf gourd), a *Cucurbita* crop that is relatively unknown in the United States but widely cultivated in Latin America and regionally important in some regions of Asia.

Because fruit and varietal terms including “pumpkin,” “summer squash,” “winter squash,” “gourd,” and “cushaw” have been inconsistently applied to the diverse subspecies and varieties of domesticated *Cucurbita*, it is sometimes difficult to distinguish between accounts of different crop subspecies. For clarity, we will use “pumpkins and squashes” to refer to *Cucurbita* crops generally. To refer to individual crop subspecies, we will use the botanical name or “pepo pumpkin and squash” for *C. pepo* ssp. *pepo*, “ovifera pumpkin and squash” for *C. pepo* ssp. *ovifera*, “cushaw” for *C. argyrosperma* ssp. *argyrosperma*, “giant pumpkin” for *C. maxima* ssp. *maxima*, “figleaf gourd” for *C. ficifolia*, and “butternut squash” for *C. moschata*, although many common and varietal names can be used to refer to these crop subspecies.

The wild ancestors of the *Cucurbita* crops likely appealed to ancient seminomadic native peoples because of their large and conspicuous easily collected fruits (Paris 2016). Wild *Cucurbita* plants are monoecious, multibranching vines that grow along the ground or over trees and other plants or structures (Erwin 1931; Bailey 1943) and bear large (12–15 cm) alternately arranged palmate leaves on long petioles (Paris 2016). Tendrils, flowers, and roots are all borne at the leaf axil. The fruits of wild *Cucurbita* vary somewhat among species but are generally round, 3.5–8.0 cm in diameter, with a green exocarp that may be striped or unstriped and may be yellow or green at maturity (Nee 1990). The rinds of wild *Cucurbita* are hard and lignified (Robinson and Decker-Walters 1997), and their flesh contains cucurbitacins

that render them inedible unless repeatedly boiled (Nabhan 1985). Therefore, *Cucurbita* plants were likely initially selected by native North Americans for their edible, high-calorie seeds as well as for the use of their durable rinds as containers; the latter was of utmost importance to seminomadic people prior in the preceramic era (Small 2014). Discovery of rare, non-bitter or less bitter *Cucurbita* fruits likely led to the eventual non-bitter *Cucurbita* crops we know today. Native North Americans also ate the stems and flowers of *Cucurbita* and used the saponin-containing flesh as soap, and archaeological evidence suggests many of the undomesticated wild species were used by humans (Nabhan 1985). All *Cucurbita* domesticates likely moved outside of their initial range of domestication into other areas of the New World before European contact (Fritz 1994; Smith 2001).

The traits that define the domestication syndrome of pumpkins and squashes include more uniform germination, a reduction in size and abundance of trichomes that interfere with harvesting, an increase in the size of fruits and seeds, and a reduction in the bitter taste of the flesh (Lira-Saade and Montez-Hernandez 1994). Some cultivated *Cucurbita* varieties have a bush habit, and most domesticated subspecies exhibit a much wider range of fruit color, shape, and size than their wild relatives. Domesticated species in general have a decreased resistance to drought and disease. Pumpkins and squashes have been important food in Mexico for millennia, where fruits are processed and consumed in a variety of ways. The seeds of pumpkins and squashes are a popular snack food and are also ground into a meal used to make sauces. Pumpkin and squash flowers are eaten stuffed or fried and are used to color and flavor soups and salads (Paris 1989). The origin, current extent of cultivation, most common uses, and cultivar groups for each domesticated species are described below and summarized in Table 6.1.

Cucurbita pepo

The domestication of pepo pumpkin and squash is among the earliest plant domestications in human history (Smith 2006). Archaeological evidence indicates that pepo pumpkin and squash was domesticated from an unidentified wild species in Mexico around ~10,000 years B.P. (Smith 2006). Prior to the 1980s, ancient remains of *C. pepo* from ~5000 years B.P. discovered in eastern North America were thought to represent the spread of domesticated pepo pumpkin and squash from Mexico (Smith 2006). However, there is now strong support for the independent domestication of ovifera pumpkin and squash from a different *C. pepo* subspecies (*C. pepo* ssp. *ovifera*) in what is currently the United States (Decker 1988; Decker-Walters 1990; Decker-Walters et al. 1993). The domestication of *C. pepo* ssp. *ovifera* (which includes cultivated scallop, acorn, crookneck, and straightneck squashes) is one of a small number of domestications that confirms the status of eastern North America as an independent center of plant domestication (Smith 2006).

Domesticated pepo and ovifera pumpkins and squashes were introduced into Europe and Asia Minor in the late 1400s, and secondary diversification of these crops occurred in Asia Minor (Robinson and Decker-Walters 1997). Detailed drawings, paintings, and writings from Europe provide evidence that two ancient lineages of domesticated *C. pepo* were initially brought to Europe from America,

Table 6.1 Cultivated North American pumpkins and squashes

Subspecies	Cultivar groups	Origin	Current cultivation	Most common uses
<i>C. pepo</i> L. ssp. <i>pepo</i> (pepo pumpkin and squash)	Pumpkin, vegetable marrow, cocozelle, zucchini, round ornamental gourds ^a	Mexico ~10,000 years B.P. ^b	Worldwide	Fruit (immature, mature, canned)
<i>C. pepo</i> L. ssp. <i>ovifera</i> (L.) D. S. Decker var. <i>ovifera</i> (L.) Harz (ovifera pumpkin and squash)	Scallop, acorn, crookneck, straightneck, oviform ornamental gourds ^a	Eastern North America ~5000 years B.P. ^b	Worldwide	Fruit (immature, mature, canned)
<i>C. argyrosperma</i> <i>C. Huber</i> ssp. <i>argyrosperma</i> (cushaw)	Silver-seed gourd, green-stripe cushaw, calabaza pipiana ^c	Southern Mexico ~7000 years B.P. ^b	Limited. Mexico, USA, Central America	Seeds (snack food, oil, meal); fruit (usually mature)
<i>C. maxima</i> Duchesne ssp. <i>maxima</i> (giant pumpkin)	Banana squash, delicious squash, buttercup squash, hubbard squash, show pumpkins, turban squash, kabocha ^d	South America ~4000 years B.P. ^b	Worldwide esp. Africa and Asia	Fruit (immature, mature, canned, decorative)
<i>C. moschata</i> Duchesne (butternut squash)	Cheese, crookneck, bell ^e	Unknown (Mexico, Central America, or South America) >5000 years B.P. ^f	Worldwide esp. Africa and Asia	Fruit (immature, mature, canned)
<i>C. ficifolia</i> Bouché (figleaf gourd)	None commercially recognized. Other names include Malabar melon and shark fin gourd	Unknown (Mexico, Central America, or South America) >3000 years B.P. ^g	Limited. Mexico, Central America, South America, China. High (>1000 m) altitudes	Fruit (immature, mature), as rootstock

^aParis et al. (2012)^bSmith (2006)^cLira-Saade and Montes-Hernandez (1994)^dDecker-Walters and Walters (2000)^eRobinson and Decker-Walters (1997)^fCohen (1978)^gTowle (1961)

“pumpkin” (*C. pepo* ssp. *pepo* var. *pepo*) and “scallop” (*C. pepo* ssp. *ovifera* var. *clypeata*), and that additional cultivar groups were developed from these lineages in Europe or Asia and were subsequently brought to America (Paris 1989). Among these varieties with probable European origins are the varieties of *C. pepo* that are most economically important today: “zucchini” and “acorn squash” (Paris 1989).

Cucurbita argyrosperma

C. argyrosperma ssp. *argyrosperma* includes cultivated silver-seed gourd, green-stripe cushaw, and Calabaza pipian. The domestication of cushaw apparently occurred in Mexico, and archaeological remains of domesticated cushaw have been dated to as early as ~7000 years B.P. (Smith 2006). In contrast to the other five *Cucurbita* crops, cushaw did not leave its origin of domestication during the Columbian exchange and today is still cultivated primarily in Mexico and Central America with minor cultivation in Asia (Robinson and Decker-Walters 1997). It is unclear why cushaw was not brought to Europe during the Columbian exchange, but the reason for its historical and current lack of cultivation compared with other *Cucurbita* crops is likely due to the inferior quality of its fruit (Lira-Saade and Montez-Hernandez 1994).

Cucurbita maxima

Domesticated *C. maxima* ssp. *maxima* is among the most widely cultivated and morphologically diverse *Cucurbita* crop subspecies (Grubben and Chigumira Ngewerume 2004). *Cucurbita maxima* ssp. *maxima* was domesticated ~4000 years ago from the South American subspecies *C. maxima* ssp. *andreana* that occurs in Argentina and Uruguay and more rarely in Bolivia (Decker-Walters and Walters 2000). *Cucurbita maxima* ssp. *maxima* was brought to the Old World during the Columbian exchange (Decker-Walters and Walters 2000) and is now cultivated all over the world, with a secondary center of diversity in Asia (Ferriol et al. 2004) where extensive breeding and improvement of new varieties have occurred.

