Chapter 2.

Squashes, pumpkins, zucchinis and gourds (*Curcurbita* species)

*This chapter deals with the biology of squashes, pumkins, zucchinis and gourds (*Cucurbita *species). It contains information for use during the risk/safety regulatory assessment of genetically engineered varieties intended to be grown in the environment (biosafety). It includes elements of taxonomy, centres of origin and distribution, morphological characters, reproductive biology, genetics, hybridisation and introgression, crop production and cultivation practices, interactions with other organisms, pests and pathogens, and biotechnological developments.*

The chapter was prepared by the OECD Working Group on the Harmonisation of Regulatory Oversight in Biotechnology, with Mexico as the lead country and the collaboration of the United States. It was initially issued in August 2012. Data from FAOSTAT have been updated.

Species or taxonomic group

The genus *Cucurbita* is well known for its cultivated species which in English are called by the general names of squashes, pumpkins, marrows and gourds, and in Spanish are commonly known as *calabazas* and *zapallos* or in some areas of the Americas by indigenous names. Other names have been given to *Cucurbita* species in countries where these species have been adopted into local agriculture, e.g. in the French language, *citrouille*, *courgette* and *potiron*. The cultivated *Cucurbita* species are: *C. argyrosperma*, which includes the cushaw type (long curved neck) of squash; *C. maxima*, which includes pumpkins and hubbard, turban and buttercup squash; *C. moschata*, which includes the winter squashes; and *C. pepo*, which includes both summer squash (e.g. zucchini, scallop, scallopini, crookneck and cocozelle squash) and winter squash (e.g. the common or "true" pumpkin, delicata, acorn and spaghetti squash) as well as ornamental gourds. *C. ficifolia* includes the fig leaf gourd and lacayote. The most important of these species in terms of agricultural production worldwide are *C. maxima*, *C. moschata* and *C. pepo*.

The genus *Cucurbita* is exclusively native to the Americas. Prior to the European contact (i.e. prior to 1492 of the Common Era), various *Cucurbita* were a mainstay of traditional Native American agriculture. In the Americas, *Cucurbita* have traditionally been one of the "three sisters" of native agriculture together with beans (*Phaseolus vulgaris*) and maize (*Zea maize*). The three crops were grown together, with the maize providing support for the climbing beans, and shade for the *Cucurbita*. The *Cucurbita* provide ground cover to limit weeds and keep the soil moist. The beans fix nitrogen for all three crops. Subsequent to the European contact, *Cucurbita* species were disseminated worldwide and cultivated on other continents (Paris, 1989). Today, *Cucurbita* species are cultivated worldwide, and are an important food source for much of the world's population. In 2013, Asia region (primarily the People's Republic of China, and India) was the largest producer of squashes, pumpkins and gourds with more than 65% of the total hectares planted to *Cucurbita* species worldwide, followed by Africa with 15% of the global acreage, then North and Central America and the Caribbean with 8%, Europe with 7.5%, South America with 3% and Oceania with 0.9 % (FAOSTAT, 2013).

Domesticated species are cultivated in large production areas for processing and the fresh market, as well as in home gardens. Cultivated *Cucurbita* species are grown primarily for their seeds, fruits and gourds. *Cucurbita* seeds can be eaten directly, ground into paste, meal, "nut" butter or fine flour. The seeds are also sources of oils and proteins (Robinson and Decker-Waters, 1997). After the hull is removed, the seeds contain about 50% oil and up to 35% protein. Most of the oil is made up of non-saturated fatty acids, and thus is of high nutritional value. Conjugated fatty acids among some *Cucurbita* oils make them highly useful as drying oils, as they combine readily with oxygen to form an elastic, waterproof film. Mature and immature *Cucurbita* fruits are edible and eaten as a vegetable. The flesh of some fruits (e.g. *C. maxima*) can be dried, ground into a powder and used with cereals to make bread, cakes, etc. (Chiej, 1984; Facciola, 1990; See, Wan Nadiah and Noor Aziah, 2007). The fruits of one *Cucurbita* (*C. ficifolia*) are used to make confections and beverages, some alcoholic. In addition, in many places in Latin America and elsewhere in the world, flowers and some vegetative parts (e.g. tender stem tips, leaves, tendrils) are also eaten as vegetables (Nee, 1990; Merrick, 1991; Lira, Andres and Nee, 1995). The vines and fruits can also be used as fodder for domesticated animals (Mariano and Dirzo, 2002). The gourds can be used for ornamental purposes or, as has been the case historically, as containers. Few people grow *Cucurbita* flowers for decorative purposes as a flower lasts only one morning. Only one species (*C. maxima*) is known to have very aromatic flowers (Lira, Andres and Nee, 1995). Several *Cucurbita* species are used in traditional medicine; as an anthelmintic (Chou and Huangfu, 1960; Schabort, 1978; Chiej, 1984; Argueta, 1994); to treat benign prostatic hypertrophy (Duke and Ayensu, 1985; Kreuter, 2000; Gossell-Williams, Davis and O'Connor, 2006); as a diuretic (Chiej, 1984); as a nerve tonic and to sooth burns, inflammations and boils (Chopra, Nayar and Chopra, 1956); and as an antihyperglycemic agent (Andrade-Cetto and Heinrich, 2005; Xia and Wang, 2006). Lira, Andres and Nee (1995) discuss several of these uses.

Cultivated species of *Cucurbita* are very diverse locally, regionally and worldwide, having a wealth of innumerable strains, landraces and varieties (e.g. Esquinas-Alcazar and Gulick, 1983; Jeffrey, 1990; Nee, 1990; Lira, Andres and Nee, 1995; Sanjur et al., 2002). It should be noted that commonly used descriptors such as "pumpkin" or "squash" apply broadly to morphotypes across all of the cultivated *Cucurbita*, as does the term "gourd". Thus, the term "pumpkin" is applied to certain fruits of *C. maxima* as well as certain fruits of *C. moschata*, *C. argyrosperma* and *C. pepo*; and the term "squash" is applied to certain fruits of *C. pepo* as well as certain fruits of *C. maxima*, *C. moschata* and *C. argyrosperma*. Similarly, in English the word "pumpkin" or "squash" as used colloquially could be describing a variety, a subspecies, a species or, at the extreme, a genus. In order to avoid confusion, this chapter will rely on taxonomic identifiers to the extent possible.

Taxonomy

The genus *Cucurbita*, which is native to the Americas, is in the order Cucurbitales, the family Cucurbitaceae, the subfamily Cucurbitoideae and the tribe Cucurbiteae (Jeffrey, 1990). The *Cucurbita* are not closely related to other Cucurbitaceae genera.

Cucurbita traditionally has been considered a distinct genus of 20-27 species (Bailey, 1943, 1948; Cutler and Whitaker, 1961; Esquinas-Alcazar and Gulick, 1983), which, due to the ecological characteristics of their habitats and duration of their life cycles, are divided into two large groups: the xerophytic species, perennials adapted to dry climates with tuberous storage roots; and the species adapted to moister or mesophytic environments, either annuals or short-lived perennials with fibrous roots. Within this second group are the five cultivated species, whose amazing morphological variation – especially of fruits and seeds – has led to multiple names and classification schemes. Crossability experiments have more recently revealed that some of the species considered separate members of the 27-member cohort were merely from different wild populations. Nee (1990) recognises 12 or 13 species. Lira, Andres and Nee (1995) recognise 15 species and 20 taxa.

The *Cucurbita* can be categorised into seven groups (Table 2.1): the *Argyrosperma* group, the *Maxima* group, the *Pepo* group, the *Okeechobeensis* group, the *Digitata* group, the *Foetidissima* group and a seventh group, those species with no defined group (i.e. *C. ecuadorensis*, *C. ficifolia*, *C. lundelliana* and *C. moschata*). The five cultivated *Cucurbita* species are listed amongst these seven groups, and highlighted in Table 2.1 in bold.