Cucurbita moschata

The origin of butternut squash is unclear. As recently as the early 1900s, butternut squash was thought to be of Asian origin (Lira-Saade and Montes-Hernandez 1994) although all wild *Cucurbita* species are native to the New World. Multiple lines of evidence now confirm that *C. moschata* was domesticated somewhere in Mexico, Central America, or South America. The oldest archaeological remains of *C. moschata* were found in the Ocampo caves of Northwestern Mexico and date from ~5000 years B.P. More recent archaeological remains have also been found in northern Belize (2000 B.P.), Guatemala (2000 B.P.), and Peru (3000 B.P.) (Cohen 1978).

Cucurbita moschata moved outside of its area of domestication prior to European contact. For example, the *C. moschata* landrace “Seminole pumpkin” was first grown by indigenous groups of Florida in the United States before Europeans arrived (Lira-Saade and Montes-Hernandez 1994). By the end of the 1800s, *C. moschata* was cultivated in Asia and Africa (Robinson and Decker-Walters 1997).

Cucurbita ficifolia

The origin of figleaf gourd is also unclear, and, like *C. moschata*, the figleaf gourd was thought to have had its origin in Asia (Lira-Saade and Montes-Hernandez 1994). Some authors have suggested Central America or southern Mexico as the site of domestication for figleaf gourd based on etymological evidence (Andres 1990), but archaeological evidence points instead to the Andean region of South America

(Andres 1990). Phylogenetic studies have been unable to support any of these hypotheses as *C. ficifolia* is not closely related to any single wild *Cucurbita* species (e.g., Sanjur et al. 2002; Zheng et al. 2013; Kistler et al. 2015; Kates et al. 2017). Figleaf gourd spread from the New World to Europe and Asia as early as the 1600s, and its cultivation has since spread to many other parts of the world (Andres 1990).

6.1.2 Current Agricultural and Economic Importance of Pumpkins, Squashes, and Gourds

The current agricultural and economic importance of the domesticated lineages of *Cucurbita* differs substantially. Because of the inconsistent and ambiguous nomenclature of cultivated forms, it is impossible to determine the precise contribution of individual subspecies to total *Cucurbita* agricultural production. *Cucurbita moschata*, *C. maxima* ssp. *maxima*, *C. pepo* ssp. *pepo*, and *C. pepo* ssp. *ovifera* are the most economically important, and references to production and consumption of “pumpkins, squashes, and gourds” refer to all of these subspecies. The terms “pumpkin” and “squash” are also used; in this case, pumpkin still refers to all subspecies, but squash is more likely to refer to varieties of *C. pepo* ssp. *pepo* or *C. pepo* ssp. *ovifera*.

China and India are the largest producers of pumpkins, squashes, and gourds today, and in these countries, *C. moschata* and *C. maxima* ssp. *maxima* are the most commonly grown *Cucurbita* crops (Yang and Walters 1992; Sharma and Lal 1998). This contrasts with the relative importance of *Cucurbita* crop subspecies consumed in the United States, where pepo and ovifera pumpkins and squashes are the most popular *Cucurbita* crops. The “pumpkin” types of *Cucurbita* consumed in the United States are mostly produced domestically (Minor and Bond 2017, and in 2014 750 K tons of pumpkins were produced in the United States (Minor and Bond 2017). In contrast, most of the “squash” types of *Cucurbita* consumed in the United States are imported (FAOSTAT 2002), and the United States is the largest importer of squash worldwide.

Cushaw and figleaf gourd are of regional importance rather than worldwide economic importance. Cushaw is rarely grown outside of the Western Hemisphere and is not widely grown outside of its origin of domestication in Mexico (Robinson and Decker-Walters 1997). Figleaf gourd is regionally popular in some areas outside of its likely area of domestication but is still relatively rare outside of Mexico, Central America, and South America (Andres 1990).

There is a wide range of modern uses of pumpkins and squashes that often vary by species and by variety. The commercial uses of pumpkins and squashes include (in order of importance) immature and mature fruit as food (fresh market and processed), seeds for direct consumption, seeds for vegetable oil, mature fruit as animal feed, seeds for meal, and nonedible types for ornamental use. In general, round-fruited types are usually grown for mature fruits or seed (Paris 2016), and the long

or flat-fruited types are primarily grown for consumption of immature fruits (Paris 1989). *Cucurbita* fruits are a good source of Vitamin A, with levels comparable to that of avocados, asparagus, musk melon, Brussels sprouts, artichokes, and green olives (Whitaker and Davis 1962), and are an excellent source of starch. The fat and oil content of *Cucurbita* seeds is very high and is comparable to sunflower and soybean oil in its fatty acid profile (Whitaker and Davis 1962). In some countries including the United States, most varieties of “pumpkins” are seasonal crops, and up to 90% of annual consumption occurs between October and January.

Cucurbita pepo

The popularity and importance of edible varieties of pepo and ovifera pumpkins and squashes have increased tremendously since the 1970s (Small 2014). The United States produces a modest amount of pepo and ovifera pumpkins and squashes (less than 900 K tons in 2014 compared with 7 M tons in China and 5 M tons in India) (FAOSTAT 2002) but is the largest importer of pumpkins, squash, and gourds in the world. Ninety-five percent of squash consumed in the United States is grown in Mexico (FAOSTAT 2002). There are four cultivated varieties of edible pepo pumpkins and squash and four cultivated varieties of edible ovifera pumpkin and squash.

Currently, the zucchini variety of pepo pumpkin and squash (*C. pepo* ssp. *pepo* var. *cylindrica*), also known as “summer squash,” is the most popular *Cucurbita* crop in the United States (Paris 2008). This pepo pumpkin and squash variety is consumed as a fresh vegetable in its immature state (Robinson and Decker-Walters 1997). Prior to the 1980s, yellow and green “summer squash” consumed in the United States and around the world included immature fruits of nearly all eight edible varieties of pepo and ovifera pumpkin and squash. These diverse varieties of “summer squash” have been replaced with uniform-inbred and highly improved types of *C. pepo* ssp. *pepo* var. *cylindrica*, reflective of a pattern of reduced genetic and morphologic variety in *C. pepo* produced worldwide (Paris 1989). Breeding and cultivation of pepo pumpkin and squash is increasingly dependent on inbreeding, as the importance of virus-resistant transgenic zucchini increases. Approval for production in Mexico is under consideration and is likely to exacerbate this trend (Reyes et al. 2015). The other three varieties of edible pepo pumpkin and squash are “pumpkin” (*C. pepo* ssp. *pepo* var. *pepo*), which includes creeping cultivars that produce round, flat-ended fruits (most famously the Halloween “jack-o-lantern” type); “cocozele” (*C. pepo* ssp. *pepo* var. *longa*), a variety that produces long, cylindrical fruits eaten in the unripe state; and “vegetable marrow” (*C. pepo* ssp. *pepo* var. *fastigata*), a semi-creeping variety that bears short, cylindrical fruits most commonly eaten when mature.

The four varieties of ovifera pumpkin and squash are the semi-shrubby “scallop” (*C. pepo* ssp. *ovifera* var. *clypeata*), which is eaten in its immature state and is the cultivated ovifera pumpkin and squash variety that most resembles a wild ancestor based on phenotype; “acorn” (*C. pepo* ssp. *ovifera* var. *turbinata*), a variety that can be shrubby or creeping and bears soft-rinded fruit that can be eaten in its mature state; and “crookneck” (*C. pepo* ssp. *ovifera* var. *torticollia*) and “straightneck” (*C. pepo* ssp. *ovifera* var. *recticollis*), two similar varieties that include shrubby plants that produce yellow fruits eaten in their immature state.

Cucurbita argyrosperma

Three varieties of cushaw are grown, primarily in Mexico where they are cultivated near the range of their wild ancestor, *C. argyrosperma* ssp. *sororia*. *Cucurbita argyrosperma* ssp. *argyrosperma* var. *argyrosperma* (silver-seed gourd) likely represents the initial domesticate from which the other cultivated varieties were subsequently developed in different parts of its range of cultivation in Mexico. Limited genetic data reveals a high proportion of wild ancestry for samples of silver-seed gourd (Kates et al., unpublished), but more extensive sampling at the varietal level is needed to determine whether this variety truly represents the initial domesticate of this species. The large seed size of this variety suggests that its seeds, rather than its flesh, were the target of initial domestication (Lira-Saade and Montez-Hernandez 1994). Silver-seed gourd is grown infrequently by home gardeners in the United States as a curiosity (Lira-Saade and Montez-Hernandez 1994). *Cucurbita argyrosperma* ssp. *argyrosperma* var. *callicarpa* (green-stripe and white cushaw; Japanese pie pumpkin) is considered the most recent or specialized variety of cushaw, and the diversity of shapes, colors, and size of the fruits and seeds suggests it was domesticated for its flesh and its seeds (Lira-Saade and Montez-Hernandez 1994).

Outside of Mexico, cushaw is a crop of minor importance in South America and in the United States (Lira-Saade and Montez-Hernandez 1994). A third cultivated variety, *C. argyrosperma* ssp. *argyrosperma* var. *stenosperma* (calabaza pipiana), is another more recently derived variety of cushaw, and although it also has diverse fruit morphology (Lira-Saade and Montez-Hernandez 1994), it is now mostly grown in Mexico and Central America for its seeds (Merrick 1995). A fourth variety of cushaw, *C. argyrosperma* ssp. *argyrosperma* var. *palmeri*, is wild and thought to be a feral escape from cultivation (Lira-Saade and Montez-Hernandez 1994). Genetic data resolve a close relationship between *C. argyrosperma* ssp. *argyrosperma* var. *palmeri* and the cultivated varieties and support its status as a feral rather than a truly wild taxon (Kates et al., unpublished).

Cucurbita maxima

Outside of the Americas, *C. maxima* ssp. *maxima* is one of the two most common *Cucurbita* crops consumed. The many cultivars of *C. maxima* ssp. *maxima*, known generally as “pumpkins” (Sharma and Lal 1998), are very popular in Asia and Africa where their mature fruits are widely used in cooking and as cattle feed. In contrast to the minor nutritional importance of squash and pumpkin consumption in the United States, in Africa and Asia, *C. maxima* ssp. *maxima* pumpkins may serve as a staple food when grain production is limited (Sharma and Lal 1998).

Attempts to classify the diverse *C. maxima* ssp. *maxima* into cultivar groups are inconsistent, but popular named varieties include banana squash, delicious squash, buttercup squash, hubbard squash, show pumpkins, turban squash, and kabocha (Decker-Walters and Walters 2000). Varieties of *C. maxima* ssp. *maxima*, especially the “buttercup” variety, are the most popular type of pumpkins and squashes consumed in Africa. *Cucurbita maxima* ssp. *maxima* also includes all “giant pumpkins,” varieties that produce the largest fruits in the world. Giant pumpkins are popular as

ornamental pumpkins in the United States for Halloween and are celebrated in many festivals and competitions.

Cucurbita moschata

Cucurbita moschata is one of the two most popular *Cucurbita* species outside of the Americas. Like *C. maxima*, its many regional varieties, which were developed in Central and South America, Africa, and the United States (Lira-Saade and Montes-Hernandez 1994), are often referred to as “pumpkins.” Among these, the three cultivar groups commercially recognized in North America are cheese, crookneck, and bell (including the popular “butternut” cultivar) (Robinson and Decker-Walters 1997). In the United States, all canned pumpkin is *C. moschata*, and the most popular variety of canned pumpkin is Libby’s Select Dickinson (Geisler 2014).

Cucurbita ficifolia

Figleaf gourd is not common in industrialized countries (Robinson and Decker-Walters 1997) but is used as food and cattle feed in Mexico, Central America, and South America. *Cucurbita ficifolia* is also popular in some regions of China where it is known as “shark fin melon” because of its use in a soup that resembles shark fin soup. *Cucurbita ficifolia* is also used as a rootstock for grafting cucumber (Robinson and Decker-Walters 1997). Research has demonstrated the potential of the proteolytic enzymes in the pulp of *C. ficifolia* fruit to treat wastewater from the industrial processing of foods derived from fish (Illanes et al. 1985), but this use of *C. ficifolia* has never been implemented.

6.1.3 Challenges in Cultivation of Squashes, Pumpkins, and Gourds

Viral, Bacterial, and Fungal Diseases

Disease susceptibility is common in all Cucurbitaceae crops (e.g., *Citrullus* (watermelon) and *Cucumis* (cucumber and melon)) but is comparatively understudied in *Cucurbita*. For example, fewer disease resistance genes have been reported for pumpkins, squashes, and gourds than for the other cucurbit crops (Robinson and Decker-Walters 1997). Insufficient funding is mostly responsible for the relative lack of research to screen germplasm and identify disease resistance in *Cucurbita*, but the large genome size of *Cucurbita* compared to other cucurbits and the fact that certain cucurbit diseases, including downy mildew, are less of a problem in *Cucurbita* than in other cucurbit crops may also play a role.

Diseases attack pumpkins and squash at every stage of development, from germinating seeds to mature fruits (Robinson and Decker-Walters 1997). The major challenge in the cultivation of the North American squashes, pumpkins, and gourds are viral diseases, especially those transmitted by aphids, whiteflies, and other insects (Paris 2016); virus resistance is one of the most important goals of *Cucurbita* breeding. Virus susceptibility in *Cucurbita* is a moving target; the most damaging viruses vary by region and change over time, and newly damaging viruses are

reported frequently (Paris 2016). Some of the viruses that infect pumpkins and squashes are the cucumber mosaic virus (CMV), watermelon mosaic virus (WMV), zucchini yellow mosaic virus (ZYMV), and papaya ringspot virus (PRV) (Robinson and Decker-Walters 1997). Among these, ZYMV has been the most destructive since the 1970s (Paris 2016). Because there are no chemical tools to control these viruses, the only way to limit the damage is through breeding resistant crops or management of the insect vectors using pesticides (Molinar et al. 2012).

Fungal and bacterial diseases that are the most damaging to pumpkin and squash crops include powdery mildew (*Erysiphe cichoracearum* DC.), downy mildew (*Pseudoperonospora cubensis* (Berkeley & M. A. Curtis) Rostovzev), gummy stem blight (*Didymella bryoniae* (Fuckel) Rehm), charcoal rot (*Macrophomina phaseolina* (Tassi) Goid), root and fruit rot caused by *Phytophthora capsici* Leonian, *P. spp.* and *Fusarium solani* f. sp. *cucurbitae* (Mart.) Sacc, bacterial wilt (*Erwinia tracheiphila* (Smith) Bergey), and bacterial leaf spot (*Xanthomonas campestris* pv. *cucurbitae* (Pammel) Dowson) (Robinson and Decker-Walters 1997). Fungal and bacterial diseases of squash are controlled by long-term rotation out of cucurbits (4 years or more), the use of clean seed, chemical treatment (Molinar et al. 2012), and generally reducing environmental stress whenever possible.

Susceptibility to diseases varies among domesticated *Cucurbita* species. With a few exceptions (see Walkey and Pink 1984; Lebeda and Křístková 1996; Křístková and Lebeda 2000), pepo and ovifera pumpkins and squashes and wild *C. pepo* do not naturally contain resistance to diseases (Paris 2016). Susceptibility of giant pumpkin to major cucurbit diseases is apparently similar to pepo and ovifera pumpkins and squashes (Provvidenti et al. 1978; Keinath 2014), though this observation is based on a small number of studies. Disease resistance in cushaw and wild *C. argyrosperma* has not been as well-studied and also appears to be rare (Provvidenti et al. 1978; Luitel et al. 2016; Wessel-Beaver 1998), but some *C. argyrosperma* germplasm exhibits resistance to downy mildew and offers a potential source for breeding downy mildew-resistant squash and pumpkins (Lebeda et al. 2016). Butternut squash is resistant to a greater number of diseases than other domesticated species (e.g., Provvidenti et al. 1978, ZYMV, PRV, tomato ringspot virus, tobacco ringspot virus, squash curl leaf virus; Chavez et al. 2011, crown rot; Zhou et al. 2010, downy mildew). The prospects and limitations of utilizing pest and disease-resistant crop wild relatives (CWR) for crop enhancement are discussed in Sect. 6.2. To avoid the loss of susceptible crops, farmers apply pesticides to target insect vectors, rotate pumpkin and squash crops, and avoid irrigation practices that excessively wet squash leaves or create standing water (Sharma and Lal 1998). To address the need for disease-resistant *C. pepo* crops, geneticists and breeders in the United States created a transgenic zucchini with virus-resistance genes.

The transgenic variety of zucchini called “Freedom II” was the second transgenic crop to be deregulated for commercial use in the United States in 1995 (Tricoli et al. 1995). There are currently at least six transgenic cultivars of *C. pepo* ssp. *cylindrica* being sold in the United States that are resistant to WMV, ZYMV, and cucumber mosaic virus (Gaba et al. 2004). The impact of transgenic zucchini on worldwide pepo pumpkin and squash production is very limited for several reasons.

Resistance to the three viruses listed above apparently increases the vulnerability of the resistant squash to other viruses and to some insect pests (Sasu et al. 2009). Additionally, the United States is not a major producer of pepo pumpkin and squash; Canada is the only country that allows the import of transgenic pepo pumpkin and squash from the United States (CBAN 2018), and nearly all zucchini sold in the US market is imported from Mexico (FAOSTAT 2002), where transgenic squash has not been deregulated (Cruz-Reyes et al. 2015). The potential deregulation of transgenic pepo pumpkin and squash cultivars in Mexico is discussed in Sect. 6.4.1.

Non-disease Challenges to Cultivation

The severity of some non-disease challenges to cultivation differs among the species and varieties of ovifera and pepo pumpkins and squashes and cushaw due to the phenotypic diversity of the cultivated types. All pumpkin and squash crops are sensitive to very low temperatures and continuous frost (Lira-Saade and Montes-Hernandez 1994; Sharma and Lal 1998) and to heavy precipitation and standing water, which can cause fruit to rot. Cultivation of varieties of pepo and ovifera pumpkins and squashes and of cushaw that are grown for mature fruits (e.g., the acorn variety of ovifera pumpkin and squash, most important cultivars of cushaw) requires high water use. Pumpkins and winter squash are among the highest water-using vegetable crops (Daniello 2003) in contrast to summer squashes (e.g., zucchini, straightneck, crookneck), which have the lowest water requirements. Pumpkins and winter squash also require large amounts of arable land to support their vine or semi-bush habit. The bush habit has been selected for in nearly all summer squash varieties (Paris 2016), but these types require larger applications of fertilizer (Sharma and Lal 1998).