The cultivated species *C. argyrosperma*, *C. maxima*, *C. moschata* and *C. pepo* each are comprised of a large series of convarieties, varieties and forms, including numerous local races (landraces) or varieties, and commercial cultivars. At least three of the cultivated species, *C. argyrosperma*, *C. maxima* and *C. pepo* are known to interbreed naturally with wild relatives, and the appropriate taxonomic assignments for these wild relatives *vis-à-vis* the cultivated species is still in flux as new information becomes available. In some instances the wild relative has been classified as a distinct species, in others it has been classified as a subspecies of the cultivated species. Annex 2.A1 provides a listing of the various names associated with 13 of the species. The taxonomic relationships of two *Cucurbita* species, *C. argyrosperma* and *C. pepo*, have been studied more intensively, and these studies have provided a much clearer perspective of the relationships within these cultivated species, and between the cultivated species and their wild relatives. The other three domesticated species have been less studied in terms of relationships within the species and between the cultivated species and their wild relatives.

Morphological, ecogeographical, archaeological and biosystematic evidence, such as those derived from studies on hybridisation and molecular biology (e.g. Decker, 1988, 1986; Andres, 1990, 1987a, 1987b, 1987c; Decker-Walters et al., 2002, 1993; Decker and Wilson, 1987; Kirkpatrick and Wilson, 1988; Wilson, 1990, 1989; Merrick, 1990; Rodríguez and Lira, 1992; Wilson, Doebley and Duvall, 1992; Wilson, Lira and Rodríguez, 1994; Sanjur et al., 2002), as well as field observations, contribute to the development of the currently recognised limits and relationships of the five cultivated species. Table 2.1 and Annex 2.A1 are syntheses of information from various sources describing the most commonly referred to *Cucurbita* taxa, both wild and domesticated.

Table 2.1**. List of taxa in the genus *Cucurbita* and their natural distributions**

Cucurbita group	Taxa	Natural distribution
Argyrosperma group	***C. argyrosperma*** **Huber ssp.** ***argyrosperma***	Southwestern United States, Mexico, Mesoamerica
	C. argyrosperma ssp. *sororia* (L.H. Bailey) Merrick & Bates	Mesoamerica (Pacific coast from Mexico to Nicaragua)
Maxima group	***C. maxima*** **Duchesne ex Lam. ssp.** ***maxima***	South America (Argentina, Bolivia , Chile)
	C. maxima ssp. *andreana* (Naudin) I.A. Filov	South America (Argentina, Bolivia, Uruguay)
Pepo group	***C. pepo*** **L.**	Northern Mexico, southern and central United States
	C. pepo ssp. *fraterna* (L.H. Bailey) Andres	Northeastern Mexico
	C. pepo ssp. *texana* (Scheele) I.A. Filov	Central, southcentral, southeastern United States
Okeechobeensis group	*C. okeechobeensis* (J.K. Small) L.H. Bailey ssp. *okeechobeensis*	Southern United States (Florida)
	C. okeechobeensis ssp. *martinezii* (L.H. Bailey) Walters & Decker-Walters	Mexico
Digitata group	*C. digitata* A. Gray *	Mexico, United States
	C. cordata S. Watson *	Mexico
	C. palmata S. Watson *	Mexico, United States
Foetidissima group	*C. foetidissima* H.B.K. *	Mexico, United States
	C. pedatifolia L.H. Bailey *	Central Mexico
	C. scabridifolia L.H. Bailey *	Northeastern Mexico
	C. radicans Naudin *	Mexico
Species with no defined group	*C. ecuadorensis* Cutler & Whitaker	Ecuador (Pacific coast)
	C. lundelliana L.H. Bailey	Belize, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua
	C. ficifolia **Bouché**	Mexico to Argentina and Chile
	C. moschata **(Duchesne ex Lam.) Duchesne ex Poiret**	Mesoamerica and South America

Note: Names in bold correspond to domesticated taxa; those with an asterisk (*) correspond to perennial species. Names used preferentially in this table and in the text are based on the nomenclature used by Lira, Andres and Nee (1995); Lira Saade, Eguiarte Fruns and Montes Hernández(2009); and Gong et al. (2012).

Cucurbita argyrosperma

A number of researchers have investigated *Cucurbita argyrosperma*, which was formerly known as *C. mixta* Pang (e.g. Nabhan, 1984; Merrick and Nabhan, 1985; Merrick and Bates, 1989; Merrick, 1991, 1990). *C. argyrosperma* is a collection of interfertile domesticated, feral and wild plants. Based on morphological variation, geographical distribution and allozyme variation, Merrick and Bates (1989) and Merrick (1990) have divided *C. argyrosperma* into two subspecies: 1) ssp. *argyrosperma*, with four varieties, three of which (var. *argyrosperma*, var. *callicarpa*, var. *stenosperma*) encompass all the cultivated types of the species, and one that encompasses the wild populations from northern Mexico (var. *palmeri*); and 2) ssp. *sororia*, which is considered the evolutionarily ancestral wild stock (based on its ecogeographical distribution, morphological similarity and reproductive compatibility) and is comprised of the wild populations from Mexico through Central America. Hybridisation studies (Merrick, 1990) and field data (Nabhan, 1984; Merrick and Nabhan, 1985; Decker, 1986; Lira, 1991) have revealed that all five of these taxa are completely interfertile and thus belong to the same biological species.

Spontaneous hybrids between the wild and cultivated plants of the group have been documented for some regions of Mexico in populations quite separated from each other, as reported by Decker (1986), between plants from various taxa of ssp. *argyrosperma* in the state of Jalisco. Moreover, the characteristics of cultivated varieties do not differ much from those that can be found in the wild plants of the group, nor from those of spontaneous hybrids between the wild and cultivated plants of the group. It is therefore not easy to readily distinguish between the various subspecies and varieties. For these reasons, this chapter follows the general convention and recognises only the two subspecies, placing all the cultivated types within ssp. *argyrosperma*, and the wild or spontaneous plants within ssp. *sororia* (as in Table 2.1).

Cucurbita pepo

Cucurbita pepo is probably the most well-studied species of the genus. Systematic, ethnobotanical and morphometric research, together with archaeological information, constitute the main sources of information concerning its origin and domestication. Similar to *C. argyrosperma, C. pepo* is a collection of interfertile domesticated, feral and wild plants.

Morphometric and molecular research, as well as studies on artificial and spontaneous hybridisation, indicate that the wild taxa most closely related to *C. pepo* L. are: 1) *C. pepo* ssp. *fraterna* (also known as *C. fraterna*), only found currently in a few localities in northeastern Mexico (in the states of Tamaulipas and Nuevo León; Bailey, 1943; Andres, 1987a; Nee, 1990; Rodríguez and Lira, 1992; Wilson, Lira and Rodríguez, 1994); and 2) two wild *Cucurbita* originally identified as *C. texana* (identified now as *C. pepo* ssp. *ovifera* var. *texana* and *C. pepo* ssp. *ovifera* var. *ozarkana*), which are endemic to parts of the United States (Gray, 1850; Bailey, 1943; Fursa and Filov, 1982; Decker, 1988, 1986; Andres, 1987a; Decker and Wilson, 1987; Kirpatrick and Wilson, 1988; Wilson, 1990, 1989; Decker-Walters et al., 1990; Wilson, Doebley and Duvall, 1992; Sanjur et al., 2002).