Insect pests that damage pumpkin and squash crops include seed-corn maggot larva (*Delia platura* Meigen), which are associated with high amounts of decaying organic matter in the soil; wireworms (*Limonius* spp. and others); squash bugs (*Anasa tristis* DeGeer); whiteflies (*Bemisia argentifolii* Gennadius and *Trialeurodes vaporariorum* Westwood); aphids (*Aphis gossypii* Glover and *Myzus persicae* Sulzer), which are also disease vectors; cucumber beetles (*Diabrotica undecimpunctata* Mannerheim and *Acalymma trivittatum* Mannerheim); larvae of several species of armyworm (*Spodoptera* spp.); and cabbage looper (*Trichoplusia ni* Hübner) (Molinar et al. 2012; Robinson and Walters 1997). Bitter cucurbitacins present in *Cucurbita* (see Sect. 5.2.3) attract squash bugs, corn rootworm, and cucumber beetle, and wild and domesticated *Cucurbita* species are used as perimeter trap crops in integrated pest management (e.g., Adler and Hazzard 2009; Metcalf et al. 1979).

The Effect of Climate Change on Challenges to Cultivation

Some of the challenges that *Cucurbita* faces in cultivation may intensify under climate change (Chakraborty and Newton 2011). Although the impacts of climate change on cucurbit crops have not been widely modeled and studied, some plant pathogens are expected to spread and infect plants more readily under current climate change scenarios (Pautasso et al. 2012), and environmentally stressed pumpkins and squash are more susceptible to initial infection and subsequent

disease development (Robinson and Decker-Walters 1997). Changes in precipitation also pose a threat to *Cucurbita*, especially to winter squash and pumpkin cultivars that require high water input and bear fruits that are vulnerable to rot while they mature. In 2015, unusually heavy summer rains drastically reduced pepo pumpkin and winter squash yield (Kennedy 2015). In the previous year, drought in California reduced yield of *Cucurbita* grown in that state and increased pest damage (CBS News 2014).

There are also characteristics of *Cucurbita* cultivation that may make it resilient to climate change. For example, compared with crops that rely entirely on honey bee pollination, *Cucurbita* crops are also pollinated by native bees (Giannini et al. 2011). Though the potential effects of climate change on pollination of *Cucurbita* crops has not yet been studied, pollination by native bees was found to be a potential buffer against climate change in watermelon (Radar et al. 2013). Pumpkin and squash production as a whole may be less affected by climate change than that of some other crops due to the diversity of cultivated types and the wide range of elevations and temperatures at which they can be grown.

6.2 Crop Wild Relatives of Pumpkins, Squashes, and Gourds

The wild relatives of pumpkins and squashes that occur in North America include six arid-adapted (xerophytic) perennial species and seven non-arid-adapted (mesophytic) annual species, subspecies, or varieties. The greatest species diversity occurs in Mexico (Fig. 6.1), although phylogenetic data suggests the genus likely originated in Central or South America (Schaefer et al. 2009). The wild xerophytic perennial *Cucurbita* species grow in the deserts and dry scrub of Mexico and the Southwestern United States, and wild mesophytic annual species grow in the moist or dry forests and plains of Mexico and the Southern and Central United States. All domesticated *Cucurbita* species and subspecies are derived from the mesophytic annual species group; therefore, all mesophytic annual species are more closely related to cultivated pumpkins and squashes than are any of the xerophytic perennial species. Table 6.2 lists the habitat, distribution, genepool classification, and potential agronomic traits for 13 *Cucurbita* CWRs native to North America. Likely due to the recent divergence of the wild *Cucurbita* species (Zheng et al. 2013), all *Cucurbita* CWR can be crossed with one or more other species in the genus. Introgression of traits from wild to cultivated *Cucurbita* can be made directly from a CWR with desirable traits or using another CWR as a genetic bridge (Yi-Hong Wang et al. 2012).

Because there are multiple domesticated *Cucurbita* species, each *Cucurbita* CWR may be a primary, secondary, and/or tertiary genepool CWR. Below, each CWR is grouped into the genepool rank that denotes its closest relationship to a domesticated *Cucurbita* crop species or subspecies. If a CWR is also in a subsequent genepool group, this is noted.

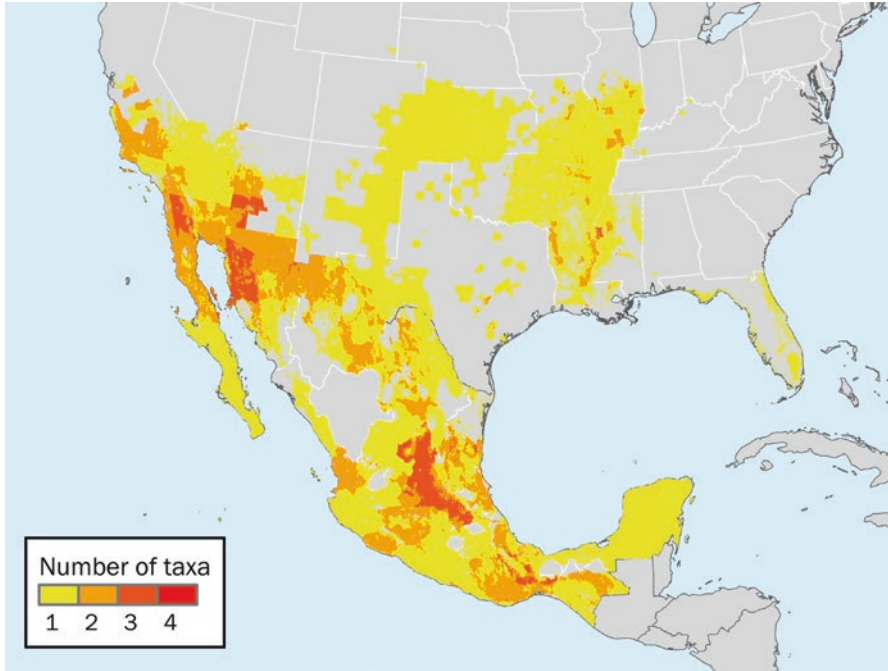


Fig. 6.1 Species richness map of modeled potential distributions of North American *Cucurbita* taxa, based on climatic and edaphic similarities with herbarium and genebank reference localities. Warmer colors indicate areas where greater numbers of taxa potentially occur in the same geographic localities. Full methods for generation of maps and occurrence data providers are given in Appendix 1

6.2.1 Primary Genepool CWR

Cucurbita argyrosperma ssp. *sororia* (L. H. Bailey) L. Merrick & D. M. Bates
Cucurbita argyrosperma ssp. *sororia* is the putative wild ancestor of cushaw (Merrick 1995), and the two subspecies form fully fertile offspring when hybridized (Merrick 1995). *Cucurbita argyrosperma* ssp. *sororia* is also a secondary genepool CWR of the pepo and ovifera pumpkins and squashes and butternut squash and a tertiary genepool CWR of giant pumpkin and figleaf gourd (Table 6.2). *Cucurbita argyrosperma* ssp. *sororia* is locally widespread and occurs in the lowland thornscrub vegetation of the Pacific and, less often, the Gulf of Mexico coasts and from Southern Sonora in Mexico south to Nicaragua (Nee 1990) (Fig. 6.2). Like most *Cucurbita* CWR, *C. argyrosperma* ssp. *sororia* has a weedy growth habit and is most common along roadsides, near agricultural fields, and other disturbed areas (Merrick 1995). It thrives in high-light environments and is often found growing over other plants or manmade structures (Merrick 1995).

Table 6.2 *Cucurbita* CWR

CWR	Genepool (A; B; C; D; E)	Native range	Potential agronomic traits
<i>C. argyrosperma</i> C. Huber ssp. <i>sororia</i> (L. H. Bailey) L. Merrick & D. M. Bates	2; 1; 2; 3; 3	Pacific coast from Sonora in Mexico south to Nicaragua	Resistant to BYMV and TmRSV
<i>C. cordata</i> S. Watson	3; 3; 3; 3; 3	Baja California (Mexico)	Drought tolerance, resistant to CMV, TRSV, BYMV
<i>C. digitata</i> A. Gray	3; 3; 3; 3; 3	Southwestern United States and Northwestern Mexico	Drought tolerance; resistant to CMV, TmRSV
<i>C. foetidissima</i> Kunth	3; 3; 3; 3; 3	Southwestern United States and Northern Mexico	Drought tolerance, resistant to CMV, TRSV, BYMB, WMV, and squash vine borer
<i>C. lundelliana</i> L. H. Bailey	2; 3; 2; 2; 2	Southern Mexico (Tabasco to Yucatan) (and Northern Central America)	Resistant to SqLCV, CMV, powdery mildew; used as a genetic bridge for breeding non-interfertile species
<i>Cucurbita okeechobeensis</i> (Small) L. H. Bailey ssp. <i>martinezii</i> (L. H. Bailey) T. C. Andres & Nabhan ex T. W. Walters & D. S. Decker	2; 3; 2; 3; 3	Southern Mexico (gulf coast)	Resistant to CMV, BYMV, TRSV, bacterial leaf spot, powdery mildew
<i>C. okeechobeensis</i> (Small) L. H. Bailey ssp. <i>okeechobeensis</i>	2; 3; 2; 3; 3	Florida (United States)	Resistant to CMV, BYMV, TRSV, bacterial leaf spot, powdery mildew
<i>C. palmata</i> S. Watson	3; 3; 3; 3; 3	Southwestern United States and Baja California	Drought tolerance; resistant to CMV, TRSV, BYMV, TmRSV
<i>C. pedatifolia</i> L. H. Bailey	3; 3; 3; 3; 2	North-central to Southern Mexico	Drought tolerance; disease resistance unstudied
<i>C. pepo</i> ssp. <i>pepo</i> var. <i>texana</i>	1; 2; 2; 3; 3	Texas (United States)	Undiscovered
<i>C. pepo</i> ssp. <i>pepo</i> var. <i>ozarkana</i>	1; 2; 2; 3; 3	Central United States	Undiscovered
<i>C. pepo</i> L. ssp. <i>fraterna</i> (L. H. Bailey) Lira et al.	1; 2; 2; 3; 3	Northern Gulf coast of Mexico	Undiscovered
<i>C. radicans</i> Naudin	3; unknown; 2; 3; unknown	North-central to Southern Mexico	Drought tolerance; resistant to CMV, TmRSV, BYMV; production of potato-sized tubers