There is still some disagreement concerning the appropriate taxonomic relationship of the members of the *Pepo* group, with no fewer than three different reclassifications suggested, including those from Decker (1988, 1986); Andres (1987a); Decker-Walters et al. (1993, 1990). The first proposal by Decker (1988, 1986) recognised two subspecies: 1) ssp. *pepo*, composed of two varieties: var. *pepo*, in which all edible cultivars are included, and var. *fraterna*, corresponding to the wild ancestor of this part of the group; and 2) ssp. *ovifera*, also with two varieties: var. *ovifera*, which includes cultivars used as decoration, and var. *texana*. The second classification (Andres, 1987a) is simpler and proposes that *C. pepo* is only constituted by three subspecies: ssp. *pepo*, which includes all edible and ornamental cultivated types, and the subspecies *texana* and *fraterna*, in which the wild ancestors of the group are located. The third proposal (Decker-Walters et al., 1993) is a modification of the first, as it has three subspecies: ssp. *pepo*, which includes local races and commercial cultivars, ssp. *fraterna* and ssp. *ovifera*. Under this proposal, subspecies *ovifera* is composed of three varieties: 1) var. *ozarkana* (wild plants in the states of Arkansas, Illinois, Louisiana, Missouri and Oklahoma in the United States), 2) var. *texana* (wild plants in the states of Louisiana, Mississippi, New Mexico and Texas in the United States), and 3) var. *ovifera* (mainly ornamental cultivars). For simplicity, this chapter, in developing the *C. pepo* grouping in Table 2.1, follows the classification proposed by Andres (1987a), but recognises that the classification is still in flux as new molecular information is developed, as discussed below.

Work by Wilson, Doebley and Duvall in 1992 using restriction fragment length polymorphism analysis on 15 species in the genus supports the separation of cultivars of *C. pepo* into two distinct lineages, *C. pepo* ssp. *pepo* and *C. pepo* ssp. *ovifera*, as do isozyme studies of these taxa (Decker-Walters et al., 1993; Jobst, King and Hemleben, 1998). Analysis of the sequence of an intron of the mitochondrial *nad1* gene has also been used to elucidate the relationship between the various members of the *Pepo* group (Sanjur et al., 2002), and this analysis also suggests that *C. pepo* can be subdivided into two subspecies: *C. pepo* ssp. *pepo* and *C. pepo* ssp. *ovifera*.

Smith (2006) agrees that *C. pepo* is comprised of two subspecies: *C. pepo* ssp. *pepo* and *C. pepo* ssp. *ovifera*. *C. pepo* ssp. *pepo* includes pumpkin, zucchini and other marrow squashes, Mexican landraces and a few ornamental gourds. *C. pepo* ssp. *ovifera* comprises both domesticated and free-living populations, and is further divided into three taxa: *C. pepo* ssp. *ovifera* var. *ovifera*, which includes some cultivars (e.g. acorn, crookneck and scallop squash and some pumpkin) and most ornamental gourds; and the free-living populations in the United States, which represent two molecularly distinct populations; *C. pepo* ssp. *ovifera* var. t*exana* and *C. pepo* ssp. *ovifera* var. *ozarkana* (Decker-Walters et al., 1993, 2002).

The analysis by Sanjur et al. (2002) of an intron of the mitochondrial *nad1* gene shows that *C. fraterna*, *C. pepo* var. *texana*, *C. pepo* var. *ozarkana* and cultivated *C. pepo* ssp. *ovifera* form a closely related clade, with any of the three wild species a potential progenitor of the domesticated species. The *C. pepo* ssp. *pepo* lineage is separated from the *ovifera* clade on the basis of a three base pair difference in an intron of the gene *nad1* of the mitochondrial DNA, a finding which supports the hypothesis that *C. pepo* ssp. *pepo* and *C. pepo* ssp. *ovifera* arose from two separate domestication events.

All of the *C. pepo* subspecies and variants can successfully hybridise with each other, suggesting that the *C. pepo* progenitors for both subspecies *pepo* and *ovifera* were once part of an extended contiguous population reaching from Mexico through the eastern United States. Whether this extended range occurred naturally or was influenced by humans is still uncertain (Newsom, Webb and Dunbar, 1993; Smith, 2006). Upon reviewing archaeological evidence found in the state of Florida (United States), Hart, Daniels and Sheviak (2004) suggest that the pepo gourd may have first been employed in North America as a float for fish nets, and this use may have facilitated spread of the species in North America.

Cucurbita maxima

Taxonomically, the species *C. maxima* is composed of two subspecies, *maxima* and *andreana*. *C. maxima* ssp. *maxima* contains ornamental and cultivated forms, while *C. maxima* ssp. *andreana* contains only the wild forms. Gene sequence analysis work by Sanjur et al. (2002) on the mitochondrial *nad1* gene detects no base pair differences in an intron of the mitochondrial *nad1* gene between *C. maxima* and *C. andreana*, supporting the assignment based on ecological and morphological evidence that these two species form a wild/domesticated species pair (Nee, 1990). The work of Sanjur et al. (2002) also shows that *C. maxima* is closely related to the free-living South American species, *C. ecuadorensis*. This supports research using chloroplast DNA analysis which shows that *Cucurbita ecuadorensis* groups with *C. maxima* and *C. andreana* to form a South American group of allied species (Wilson, Doebley and Duvall, 1992). Nee (1990) suggests that *C. andreana* appears to be ancestral to *C. maxima,* while Wilson, Doebley and Duvall (1992) suggest that *C. ecuadorensis*, *C. maxima* and *C. andreana* are derived from the same ancestor. *Cucurbita ecuadorensis* itself has been regarded as a species subjected to an incipient domestication process which, however, did not continue (Nee, 1990; Sanjur et al., 2002).

Cucurbita moschata

Although a very important vegetable crop in many parts of the world (e.g. Africa), *C. moschata* has been subject to less scientific scrutiny aimed at elucidating taxonomic relationships within the species than *C. argyrosperma* or *C. pepo*. Filov in 1966 classified more than 20 varieties of *C. moschata* into geographical subspecies. This classification reflects several centres of diversity of *C. moschata* such as Columbia, Japan, Mexico, Central America, the western United States, Florida, India and Asia Minor. Gwanama, Labuschagne and Botha (2000), using random amplified polymorphic DNA analysis, elucidated the relationship between 31 landrace genotypes obtained from Malawi and Zambia. That analysis revealed four clusters, with genotypes from Malawi mainly grouping in three clusters, while all genotypes from Zambia and three from Malawi clustered in another group.

That *C. moschata* has a closer affinity to the *Argyrosperma* group taxa than to other *Cucurbita* species has been argued from floral, seed and ecological similarities, and the fact that these species are partially interfertile (Merrick, 1995, 1990). Sanjur et al. (2002) confirmed this relationship through mitochondrial *nad1* gene sequence analysis.

Cucurbita ficifolia

C. ficifolia has been subject to less scientific scrutiny aimed at elucidating taxonomic relationships within the species than other cultivated *Cucurbita*. The species is reproductively incompatible with the other species of the genus and shows far less variability than the other species of the genus. The scant morphological variation of this species is consistent with the limited variability in the pattern of isozymes studies conducted so far (Andres, 1990). It has no associated wild ancestor in studies to date (e.g. Sanjur et al., 2002).

Work by Sajur et al. (2002) examining a sequence of an intron region from the mitochondrial gene *nad1*, and work by Wilson, Doebley and Duvall (1992) using chloroplast restriction fragment length polymorphism, suggest that *C. ficifolia* is basal to all other mesophytic *Cucurbita* species. More work is needed to decipher the relationship of *C. ficifolia* to the xerophytic species of the genus with which it shares some morphological features.

Centres of origin and distribution

All of the *Cucurbita* are native to the Americas. The centres of origin and domestication for cultivated *Cucurbita* species can be identified as various areas in North and South America (Jeffrey, 1990). Table 2.1 lists the natural distribution for both cultivated and wild *Cucurbita* species. At least five species of the genus *Cucurbita* were domesticated before the European contact in the late 15th century, forming important food sources in Native American economies, and some of these species were among the earliest plants taken under cultivation and domestication in the New World (Smith, 2001; Sanjur et al., 2002).