Genepool relative to A, pepo and ovifera pumpkins and squashes; B, cushaw; C, butternut squash; D, giant pumpkin; E, figleaf gourd. Diseases: cucumber mosaic virus (CMV), watermelon mosaic virus (WMV), tomato ringspot virus (TmRSV), bean yellow mosaic virus (BYMV), tobacco ringspot virus (TRSV), squash leaf curl virus (SqLCV)

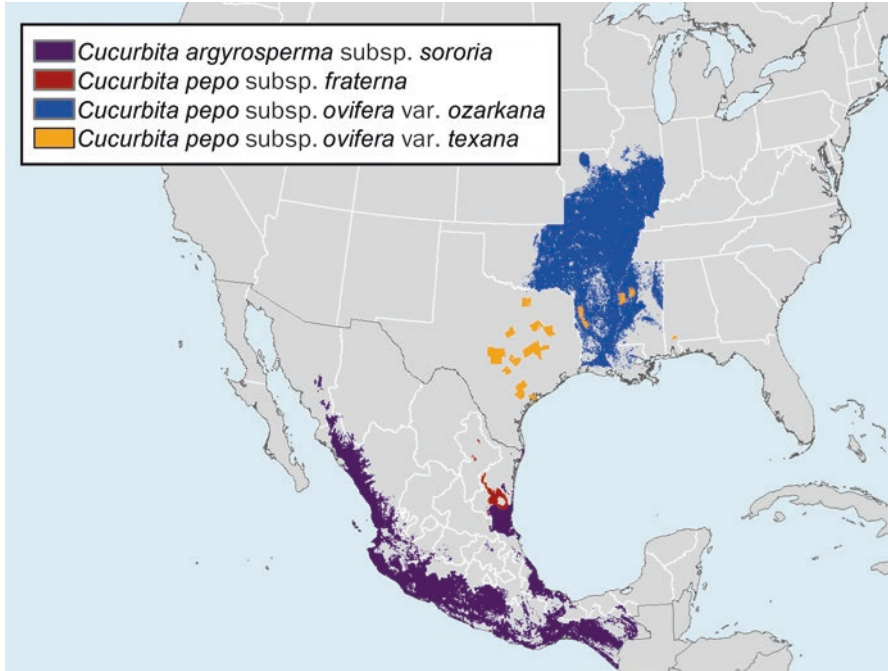


Fig. 6.2 Modeled potential distribution maps of *Cucurbita* primary CWR species (*Cucurbita pepo* L. ssp. *fraterna* (L. H. Bailey) Lira et al., *C. pepo* L. ssp. *ovifera* (L.) D. S. Decker var. *ozarkana* D. S. Decker, *C. pepo* L. ssp. *ovifera* (L.) D. S. Decker var. *texana* (Scheele) Filov, *C. argyrosperma* C. Huber ssp. *sororia* (L. H. Bailey) L. Merrick & D. M. Bates), based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are given in Appendix 1

It is possible to distinguish between *C. argyrosperma* ssp. *sororia* and cultivated cushaw by the wild subspecies' larger and more deeply lobed leaves, later flowering time (Jones 1992), and smaller fruits and seeds. The fruits of *C. argyrosperma* ssp. *sororia* are ovate and relatively small (about 8 cm in diameter) and contain seeds that are around 50–80% smaller by weight than seeds of the cultivated subspecies (Merrick 1995). *Cucurbita argyrosperma* ssp. *sororia* commonly grows near fields of cultivated cushaw in some areas in Mexico, and gene flow between the two subspecies can introduce bitterness into the fruit of the crop (Nabhan 1985; Montes-Hernandez et al. 2005). Gene flow between these two subspecies also introduces characteristics of the crop into wild populations; wild squashes are found with green and white striped rinds, thickened stems, and non-bitter flesh (Nabhan 1985).

Cucurbita argyrosperma ssp. *sororia* is resistant to two viruses: bean yellow mosaic virus (BYMV) and tomato ringspot virus (TmRSV) (Table 6.2). Neither of these viruses is a major threat to *Cucurbita* crop production, and resistance to these viruses is common in *Cucurbita*. Resistance to other viruses including cucumber mosaic virus and watermelon mosaic virus has not been found in *C. argyrosperma* ssp. *sororia* (Provvidenti et al. 1978). There are accounts of wild *C. argyrosperma* ssp. *sororia* being used in rural areas of Mexico medicinally and for its edible seeds (Montes-Hernandez et al. 2005)

***Cucurbita pepo* L. (wild)**

Cucurbita pepo ssp. *fraterna* (L. H. Bailey) Lira et al. and the two wild varieties of *C. pepo* ssp. *ovifera* are primary genepool CWR of both *ovifera* and *pepo* pumpkin and squash. These three taxa are also secondary genepool CWR of cushaw and butternut squash and tertiary genepool CWR of giant pumpkin and figleaf gourd (Table 6.2). Wild populations of *C. pepo* ssp. *ovifera* that occur in the Midwestern United States are classified as *C. pepo* ssp. *ovifera* (L.) var. *ozarkana* D. S. Decker (Ozark gourd). Those that occur in Texas are classified *C. pepo* ssp. *ovifera* (L.) D. S. Decker var. *texana* (Scheele) Filov (Texas gourd) (Fig. 6.2). Ozark gourd occurs along riverbanks and in other disturbed lowland habitats throughout the Ozark plateau and Greater Mississippi Valley (Smith et al. 2007) and is a persistent weed in agricultural fields (Decker and Wilson 1987), and Texas gourd occurs along riverbanks and in moist thickets in Texas (Erwin 1938). Ozark gourd has been proposed as the wild ancestor of *ovifera* pumpkin and squash based on isozyme studies (Decker-Walters et al. 1993). Modern molecular phylogenetic analyses have not found support for the separation of Ozark gourd and Texas gourd and thus have not been able to clearly suggest either as the ancestor of *ovifera* pumpkins and squashes (Kates et al. 2017). However, Ozark gourd and Texas gourd are geographically distinct and can be distinguished from each other based on fruit color and germination time (Decker-Walters et al. 1993, 2002), and the relationships of these two groups of wild *C. pepo* to *ovifera* pumpkin and squash should be studied further.

Cucurbita pepo ssp. *fraterna* is known from a small number of populations in the upland, seasonally dry thornscrub in Northeastern Mexico (Nee 1990) (Fig. 6.2). Although *C. pepo* ssp. *fraterna* was initially considered as a possible wild ancestor of *C. pepo* ssp. *pepo*, multiple phylogenetic studies of *Cucurbita* do not support that hypothesis (Sanjur et al. 2002; Zheng et al. 2013; Kates et al. 2017). Phylogenetic analysis indicates that *C. pepo* ssp. *fraterna* is highly diverged from the rest of wild *C. pepo* (Kates et al. 2017).

Few cases of disease resistance have been documented in wild *C. pepo* (Paris 2016). To introduce virus resistance into cultivated *pepo* and *ovifera* pumpkins and squashes, virus resistance has been introgressed from other less closely related CWR and cultivated *Cucurbita* subspecies (Paris 2016), but these hybridizations are challenging for breeders.