Cucurbita argyrosperma

The natural distribution of *C. argyrosperma* ranges from the southwestern United States through Mexico into Central America (Table 2.1). The area of domestication for *C. argyrosperma* is considered to be from the southwestern United States to the centre-south region of Mexico (Merrick and Bates, 1989). Archaeological remains of *C. argyrosperma* found from southwestern United States to the centre-south region of Mexico suggest that domestication of this species occurred in the region several thousand years ago (Table 2.2). Unlike the other cultivated *Cucurbita* species, data on the distribution of *C. argyrosperma* outside the Americas are scarce and there is some question as to whether this species was cultivated at any time in other parts of the world. Today, it is cultivated primarily in South America, Mexico, and on very limited areas in the United States.

Cucurbita ficifolia

The natural distribution of *C. ficifolia* ranges from the Mexican highlands south to northern Chile and Argentina (Table 2.1). It grows as an annual in temperate climates and can appear to be a perennial in tropical zones. The precise location of the centre of domestication of *Cucurbita ficifolia* is still uncertain. Some have proposed that its centre of origin is Central America or southern Mexico/Central America. Linguistic evidence tends to support this hypothesis because of the wide use of names based on the Nahuatl name "*chilacayohtli*" as far south as Argentina. Others suggest that its centre of domestication is located in South America and, more specifically, in the Andes (Nee, 1990). Andres (1990) compared diverse types of evidence and was not able to determine precisely the probable domestication site of this crop. So, while native names from indigenous Nahua influence like "*chilacayote*" and "*lacayote*" suggest a Mexican origin, systematic evidence has been inconclusive because a strong reproductive incompatibility has been found between *C. ficifolia* and the wild taxa of *Cucurbita* native to Mexico. While archaeological evidence favours a South American origin since the most ancient remains have been found in Peru (Table 2.2), it has not been possible to support this evidence by means of systematic studies, including those involving the two wild South American taxa (*C. maxima* ssp. *andreana* and *C. ecuadorensis*) as both prosper in habitats different from those in which *C. ficifolia* is cultivated (Nee, 1990). Also, the bee *Peponapis atrata*, until recently considered a pollinator specific to *C. ficifolia*, has not been found in South America. *Cucurbita ficifolia* differs in its karyotype from all other taxa of the genus and is always clearly separated in analyses with various molecular markers (Weiling, 1959; Andres, 1990; Wilson, Doebley and Duvall, 1992; Sanjur et al., 2002). All of these data have led to the proposition that the wild ancestor of *C. ficifolia* could be an undiscovered (or possibly extinct) species from South America (Andres, 1990; Nee, 1990; Sanjur et al., 2002). Although archaeological records show that it was the most cultivated *Cucurbita* species in the Americas prior to the European contact (Bisognin, 2002), currently *C. ficifolia* is the least cultivated of the *Cucurbita* species in the Americas. In the 16th and 17th centuries, Europeans introduced *C. ficifolia* to the Mediterranean countries (specifically France and Portugal) and India. It was also spread to other parts of the world and picked up other names, e.g. shark skin melon in Asia, Malabar gourd in India, and pie melon in Australia and New Zealand.

Table 2.2. **Synthesis of archaeological records of cultivated species of *Cucurbita***

C. argyrosperma	*C. ficifolia*	*C. maxima*	*C. moschata*	*C. pepo*
– Valley of Tehuacán, Puebla, Mexico (before 5200 BCE) – Ocampo, Tamaulipas, Mexico (200-900 CE) – Southwest United States (380-1340 CE) – Zape River, Durango, Mexico (700 CE)	– Huaca Prieta, Peru (2700-300 BCE) – Casma Valley, Peru (2000-1500 BCE) – North of Belize and Tikal, Guatemala (remains of doubtful identification) (2000 BCE-850 CE) – Valley of Oaxaca, Mexico (700 CE)	– Casma Valley, Peru (2000-1500 BCE) – Viru Valley, Peru (1800 BCE-600 CE) – Pampa Grande North of Argentina (500-1000 CE) – Ica, Peru (500-1400 CE) – San Nicolás, Peru (1200 CE)	– Ocampo, Tamaulipas and Valley of Tehuacán, Puebla, Mexico (4900-3500 BCE) – Huaca Prieta, Peru (2700-300 BCE) – North of Belize and Tikal, Guatemala (2000 BCE-850 CE) – Valle Casma, Peru (500 BCE) – Southwest United States (300 BCE) – Viru Valley, Peru (600-1100 CE) – Chincha, Peru (1310-1530 CE) – Great Plains, west of the Mississippi River, United States (1700 CE)	– Valley of Oaxaca (8750 BCE-700 CE) – Ocampo, Tamaulipas (7000-5000 BCE) – West-Center, Illinois (5000-2000 BCE) – Ozark Highlands, Missouri, United States (4000 BCE) – West of Kentucky, United States (3000-600 BCE) – Philips Spring, Missouri, United States (2300 BCE) – Valley of Tehuacan, Mexico (2000-1000 BCE) – Southwest United States (300 BCE) – Zape River, Durango, Mexico (600-700 CE) – Edzna, Campeche, Mexico (850 CE) – Great Plains, west of the Mississippi River, United States (1400 CE)

Source: Adapted from Lira, Andres and Nee (1995).

Cucurbita maxima

The natural distribution of *Cucurbita maxima* is comprised of Argentina, Bolivia and Chile (Table 2.1). *C. maxima* was domesticated in South America. Historical chronicles indicate that during the time of the conquest of Río de La Plata (16th century), this species was one of the main crops of the Guaraní people living in what is now northeastern Argentina and Paraguay (Parodi, 1935). Then, as now, there were many variants under cultivation in the Andean valleys (Cárdenas, 1944). Archaeological evidence for *C. maxima* uses and domestication has been found from Peru to northern Argentina as shown in Table 2.2. The wild species that have shown higher genetic affinity or otherwise are more similar to this crop (Puchalski and Robinson, 1990; Wilson, Doebley and Duvall, 1992; Sanjur et al., 2002) are *C. maxima* ssp. *andreana*, endemic to Argentina and Uruguay (Martínez-Crovetto, 1974; 1965; 1954), and *C. ecuadorensis*, known only from the coast of Ecuador (Cutler and Whitaker, 1969; Nee, 1990). *C. maxima* ssp. *andreana* is the most probable wild ancestor of this crop (Millán, 1945; Fursa and Filov, 1982; Nee, 1990; Sanjur et al., 2002).

From the 16th century, several types of *C. maxima*, such as the turban type, were transported directly from South America to Europe. Many other cultivars reached Australia, Africa and Asia, where local landraces evolved. In the 19th century, several cultivars were introduced into the United States from South America (Decker-Walters and Walters, 2000). Secondary centres of diversity include Bangladesh, Burma, India and the southern Appalachians of the United States, e.g. the landrace "Candy Roaster" was originally developed by the Cherokee people in the southern Appalachians. These findings suggest that for *C. maxima*, in addition to the regions of South America mentioned above, multiple centres of diversity, primarily composed of landraces, exist around the world.