6.2.2 Secondary Genepool CWR***Cucurbita lundelliana* L. H. Bailey**

Cucurbita lundelliana is a secondary genepool CWR of both *ovifera* and *pepo* pumpkin and squash and of butternut squash, giant pumpkin, and figleaf gourd and a tertiary genepool CWR of cushaw. *Cucurbita lundelliana* is a mesophytic annual species that is native to Southern Mexico and to parts of Central America where it occurs at low elevations in tropical deciduous forests and as a weed in agricultural fields (Lira et al. 2009) (Fig. 6.3). Before the multiple independent domestications



Fig. 6.3 Modeled potential distribution maps of *Cucurbita* secondary CWR species (*Cucurbita lundelliana* L. H. Bailey, *C. okeechobeensis* (Small) L. H. Bailey ssp. *okeechobeensis*, *C. okeechobeensis* (Small) L. H. Bailey ssp. *martinezii* (L. H. Bailey) T. C. Andres & Nabhan ex T. W. Walters & D. S. Decker, *C. radicans* Naudin, *C. pedatifolia* L. H. Bailey), based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are given in Appendix 1

in *Cucurbita* were hypothesized, *C. lundelliana* was considered as a possible ancestor of all domesticated *Cucurbita* because it is interfertile with all the cultivated *Cucurbita* species other than *C. pepo* (Nee 1990). The ability of *C. lundelliana* to hybridize with many wild and domesticated *Cucurbita* species has led to its use as a bridge to transfer genes between species that are difficult to cross (Whitaker and Robinson 1986). *Cucurbita lundelliana* exhibits resistance to squash leaf curl virus, cucumber mosaic virus, and powdery mildew (Grubben and Chigumira Ngwerume 2004) (Table 6.2). Resistance to squash leaf curl virus has been transferred from *C. lundelliana* to the cultivated species *C. moschata* (butternut squash), but not to the North American crop subspecies. In addition to its importance as a genetic bridge species and as a source of virus resistance, *C. lundelliana* produces fruit that are sometimes used locally as a soap substitute and as a container (Lira et al. 2009).

Cucurbita okeechobeensis (Small) L. H. Bailey

Cucurbita okeechobeensis (Okeechobee gourd) includes two geographically disjunct subspecies. These subspecies are secondary gene pool CWR of pepo and ovifera pumpkins and squash and of butternut squash, and they are tertiary gene pool

CWR of cushaw, giant pumpkin, and figleaf gourd. *Cucurbita okeechobeensis* ssp. *martinezii* (L. H. Bailey) T. C. Andres & Nabhan ex T. W. Walters & D. S. Decker is native to Mexico where it grows at a wide range of elevations from sea level to the mountain cloud forest and is a weed in coffee plantations and agricultural fields (Lira et al. 2009) (Fig. 6.3). *Cucurbita okeechobeensis* (Small) L. H. Bailey ssp. *okeechobeensis* occurs in only two locations in Central Florida in the United States where it grows in the permanently wet soil of riverbanks or lakeshores (Fig. 6.3) (Walters and Decker-Walters 1993). The Okeechobee gourd is one of only two federally listed endangered species native to the United States that were identified as high priority for their value as genetic resources for important food crops (Khoury et al. 2013). The conservation status of the Okeechobee gourd is discussed in Sect. 6.4.1. Both subspecies of *C. okeechobeensis* are resistant to CMV, BYMV, TRSV, powdery mildew (Lira et al. 2009; Jahn et al. 2002; Formisano et al. 2010), and bacterial leaf spot (Robinson and Decker-Walters 1997) (Table 6.2). Resistance to powdery mildew has been introgressed from wild *C. okeechobeensis* to *C. pepo*, and the resistant offspring are commercially produced (Jahn et al. 2002; Formisano et al. 2010).

***Cucurbita pedatifolia* L. H. Bailey and *C. radicans* Naudin**

Cucurbita pedatifolia and *C. radicans* are secondary genepool CWR to figleaf gourd and butternut squash, respectively, and tertiary genepool CWR to all other *Cucurbita* crops. Of the six xerophytic perennial *Cucurbita* species, the closely related and interfertile xerophytic perennial species *C. pedatifolia* and *C. radicans* (along with tertiary genepool CWR *C. foetidissima*) are the most closely related to the cultivated pumpkins and squashes (Kates et al. 2017). *Cucurbita pedatifolia* and *C. radicans* occur in dry forests of Mexico from Zacatecas at the northern end of their range south to Chiapas (Fig. 6.3). Collections of *C. radicans* suggest that it occurs between and to the west of disjunct northern and southern distributions of *C. pedatifolia* (Fig. 6.3), but the morphological, ecological, and genetic differences of these two species are not documented, and additional work is needed to clarify whether they are truly different species.

Because of their closer relationship to the mesophytic species and because they are sometimes referred to as semixerophytic (though it is unclear how their adaptation to aridity differs from the other xerophytic species), it has been proposed that any of *C. pedatifolia* or *C. radicans* could be used as a possible genetic bridge between the xerophytic and perennial species (Bemis and Whitaker 1969). However, crosses between these species and mesophytic species have been unsuccessful (Robinson and Decker-Walters 1997).

The development of multiple potato-size tuberous roots by *C. pedatifolia* rather than the huge taproots produced by other xerophytic species is a trait that may be beneficial for the development of a drought-tolerant *Cucurbita* starch crop (Andres 1987) (Table 6.2). *Cucurbita radicans* is resistant to CMV, TRSV, and BYMV, but it is susceptible to WMV (Provvidenti et al. 1978) (Table 6.2). *Cucurbita pedatifolia* has not been screened for virus resistance, but considering its very close relationship to *C. radicans*, it may harbor similar traits.

6.2.3 Tertiary Genepool CWR

The four xerophytic perennial *Cucurbita* species that are tertiary genepool CWR for all *Cucurbita* crops occur in the hottest and driest regions in North America: the deserts of Northwestern Mexico and the Southwestern United States (Bemis and Whitaker 1969) (Fig. 6.4). Previously it was thought that the xerophytic species of *Cucurbita* were derived from non-xerophytic species and had subsequently evolved an adaptation to hot, dry climates. However, recent studies suggest that wild squashes tolerant to prolonged drought and extreme temperatures represent the ancestral state of pumpkins and squashes and that domesticated pumpkins, squashes, and gourds and their non-arid-adapted CWR are derived from a drought-tolerant ancestor (Zheng et al. 2013; Kates et al. 2017).

The xerophytic *Cucurbita* CWR species grow at low elevations (generally less than 1300 m) in coarse, dry, sandy soils. They are most common along roadsides and washes where water accumulates during rare periods of precipitation. Compared with the wild species of *Cucurbita* that grow in temperate to tropical grasslands and forests, the species of pumpkins and squashes that grow wild in the deserts and dry forests of North America are conspicuous, and some are quite frequent throughout

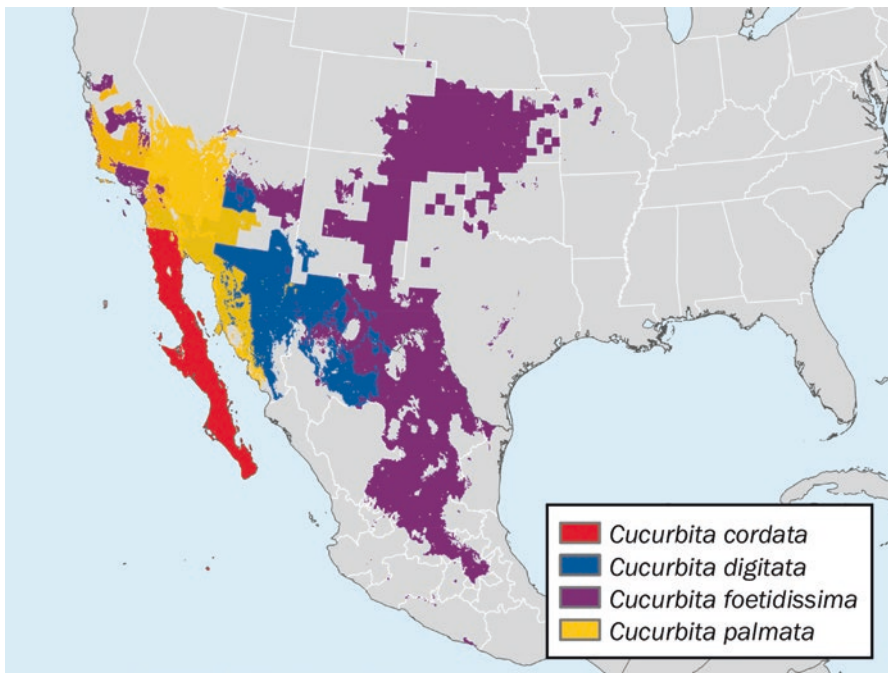


Fig. 6.4 Modeled potential distribution maps of *Cucurbita* tertiary CWR species (*Cucurbita foetidissima* Kunth, *C. palmata* S. Watson, *C. digitata* A. Gray, *C. cordata* S. Watson) based on climatic and edaphic similarities with herbarium and genebank reference localities. Full methods for generation of maps and occurrence data providers are given in Appendix 1

their native ranges due to the lack of competition from other plant species. The xerophytic *Cucurbita* CWR can be divided into two groups, one of which is more closely related to cultivated pumpkins and squashes, though more research is needed to understand the relationships among the xerophytic *Cucurbita* CWR. The Spanish or English common names chichicoyota, calabaza de coyote, calabacilla, and coyote melon/gourd may refer to any wild, arid-adapted *Cucurbita* (and rarely to non-arid-adapted wild *Cucurbita*), so here we only use common names that refer to a single species.

Cucurbita foetidissima **Kunth**

Among the xerophytic *Cucurbita* CWR, *C. foetidissima* (buffalo gourd) may be the most well-known due to its weedy, common occurrence, conspicuous folded leaves, and typically abundant, round fruit that is golden yellow at maturity (DeVeaux and Shultz 1985). Buffalo gourd is native to the deserts of the Southwestern United States and Northern Mexico (Bailey 1943) (Fig. 6.4) and grows as a weed, producing dense groundcover on disturbed soils (Deveaux and Schultz 1985). “Fetid gourd” is another common name for buffalo gourd and refers to the unpleasant smell of its leaves and flesh (Nabhan 1985). Like other xerophytic *Cucurbita* CWR, buffalo gourd reproduces primarily asexually (Deveaux and Schultz 1985); although its vines may bear many fruits, both germination and survival of young seedlings are uncommon. Like other xerophytic perennial species, buffalo gourd has low water requirements (Deveaux and Schultz 1985). It is also highly resistant to many insects and diseases that threaten cultivated pumpkins and squashes (Curtis 1946; Shahani et al. 1951; Paur 1952) (Table 6.2), though it is susceptible to squash mosaic virus (Rosemeyer et al. 1982). Buffalo gourd is resistant to some insect pests, including squash vine borer, but cucumber beetles are attracted to the high level of cucurbitacins found in its fruit, roots, and cotyledons (Deveaux and Schultz 1985) (Table 6.2).

Cucurbita palmata **S. Watson**, *C. digitata* **A. Gray**, and *C. cordata* **S. Watson**

This group of tertiary genepool CWR includes the three wild *Cucurbita* species commonly known as “coyote gourd” or “coyote melon,” which are the most distantly related to cultivated pumpkins and squashes (Kates et al. 2017). Although there are morphological differences among these interfertile and partly sympatric species, at some point they were reclassified as three subspecies of *C. digitata* (Scheerens et al. 1991). It does not appear that this taxonomy was ever adopted. All three species are native to the lowland deserts of the Southwestern United States and Western Mexico and typically occur in disturbed, gravelly soils (Shcheerens et al. 1991). *Cucurbita cordata* is narrowly distributed in Baja California in Mexico (Fig. 6.4). The distribution of *Cucurbita palmata* extends from Northeastern Baja California through California into the San Joaquin Valley and the southern part of the Salinas Valley and east to near the Colorado River (Bemis and Whitaker 1969) (Fig. 6.4). The southern end of the distribution of *C. digitata* ranges from Northern Sonora, Mexico, to Southern Arizona and New Mexico (Fig. 6.4). *Cucurbita palmata* occurs between the disjunct ranges of *C. digitata* in Southern Arizona and Northern Baja California, and interspecific hybridization is common where the two species are sympatric at the periphery of their ranges (Bemis and Whitaker 1969).

Species in this group of xerophytic perennials exhibit extreme drought tolerance and resistance to many of the viruses that infect cultivated *Cucurbita* (Table 6.2), but because of the distant relationships between the xerophytic perennials and the domesticated *Cucurbita*, introgression of these resistances into the cultivated *Cucurbita* has not been possible (Provvidenti 1990). Although desirable traits from these species may not be directly introgressed into cultivated pumpkins and squashes, modern studies of the genetics underlying these traits could aid in the identification of genes important for conferring disease resistance and drought tolerance in the cultivated species and subspecies.

6.3 Wild Utilized Species

Nearly all *Cucurbita* CWR are utilized in some way by rural people who live within the native ranges of the CWR. The diverse uses for wild pumpkins and squash are based on the bitter chemicals in their flesh, nutritious seeds, and hard rinds, which are the same traits that initially attracted hunter-gatherers to wild pumpkins and squashes. There are accounts of rural desert-dwelling people in the Southwestern United States and Mexico using the undried fruit of coyote melon (*C. digitata*, *C. palmata*, *C. cordata*) for soap due to its saponin-rich flesh (Nabhan 1985). The dried roots of buffalo gourd (*C. foetidissima*) are sold in medicinal herb markets in the Southwestern United States (Nabhan 1985). The non-xerophytic subspecies *C. argyrosperma* ssp. *sororia* is also utilized by rural Mexicans who eat the seeds and sometimes sell them in markets (Merrick 1995). Rural farmers and their families report using the bitter flesh (which contains saponins and cucurbitacins) to treat intestinal worms and as a biocide to purify water (Merrick 1995). Oil from cultivated *Cucurbita* subspecies has recently been shown to have pharmacological properties (Bardaa et al. 2016) that are likely also present and exploitable in the wild *Cucurbita* species and subspecies. Although there are many potential uses for *Cucurbita* CWR, the only wild *Cucurbita* species that was developed for commercial production is buffalo gourd (*C. foetidissima*).

Interest in domestication of buffalo gourd as a dryland oilseed crop emerged following the vegetable oil shortages during the Second World War (DeVeaux and Shultz 1985). Buffalo gourd was considered as a potential oilseed crop as early as 1946, and in the decades that followed, it was the subject of several studies (e.g., Bolley et al. 1950; Shahani et al. 1951) and preliminary cultivation and domestication efforts (Paur 1952; Curtis and Rebeiz 1974; Havener 1974). During the late 1970s and early 1980s, scientists worked to rapidly domesticate the wild species as a dryland oilseed and starch crop (Gathman and Bemis 1990). Researchers determined that the buffalo gourd required 150 mm of water annually if grown for its root and 250 mm annually if grown for seed (DeVeaux and Shultz 1985) and that it could yield up to 3000 kg/ha of seed (Bemis et al. 1978). The oil of seeds produced by buffalo gourd is similar to sunflower oil (DeVeaux and Shultz 1985), and the oil yield was predicted to be up to two times that of sunflower at 91 gal/acre (DeVeaux

and Shultz 1985). Root starch from cultivated buffalo gourd was considered as a potential source of ethanol; researchers estimated alcohol yield from buffalo gourd root starch was superior to corn or grain sorghum at around 400 gal/a (DeVeax and Shultz 1985).

Despite the promise of buffalo gourd as an oilseed and ethanol crop for arid lands, interest in the development of the crop waned by 1990 (Small 2014). Commercialization of buffalo gourd failed, apparently due to its lack of unique qualities needed for breeders and farmers to shift their current practices. However, in the decades since interest buffalo gourd declined, reduced supplies of water and arable land that will only grow scarcer are increasing the demand for drought-tolerant crops and biofuel production, and interest in buffalo gourd may be renewed.

6.4 Conservation Status of CWR and WUS

6.4.1 *In Situ*

The Okeechobee gourd (*C. okeechobeensis* ssp. *okeechobeensis*) is one of only two federally endangered plants native to the United States that have been determined as high priority as genetic resources of important food crops (Khoury et al. 2013), and it faces a continued threat of extinction due to development, competition from invasive species, and climate change. The Okeechobee gourd was historically more widespread in Florida, but by 1930 95% of its habitat was destroyed when pond apple (*Annona glabra* L.) forests were cleared in attempts to develop the Everglades and other regions of Florida for agricultural fields (Ward and Minno 2002). The Okeechobee gourd now only occurs along the shore of Lake Okeechobee and a short stretch of riverbank along the St. Johns River in Central Florida. The St. Johns River populations are somewhat protected as they occur on State Parks Land, but the Lake Okeechobee populations face imminent threat by development, recreation, and water management practices. Furthermore, the populations of Okeechobee gourd that do exist are not robust. Two other CWR, the native vine *Vitis rotundifolia* Michx. and the invasive exotic *Dioscorea bulbifera* L., both appear to outcompete the Okeechobee gourd along the St. Johns River. Some plants surveyed in 2015 by the author did not reemerge in 2016, and though the vines of the Okeechobee gourd plants are extensive, they produced very little, if any, fruit, suggesting a possible lack of suitable pollinators or limitation by other environmental factors.

There are currently no active in situ Okeechobee gourd conservation projects, though multiple grant proposals have been submitted to various public and private organizations (Minno pers. comm.). Public awareness of this nearly extinct CWR is also lacking. Displays throughout the state parks where it occurs warn visitors of the threat of invasive plant and animal species and provide information about the parks' resident federally listed mammal species, the Florida manatee, but do not mention the Okeechobee gourd. Local landowners and park rangers are also

currently unaware that a federally listed endangered plant occurs in this area. Local accounts that the vine is regarded by some as a weed suggests some populations may be at risk of removal.

Although the Okeechobee gourd is the only listed endangered *Cucurbita* CWR, many *Cucurbita* CWR are geographically restricted. The current distributions of *Cucurbita* CWR are likely more restricted than they were in the past (Kistler et al. 2015). Disjunct species distributions in *C. okeechobeensis*, *C. digitata*, *C. pedatifolia*, and *C. pepo* and low genetic divergence between geographically distant occurrences of some species (Kates et al. 2017) suggest that the areas where *Cucurbita* CWR occur today represent only a fraction of the areas where they were historically distributed. The narrow present-day distribution of *Cucurbita* CWR may be due to ecological shifts and the extinctions of megafauna that consumed the bitter *Cucurbita* fruit and dispersed *Cucurbita* seeds (Kistler et al. 2015). Although this ancient shift cannot be reversed, the hypothesis that the extinction of large herbivores led to drastic decline in *Cucurbita* CWR populations highlights the importance of dispersal in maintaining the genetic diversity of extant CWR. Commonly, *Cucurbita* CWR are regarded as an agricultural nuisance in Mexico and Central America (Nabhan 1985) and appear regionally vigorous, so in situ conservation efforts are not pursued.