Cucurbita moschata

The natural distribution of *Cucurbita moschata* is from the lowlands of Mexico into Central America (Table 2.1). *Cucurbita moschata* was domesticated in Latin America (Whitaker, 1947) but there is no consensus as to the precise area where domestication likely occurred. It has been proposed that *C. moschata* was domesticated in Mesoamerica (Whitaker and Davis, 1962) or alternatively in South America, more specifically in what is now Colombia. However, available evidence has been difficult to interpret and the centre of origin/domestication question is still open to debate. The oldest archaeological remains of *C. moschata* (4900-3500 BCE) have been recovered from the Ocampo caves, in the state of Tamaulipas, in northeast Mexico; however, very early dates have been registered for several localities in Central America (2000 BCE-850 CE) and South America (2700-300 BCE; Table 2.2). One of the main arguments against the South American origin hypothesis is that *C. moschata* is capable of producing highly fertile hybrids with the wild taxa of the *C. argyrosperma* group (Merrick, 1990), which has an identified centre of origin from the southwestern United States to the centre-south of Mexico. Morphological and ecological studies as well as comparative mitochondrial, ribosomal and chloroplastic analyses (Wilson, Doebley and Duvall, 1992; Jobst, King and Hemleben, 1998; Sanjur et al., 2002) suggest that the ancestor of *C. moschata* might have derived from a wild taxon of *C. argyrosperma* ssp. *sororia*. However, *C. moschata* and *C. argyrosperma* have different isoenzymatic patterns (Sanjur et al., 2002). Although studies by Merrick (1990, 1991) and Sanjur et al. (2002) support a high level of relatedness between *C. moschata* and members of the *Argyrosperma* group, these authors do not support the possibility of the ancestor being the subspecies *sororia*. *C. lundelliana* has also been proposed as the *C. moschata* ancestor, and that wild taxon is indigenous to the Yucatan Peninsula in Central America (Whitaker, 1974). However, there are several morphological differences between *C. lundelliana* and *C. moschata* (i.e. the greenish-grayish-blue seed colour in *C. lundelliana* has not been seen in *C. moschata*). Results from molecular biology studies (Puchalski and Robinson, 1990; Wilson, Doebley and Duvall, 1992) have also lent evidence to exclude *Cucurbita lundelliana* as a possible ancestor. Some characteristics associated with *C. moschata* have been identified in landraces from Bolivia, Columbia and Panama (e.g. dark-coloured seeds, small fruits, a lignified and warty rind; Wessel-Beaver, 2000b), suggesting hybridisation between *C. moschata* and wild local species in Columbia (Nee, 1990). Based on these sets of information, some authors have suggested the existence of two independent domestications, one in Mexico and the other in northern South America. This hypothesis is supported by linguistic evidence – i.e. *C. moschata* is known by native names specific to the language used in each region (Lira, Andres and Nee, 1995; Robinson and Decker-Walters, 1997; Decker-Walters and Walters, 2000).

After its domestication, it is likely that *C. moschata* spread through the Caribbean Islands, giving rise to various native cultivars (Robinson and Decker-Walters, 1997; Piperno, Andres and Stothert, 2000). After the European contact, *C. moschata* was spread rapidly to other continents, adapting to different ecological conditions. *C. moschata* was being cultivated at the end of the 17th century in western Mississippi (United States), and in the 19th century in Angola, India, Java, Northern Africa and Japan, where the species diversified (Sauer, 1993; Lira, Andres and Nee, 1995; Decker-Walters and Walters, 2000). Wu et al. (2011) report the existence of 1 032 landrace accessions of *C. moschata* in the People's Republic of China, hereafter "China"), reflecting a large diversity in landraces developed in China. *C. moschata* accessions are among the best represented *Cucurbita* accessions at the genebank of the Center for the Conservation and Breeding of Agricultural Diversity (COMAV) at the Polytechnic University at Valencia, Spain with a strong representation of landraces still cultivated under traditional cropping systems (Esteras et al., 2008). In Spain the cultivation of this species is mainly based on landraces maintained for centuries. Ferriol et al. (2004) examined 47 COMAV accessions from the Spanish peninsula, the Canary Islands, and Central and South America. The morphological characterisation showed considerable variability. Molecular analysis using amplified fragment length polymorphism and sequence related amplified polymorphism markers showed a genetic variability concordant with the morphological variability (Ferriol et al., 2004). In addition, *C. moschata* is the best represented *Cucurbita* in gene banks of the Americas (e.g. Center for International Food and Agricultural Policy [CIFAP] in Mexico). *C. moschata* is also one of the most important vegetables cultivated in Malawi, Zambia and tropical Africa, where its cultivation is mainly based on landraces with a high degree of autogamy (Gwanama, Labuschagne and Botha, 2000). These landraces have adapted to a variety of climatic conditions and soil types (Gwanana, Labuschagne and Botha, 2000). In general, *C. moschata* is the most widely cultivated *Cucurbita* in the tropics, where it is primarily grown on a small-scale basis for local consumption (Andres, 2004). These findings indicate that for *C. moschata*, in addition to the diversity seen in the Americas, multiple centres of diversity, primarily composed of landraces, exist around the world.

Cucurbita pepo

The natural distribution of *C. pepo* ranges from the eastern United States north into the state of Illinois through the Mississippi Valley, through the state of Texas and south into Mexico (Table 2.1). The archeological record, summarised in Table 2.2, shows that *C. pepo* initially became a fundamental element of agriculture in the Americas in the highlands of Mexico thousands of years ago (Smith, 1986). The most ancient remains of this species have been found in the Valley of Oaxaca (8750 BCE-700 CE) in the Ocampo caves, in the state of Tamaulipas in northeast Mexico (Table 2.2). The appearance of *C. pepo* in the United States as a domesticated crop also dates back thousands of years (King, 1985) as supported by the archaeological record which indicates *C. pepo* was being used by native populations thousands of years ago (7000-5000 BCE; Table 2.2) in what is now west central Illinois (United States). According to archaeological records, *C. pepo* appears to be one of the first domesticated species of *Cucurbita*, with a domestication even older than that attributed to other important domesticated crops:

C. pepo domestication appears to have predated that of other American crops such as maize (*Zea maize*) and common beans (*Phaseolus vulgaris*) by some 2 000 to 5 000 years (Smith, 2006). The archeological record shows that *C. pepo* was cultivated in different ecological niches in the Americas from the high plains to fluvial systems.

The archaeological record suggests that *C. pepo* was domesticated on at least two occasions and in two different regions of North America: in Mexico and in the United States (Decker, 1988, 1986; Andres, 1987a). The hypothesis of two domestication events is supported by the grouping of allozymic patterns of the cultivated forms (Decker, 1985). The hypothesis is also supported by additional allozymic assays, comparisons of chloroplastic and mitochondrial DNA, as well as random amplified polymorphic DNA markers (Kirkpatrick and Wilson, 1988; Wilson, Doebley and Duvall, 1992; Decker-Walters et al., 1993, 2002; Sanjur et al., 2002). As evidence has accumulated, it has become clear that *C. pepo* is comprised of two molecularly divergent groups that had already differentiated through geographical isolation long before humans domesticated them (Decker-Walters et al., 1993, 2002; Smith, 2006). These two divergent groups are classified as two subspecies: *C. pepo* ssp. *pepo* and *C. pepo* ssp. *ovifera*. *C. pepo* ssp. *pepo* includes pumpkin, zucchini and other marrow squashes, Mexican landraces and a few ornamental gourds. *C. pepo* ssp. *ovifera* comprises both domesticated and free-living populations, and is further divided into three taxonomic varieties: *C. pepo* ssp. *ovifera* var. *ovifera* which includes some cultivated cultivars (e.g. acorn, crookneck and scallop squash) and most ornamental gourds, and the free-living populations in the United States, which represent two molecularly distinct populations: *C. pepo* ssp. *ovifera* var. t*exana* and *C. pepo* ssp. *ovifera* var. *ozarkana* (Decker-Walters et al., 1993, 2002). *C. pepo* ssp. *ovifera* appears to have been domesticated in what is now the United States, while *C. pepo* ssp. *pepo* appears to have been domesticated in Mexico (Sanjur et al., 2002).