The seeds of *Cucurbita* CWR are now most commonly dispersed by water (Nabhan 1985). After the fruits of *Cucurbita* CWR mature, the flesh inside dries out, and the seeds are preserved inside the lignified rind (Nabhan 1985). These dried fruits may stay in the same place for months but will eventually be carried by flash-floods (Nabhan 1985). As the buoyant *Cucurbita* CWR fruits are carried by fast-moving water, they hit against rocks and banks, and their dry rinds break open allowing the seeds to be scarified and then scattered in a new area. Because of the importance of seasonal flooding for the dispersal of *Cucurbita* CWR, unusually prolonged periods of drought in the deserts of the Southwestern United States and Mexico inhibit the dispersal of *Cucurbita* CWR. Dispersal by water is also important for non-xerophytic *Cucurbita* CWR that occur along rivers and lakes (*C. okeechobeensis* ssp. *okeechobeensis*; wild *C. pepo* ssp. *ovifera*), and lower water levels due to drought and water management practices could negatively impact the dispersal of these *Cucurbita* CWR.

Studies modeling the effect of future climate change on the distribution of *Cucurbita* CWR show that the distributions of all *Cucurbita* CWR are expected to decrease substantially in the next 60 years (Lira et al. 2009). The specialized pollinator of *Cucurbita* CWR, *Peponapis* spp., the squash bee, also faces threats due to climate change and the widespread use of agricultural pesticides (Watanabe 2013). More research is needed on these pollinator species. Because of the large vine habit of *Cucurbita* CWR, populations of *Cucurbita* CWR that grow as weeds in or near agricultural fields are removed to prevent the introduction of undesirable traits into *Cucurbita* crops or to limit their competition with non-*Cucurbita* crops (Nabhan 1985). Similarly, populations of *Cucurbita* CWR that grow on private, nonagricultural lands are also often removed because they are local weeds.

The deregulation of transgenic zucchini (*C. pepo* ssp. *pepo* var. *cylindrica*) in Mexico is currently under consideration (Cruz-Reyes et al. 2015) and has been the subject of numerous studies to examine the potential for transgenes to escape (see Cruz-Reyes et al. 2015; Sasu et al. 2009; Arriaga et al. 2006). Gene flow between populations of wild *Cucurbita* and cultivated *Cucurbita* is well-documented in multiple species, including *C. pepo* (Wessel-Beaver 2000; Wilson et al. 1994; Montes-Hernandez and Eguiarte 2002). The viability of F₁ seed has been experimentally confirmed for some crosses (Cruz-Reyes et al. 2015). Experimental crosses of transgenic squash lines to wild squash have been made to assess the relative competitiveness of the hybrids compared with the parents (Cruz-Reyes et al. 2015). Although transgenic x wild hybrids thus far do not appear to have a competitive advantage compared with wild *Cucurbita*, additional studies are needed (Cruz-Reyes et al. 2015; Arriaga et al. 2006). The need to preserve the genetic variation in wild *Cucurbita* in Mexico is especially high, as these populations likely represent the ancestors of pepo pumpkin and squash and still harbor the genetic diversity lost in the crops during their domestication.

6.4.2 *Ex Situ*

Maintenance and regeneration of genetically diverse *Cucurbita* CWR germplasm resources is critical for identifying the genes that underlie agronomically important traits in *Cucurbita* CWR. Large collections of *Cucurbita* CWR are held in seedbanks all over the world (e.g., the United States, Mexico, Costa Rica, Russia, Italy, Brazil, Colombia, Bolivia, Czech Republic, Spain, Turkey, and Portugal) (Clark et al. 1991; Nuez et al. 2000; Diez et al. 2002; Lebeda et al. 2007; Ferriol and Pico 2008; Karlova 2008). Collections of *Cucurbita* are particularly common in seedbanks in Mexico, such as the 25 community seedbanks, established in 2005 to preserve in situ conservation (Vera Sanchez et al. 2015), and in the country's largest wild plant seedbank at the Faculty of Higher Studies of Iztacala, UNAM (FESI-UNAM seedbank) (Rodríguez-Arévalo et al. 2017). However, a comprehensive understanding of genebank coverage and gaps for *Cucurbita* CWR in Mexico and other countries is lacking in part due to insufficient collaboration among seedbanks around the world that each have unique systems of cataloguing and distributing germplasm.

Collections of *Cucurbita* CWR from throughout their native ranges are the first step in conserving and increasing ex situ collections of *Cucurbita* CWR. In over 100 years of the USDA plant exploration program, there has been only one exploration for wild *Cucurbita* in the United States that has resulted in deposition of accessions into the National Plant Germplasm System. Collection of North American *Cucurbita* CWR germplasm from outside the United States for deposition into the USDA National Plant Germplasm System is limited due to the phytosanitary and political issues described below. American researchers and botanists made many collections of *Cucurbita* CWR in Mexico in the decades prior to strict regulation; although some of these collections were deposited in the National Plant Germplasm

System in the late 1980s and early 1990s and greatly increased the holdings of *Cucurbita* CWR from Mexico, many of these collections were never deposited (Robinson 1995), and seeds from these collections are unlikely to be viable.

Concerns regarding access and benefit sharing, phytosanitary issues, and a lack of funding limit or prevent sharing of germplasm resources among seedbanks and distributing germplasm to geneticists and breeders internationally. *Cucurbita* is not currently listed in Annex 1 under the Multilateral System of Access and Benefit Sharing of the International Treaty on Plant Genetic Resources for Food and Agriculture (FAO 2017) and thus does not benefit from prearranged facilitated access negotiations. Distribution of germplasm outside of the country where it is held can be critical to ex situ conservation of genetic resources, because *Cucurbita* CWR collected in a climate that differs from its storage location may not flower or fruit in the conditions of its seedbank location (Jarret pers. comm.). For seedbanks in the United States, this can be a problem for *Cucurbita* CWR that are adapted to tropical or subtropical climates. Although this issue certainly affects the ex situ conservation of other CWR, it may be especially problematic for *Cucurbita*. In contrast to the most economically important crops like corn and rice, the infrastructure required to grow and pollinate the large, monoecious *Cucurbita* plants is not in place (Paris 2016), and investing these resources is risky when the regeneration efforts are not likely to succeed.

Limited funding for seedbank activities can restrict the regeneration efforts needed to make collections available for distribution to geneticists and breeders (Jarret pers. comm.). A high proportion of *Cucurbita* CWR held in the US National Plant Germplasm System is unavailable for distribution (Fig. 6.5). Seedbanks respond to user requests. Hence, limited resources may be diverted to maintenance of collections that are more widely used by researchers. Greater demand for

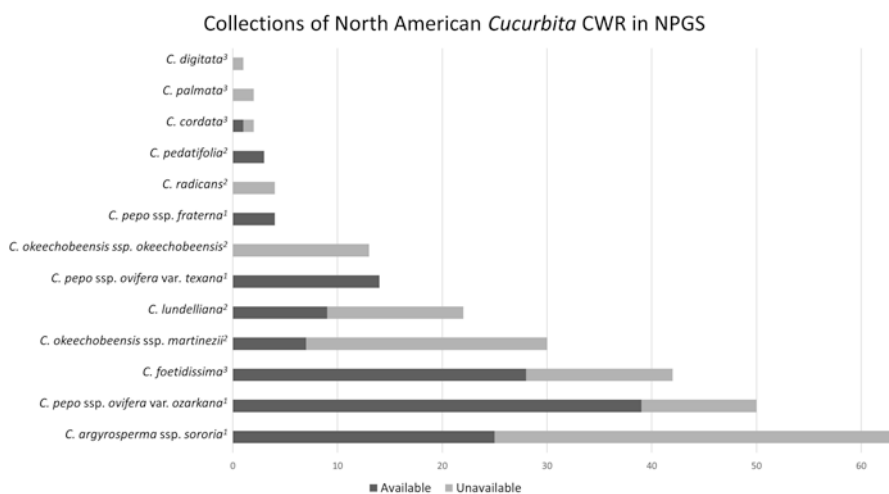


Fig. 6.5 Number of *Cucurbita* CWR accessions in the National Plant Germplasm System (NPGS). Dark gray bars indicate accessions available for distribution; light gray bars indicate accessions currently unavailable. Superscripts denote genepool designations for CWR based on most closely related domesticate

collections of modern cultivars (or specific crops) may limit the resources available for collections of *Cucurbita* CWR, although these species likely harbor some of the most useful traits for crop enhancement (Robinson 1995). Only a few studies have attempted a thorough investigation of potentially valuable agronomic traits of *Cucurbita* CWR (e.g., Provvidenti et al. 1978; Scheerens et al. 1991). The xerophytic perennial species are especially understudied even though they are known to be resistant to drought and to many of the viral diseases that pose a threat to cultivated pumpkin and squash yields. Increased research interest in *Cucurbita* CWR is needed to promote the conservation of genetically diverse CWR in genebanks and to create drought-tolerant, disease-resistant crops that can meet the present and future challenges to food security.

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