With regard to the likely ancestor(s) of the cultivated *C. pepo*, the three most closely related wild relatives are: *C. pepo* ssp. *fraterna* which is found in Mexico, and *C. pepo* ssp. *ovifera* var. *texana* and var. *ozarkana* which are found in the United States. *C. pepo* ssp. *fraterna* is known only from a few localities in the states of Tamaulipas and Nuevo León in the northeastern region of Mexico (Bailey, 1943; Andres 1987a; Nee, 1990; Rodríguez and Lira, 1992; Wilson, Lira and Rodríguez, 1994). *C. pepo* var. *texana* and var. *ozarkana* have distribution patterns associated with drainage patterns of the river systems that lead from the central United States to the Gulf of Mexico (Smith, 1992; Asch and Sidell, 1992; Wilson, 1998; US Department of Agriculture, 2011a).

With regard to the probable ancestor of *C. pepo* ssp. *ovifera*, Sanjur et al. (2002), on the basis of sequence analysis of and intron of the mitochondrial gene *nad1*, suggest that *C. pepo* ssp. *fraterna* is the most probable ancestor of *C. pepo* ssp. *ovifera*. In the Sanjur et al. studies (2002), *C. pepo* ssp. *fraterna*, *C. pepo* ssp *ovifera*, *C. pepo* ssp. *ovifera* var. *texana* and var. *ozarkana* form a group and share the same haplotype. Smith (2006), however, posits that although the analysis of the *nad1* mitochondrial gene in the studies by Sanjur et al. (2002) could not distinguish between these taxa, random amplified polymorphic DNA data (Decker-Walters et al., 2002; 1993) was able to separate ssp. *fraterna* from ssp *ovifera* var. *texana* and var. *ozarkana* and effectively excluded ssp. *fraterna* from the cluster that includes all cultivated and wild varieties of ssp. *ovifera*. Further support for excluding ssp. *fraterna* from potential contention as an ancestor of ssp. *ovifera* is provided by a recent genetic study employing amplified fragment length polymorphism, inter simple sequence repeat and simple sequence repeat markers, in which ssp. *fraterna* was placed at a greater genetic distance from the domesticates of ssp. *ovifera* than the eastern North American wild gourds (Paris et al., 2003). Smith (2006) and others (Emshwiller, 2006; Rieseberg and Harter, 2006) therefore argue that *C. pepo* ssp. *ovifera* var. *ozarkana* is the most likely ancestor of cultivated *C. pepo* ssp. *ovifera*.

With regard to the possible wild ancestor of *C. pepo* ssp. *pepo*, some authors consider it unknown or extinct (Wilson, Doebley and Duvall, 1992; Decker-Walters et al., 2002). That *C. pepo* ssp. *fraterna* is found on the muddy or volcanic plains of northeastern Mexico supports the suggestion that it might be the ancestor. Sanjur et al. (2002) suggest that *C. pepo* ssp. *fraterna* could have existed in the past in small and half-isolated populations which were genetically divergent, and some *C. pepo* ssp. *fraterna* population still not collected could be the possible ancestor of *C. pepo* ssp. *pepo*. Morphometric and molecular research, as well as studies on artificial and spontaneous hybridisation support *C. pepo* ssp. *fraterna* as a closely related wild relative. Nonetheless, at this time, no *C. pepo* ssp. *pepo* ancestor has been identified.

Today, populations composed of *C. pepo* wild relatives, *C. pepo* ssp. *fraterna*, *C. pepo* var. *texana* and *C. pepo* var. *ozarkana*, range from northeastern Mexico through the state of Texas, east to the state of Alabama and north through the Mississippi Valley to the state of Illinois in the United States. They occupy a diversity of environments and ecological niches – from upland seasonally dry thornscrub habitat in northeastern Mexico to primarily riverbanks and moist thickets in Texas, to a variety of riparian and other disturbed lowland habitats (e.g. agricultural fields, railroad tracks and highway embankments) throughout the Mississippi Valley. Different morphological and physiological adaptations have evolved in these areas, including early fruit abscission from the peduncle in response to riverine dispersal in the state of Texas, as well as relatively quick seed germination in response to a shorter growing season in the more northerly populations (Decker-Walters et al., 1993). In North America, *C. pepo* is a morphologically and ecologically diverse species composed of genetically distinct groups of cultivars and free-living populations (i.e. self-sustaining wild populations), all of which are interfertile.

Following its domestication, *C. pepo* experienced great diversification in the Americas and subsequent to the European contact, in Europe and Asia (Decker, 1988). That several cultivars were known in the Americas prior to the European contact is demonstrated by the great variability found in the first European herbaria (Whitaker, 1947; Paris, 2001, 1989). The various forms of *C. pepo* which were geographically isolated in the Americas were brought together and cultivated together in European gardens where hybridisation unavoidably occurred to produce new recombinants (Paris, 1989). *C. pepo* accessions are, for example, among the best represented *Cucurbita* accessions at the genebank of the COMAV at the Polytechnic University at Valencia Spain. Landraces still cultivated in Europe under traditional cropping systems (Esteras et al., 2008) are well represented (see also Aliu et al. [2011] for a description of *C. pepo* landrace diversity in the Balkans). The Newe Ya’ar Research Center in Israel maintains a *C. pepo* collection with 320 accessions collected almost entirely from North America, Europe and Asia (Paris, 2011). *C. pepo* is planted in all countries of Africa on a limited scale, even though it is less tolerant of tropical conditions than *C. moschata* (Grubben, 2004). Landraces or traditional varieties are maintained in traditional cropping systems in Mexico and the northern region of Central America, and the variation of this species in rural communities, at least in Mexico and Central America (mainly Guatemala), is also large. It includes variants which are cultivated at altitudes above 2000 m (during the rainy season or even the dry season on land that remains wet), and still others that can grow near the sea and in even more extreme conditions (i.e. those found on the Yucatan Peninsula). On the other hand, it is common for small farmers in Latin American to manage, in common plots, a fair representation of races or local varieties with morphological features similar to those that have been considered specific to some groups of commercial cultivars. *C. pepo* accessions are well represented in genebanks of the Americas (e.g. CIFAP). As with *C. maxima* and *C. moschata*, in addition to the diversity seen in the Americas, multiple centres of diversity exist for *C. pepo*, primarily as landraces, around the world.

Morphological characters

Cucurbita is a genus of dicotyledonous flowering plants in the family *Cucurbitaceae.* The wild and cultivated species of *Cucurbita* are trailing or climbing vines, or subshrubs (bushes) in some cultivated varieties. The cultivated and wild mesophytic species are annuals or such long-lived annuals to be seen as short-lived perennials. The xerophytic species are perennials, persisting for years due to their long tap roots. Mature stems are approximately 1 cm thick, but considerably thicker at the base of the plant. Cultivated forms have internodes that are usually 15-25 cm long, with petioles having a similar range of length and leaf laminae that are generally pentagonal in outline, ranging to 30 cm diameter or more. Wild forms have more diminutive vegetative parts. Emerging from the leaf axil are solitary branched tendrils 20 cm long and solitary flowers. Wild and cultivated species of *Cucurbita* are mostly monoecious, i.e. both male and female flowers are produced by a single plant, the exception being *C. foetidissima*, where some varieties are gynomonoecious. The large flowers are gamopetalous with tubular-campanulated corollas, very showy, light yellow or bright yellow-orange in colour. Rooting commonly occurs at the stem nodes. Some varieties produce tendrils that help secure vines, limit wind damage and improve vine growth across weedy and uneven ground.

For purposes of identification, the five domesticated species are differentiated by the following morphological characteristics: habit of growing, stems, leaves (in distal nodes), indument (petioles and primary veins in the lower surface of blades), receptacle (in staminate flowers), corolla, filaments, peduncle of fruit, size and shape of fruit, surface of fruit, colour of fruit, pulp of fruit, seeds (shape and size), and colour of seeds. Table 2.3 shows only the most outstanding features of the cultivated species. A complete treatment (descriptions, synonyms, illustrations, distribution maps, etc.) of *Cucurbita* is available in Lira, Andres and Nee (1995). Note, however, that cultivated species of *Cucurbita* are very diverse locally, regionally and worldwide (e.g. Jeffrey, 1990; Nee, 1990; Lira, Andres and Nee, 1995; Sanjur et al., 2002), having a wealth of innumerable strains, landraces and varieties that defy facile description (Esquinas-Alcazar and Gulick, 1983; Lira, Andres and Nee, 1995). As more plants are considered, the array of variations and combinations of notable traits increases and the differentiations become less distinct and meaningful.

This section and Annex 2.A2 offer examples of cultivars available in the retail seed market ("commercial" cultivars) for four of the five cultivated *Cucurbita* species; commercially available cultivars for *C. ficifolia* are scarcely found, but some are available online, e.g. from heirloom seed vendors.

Table 2.3. **Principal morphological characters that generally differentiate the domesticated species of *Cucurbita***

	C. argyrosperma	*C. ficifolia*	*C. maxima*	*C. moschata*	*C. pepo*
Stems	Rigid, angulated and sulcated	Rigid, angulated and only slightly sulcated	Soft, rounded or slightly angulated in lateral view, not sulcated	Rigid, angulated and only slightly sulcated	Rigid, angulated and sulcated
Leaves (in distal nodes)	Generally deeply lobed, but not palmatifid with the terminal lobe pinnatifid	Moderately lobed, rounded	Not lobed or only occasionally very slightly so	Never or very rarely with lobed acute or rounded lobes	Generally deeply lobed almost palmatifid with the terminal lobe pinnatifid, rounded or acute
Indument (petioles and primary veins in the lower surface of blades)	Soft and shortly pubescent to pilose	With short glandular hairs that stain dark brown or black	Hirsute to hispid, aculeate, but not conspicuously speculate	Soft, short to long pubescent or villous	Sometimes spiculate with persistent, conic bases of the hairs, strongly aculeate
Peduncle of fruit	Rigid, angulated to non-angulated except where it joins the fruit, smooth or costate, frequently very thickened, becoming cylindrical, claviform or subglobous	Rigid, angulate with obtuse ribs, without obtuse lobes and moderately widened where it joins the fruit, the ribs not having to extend or spread towards the apex of the fruit	Rigid or soft, cylindrical, not angulate, with irregular suberous strias, commonly not widening where it joins the fruit	Rigid, angulate with obtuse ribs, with obtuse lobes and notably widened where it joins the fruit, the ribs not tending to extend or spread towards the apex of the fruit	Rigid, angulate, with acute ribs, widened where it joins the fruit, the ribs sometimes more or less tending to extend or spread towards the apex of the fruit
Colour of the seeds	Usually white, sometimes dull white, tan; margins the same colour as the centre of the seed or a little darker, sometimes yellowish to golden, not fibrillous to very slightly so, or greenish, grayish, blue	Black or brownish-black, less commonly dull white or tan when mature; margins the same colour as the centre of the seed, sometimes lighter particularly near the apex	White to tan; margins usually of different colour than the centre of the seed (never greenish, grayish, blue), except in the white ones	White, dull white to tan or dark brown; margins usually of different colour than the centre of the seed, but never greenish-grayish-blue, usually yellow to golden and fibrillous or fimbriate	Dull white to tan; margins the same color as the centre of the seed

Source: Adapted from Lira, Andres and Nee (1995).

Cucurbita argyrosperma

There is less variation within *C. argyrosperma* as compared to other cultivated species of the genus such as *C. pepo, C. maxima* or *C. moschata*, as *C. argyrosperma* is limited for the most part to races or local varieties that are cultivated in the southwestern United States, Mexico and Central America, plus several commercial cultivars which have been developed mainly in the United States, such as “green striped cushaw”, “white cushaw”, “magdalena striped”, “papago”, “Japanese pie”, “hopi”, “taos”, “parral cushaw”, “Veracruz pepita” and “silver seed gourd”. The most important variations observed between these cultivated varieties correspond to the dimensions, shape and colour patterns of fruits and seeds.

Cucurbita ficifolia

Cucurbita ficifolia is by far the least variable species of the cultivated *Cucurbita.* Morphologically, the most important variation is in colour patterns (white to green fruits with colour patterns: spots or white stripes, and tan to dark brown or black seeds), and dimensions of fruits and seeds. Its relatively low morphological variation coincides with that observed regarding isoenzymatic patterns (Andres, 1990). However, including

South American populations in the survey may uncover wider genetic diversity (e.g. collections with differential resistance to viral diseases have been identified). Field observations have shown that some average-sized fruits contain more than 500 seeds, and that each plant can produce numerous fruits (Lira, Andres and Nee, 1995).

Cucurbita maxima

Cucurbita maxima is one of the most diversified cultivated species of the genus. Its variation includes numerous races and local varieties, and many commercial cultivars, some edible and some ornamental, with trailing and subshrub habits, and with fruits and seeds that are sometimes unique in dimension, shape and colour. Some varieties have also proven to have various degrees of resistance to several viral diseases (Tapley, Enzie and Van Eseltine, 1937; Millán, 1947; Martínez-Crovetto, 1974, 1965; Rochelle, 1974; Maluf and Souza, 1984). A total of 52 cultivars of this species were described by Tapley, Enzie and Van Eseltine in 1937. These cultivars differ not only in morphological characteristics, but in aspects of agronomic interest, such as duration of the life cycle, productivity and, in some cases, in their ability to adapt to limiting ecological conditions.

Castetter (1925) and others (Whitaker and Davis, 1962; Robinson and Decker-Walters, 1997; Decker-Walters and Walters, 2000) have addressed the diversity displayed by *C. maxima* forms, and several types have been identified. The "Banana" type includes long fruits which are pointed at both ends, with a soft rind and brown seeds. The fruits of the "Delicious" type are turbinate-shaped and have shallow ribs, a hard rind and white seeds and a high-quality flesh. The "Hubbard" type includes oval fruits, with pointed or curved ends, a very hard rind and white seeds. Fruits of the "Show" type are wide and orange coloured with a smooth rind and white seeds. A wide variability in this type is seen in India. The "Turban" type contains turban shaped fruits. Most *C. maxima* fruits are eaten at maturity as the fruit is of high quality. However, fruits of the "Marrow" type are picked a few days post-anthesis for consumption, have a soft skin, are oval or pear shaped, bulbous and have white seeds (see Annex 2.A2 for additional information on horticultural types).

Of particular interest among *C. maxima* are varieties of the Mammoth group in the "Show" type ("Mammoth Chilli" or "Mammoth Whale") whose fruits reach gigantic dimensions. Some *C. maxima* fruits exceeding 450 kg in weight have been documented. Also impressive are the turbinate fruits like "French Turban" and "Turks Cap".

Cucurbita moschata

Cucurbita moschata also displays striking morphological variation: the variation of its fruits (colours, shapes and widths, and the durability of the fruits, shell, etc.) and seeds, the number of variants with life cycles of different length, the existence of numerous cultivars developed in various parts of the world, and the existence of races and local varieties with outstanding agronomic characteristics, suggest the extensive genetic variation of this species. Some examples of interesting regional variants are found in the Yucatan Peninsula (and possibly in other regions of Latin America), with two life cycles of different length (Lira, 1988; 1985), as well as the variants grown in some Mexican states (e.g. Chiapas, Guanajuato), which have been found to be resistant to certain viral diseases, and which have been used in improvement programmes (Garzón-Tiznado, Montes-Hernández and Becerra, 1993; Gallegos, 1990). The most variation of fruit and seeds of *C. moschata* occur in Columbia (Wessel-Beaver, 2000b). During the 500 years of cultivation in China, *C. moschata* has adapted to different agro-ecological conditions, and now displays high variability for many agronomic characteristics, such as fruit shapes and colours, flowering habits, leaf characters, etc. (Du et al., 2011).

C. moschata fruits are generally harvested at maturity as the fruits possess a high-quality flesh. *C. moschata* is one of the most popular species for the large number and size of seeds. A few types have been identified. The "Cheese" type includes fruits that are variable in shape, mostly oblong, and have a leather-coloured rind. Fruits of the "Crookneck" type have a rounded distal end and a long curved or straight neck. The "Bell" type presents fruits with a shape that ranges from flared to almost cylindrical. Because *C. moschata* grows well in tropical areas, it is known as "Tropical pumpkin" (see Annex 2.A2 for information on horticultural types).

Cucurbita pepo

C. pepo also displays a very high level of striking morphological variation. *C. pepo* is perhaps the most variable species for fruit characteristics in the plant kingdom. Its fruit range in size to over 20 kg; in shape from round to flat-scalloped to long bulbous cylindrical over 75 cm long; exterior colour is based on hues of green, orange and yellow, with colour intensity ranging from very pale to intense, and a grey contribution ranging from none to very dark. Variegation, including striping and bicolour, can result in as many as four colours on the surface of the same fruit. Fruit mesocarp can be relatively thin or thick, and its colour varies in the range from greenish-white to white, yellow, light orange and intense orange. Fruit rinds can be lignified or non-lignified, and smooth, warted, wrinkled or netted. *C. pepo* not only includes commercial cultivars and edible races with diverse morphological and phenological characteristics, but also several cultivars that are used as ornamentals, e.g. "Orange Ball", "Miniature Ball" and "Striped Pear". Tapley, Enzie and Van Eseltine (1937) recognise 60 edible cultivars, including some with subshrub habits such as "Black Zucchini", "Fordhook Bush" and "Boston Greek", as well as others of trailing to climbing habits and edible fruits, e.g. "Connecticut Field" and "Table Queen". Several authors have proposed organisational groupings to reflect the possible origin and evolution of the high level of morphological variation seen in *C. pepo* (Castetter, 1925; Bailey, 1929; Paris, 1989). Paris (1986, 1989, 2001) grouped the cultivated types into eight morphotypes.

"Pumpkin" (*C. pepo* L. var. *pepo* L. Bailey) includes cultivars of creeping plants which produce spherical, ovoid or oblate fruit that is rounded or flat at the ends. The fruit of this group is grown to be eaten when ripe and is sometimes used as fodder. "Scallop" (*C. pepo* L. var. *clypeata* Alefield) has a semi-shrubby habit, the fruit ranges from flat to almost discoidal, with undulations or equatorial margins, and it is eaten before maturity. "Acorn" (*C. pepo* L. var. *turbinata* Paris) is both a shrubby and a creeping plant with fruit that is obovoid or conical, pointed at that apex and longitudinally costate-grooved. The rind is soft, hence the fruit can be eaten in the ripe state. "Crookneck" (*C. pepo* L. var. *torticollia* Alefield) is a shrubby type with yellow, golden or white fruit which is claviform and curved at the distal or apical end and generally has a verrucose rind. It is eaten unripe as the rind and fruit harden when ripe. "Straightneck (*C. pepo* L. var. *recticollis* Paris) is a shrubby plant with yellow or golden fruit and a verrocose rind similar to var. *torticolla*. "Vegetable marrow" (*C. pepo* L. var. *fastigata* Paris) has creeper characteristics as semi-shrub and has short cylindrical fruit that is slightly broader at the apex, with a smooth rind which hardens and thickens on ripening and which varies in colour from cream to dark green. "Cocozelle" (*C. pepo* L. var. *longa* Paris) has cylindrical, long fruit that is slender and slightly bulbous at the apex, it is eaten in the unripe immature state. "Zucchini" (*C. pepo* L. var. *cylindrica* Paris) is the most commonly cultivated group of cultivars at present. Like the previous group, the zucchini group has a strong affinity with the vegetable marrow and its origin is also recent (19th century). Its plants are generally semi-shrubby and its cylindrical fruit does not broaden or broadens only slightly. It is eaten as a vegetable in the unripe state (see Annex 2.A2 for information on horticultural types.) Taxonomically, the morphotypes "pumpkin", "vegetable marrow", "cocozelle" and "zucchini" are subspecies *pepo.* Some authors have categorised the morphotypes "Scallop", "Acorn", "Crookneck" and "Straightneck" as subspecies *ovifera* (also known as *C. pepo* ssp. *texana*, see e.g. Paris et al., 2003); however, this chapter, which is based on the nomenclature used by Lira, Andres and Nee (1995) and Lira Saade, Eguiarte Fruns and Montes Hernández (2009) and Gong et al. (2012), would group these morphotypes in *C. pepo* ssp. *pepo*. (Both groups are shown as *C. pepo* L. in Table 2.1).

Because of their small, hard shells, ornamental gourds are typically thought of as a distinct grouping within *C. pepo*. Isozymic evidence, however, shows this not to be true, with cultivars having originated in both subspecies *pepo* and *ovifera* and possibly in subspecies *fraterna* (Decker-Walters et al., 1993). What many of these cultivars do share in common are characteristics often ascribed to free-living populations, e.g. tough pericarps and bitter flesh, which ward off predation in the wild.

Reproductive biology

Cucurbita is a genus of dicotyledonous flowering plants in the family *Cucurbitaceae.* The cultivated *Cucurbita* are annual plants, long running and climbing, or short and bushy. The flowers are monoecious and numerous and very showy. Flowers open very early in the morning, and the predominant pollinators of these flowers are bees. In the Americas, the most efficient pollinators are the solitary bees of the genera *Peponapis* and *Xenoglossa* (Hurd and Linsley, 1970, 1976, 1964; Hurd, Linsley and Whitaker, 1971), but the flowers can also be pollinated by other bees such as the honey bee, *Apis mellifera*. Fruits are of the pepo type: a berry with numerous seeds surrounded by a fleshy wall that does not open at maturity. Production of flowers, fruits and seeds varies between species (Quesada et al., 1991).

Reproductive organs

Flower

Unisexual flowers are characteristic of the Cucurbitaceae. The *Cucurbita* species are primarily monoecious with both male and female flowers on the same plant (Whitaker and Robinson, 1986; Lira, Andres and Nee, 1995; Rzedowski and Rzedowski, 2001), although some varieties of *C. foetidissima* are gynomonoecious (Whitaker and Robinson, 1986).

Cucurbita flowers are large, gamopetalous with tubular-campanulated corollas, and showy, with a cream coloured or light yellow or bright-yellow orange corolla. Flowers grow from the axil of a leaf. Male flowers have column-like stamens, with free or more or less connivent filaments, and the anthers are joined together forming a cylindrical or narrowly pyramidal structure. Female flowers have an inferior ovary with numerous horizontally positioned ovules, the styles are fused in almost their entire length or are only shortly free in the apex; stigmas are large, fleshy or more or less sunken or lobulated, and slight modifications can be seen in the structure of the perianth regarding the staminate ones, mainly corresponding to differences in size of one or some of its parts (e.g. the receptacle is always much more reduced). After pollination, fruit develops from the pre-formed ovary at the base of the female flower. The shape of the ovary prior to pollination is indicative of the mature fruit shape.

Cross-pollination is favoured by the monoecious nature of the plants, and in some cases the male flowers are slightly larger than the female ones on the same plant. *Cucurbita* can exhibit wide variation in the proportion of male to female flowers on a plant (Janick and Paull, 2007). Zomlefer (1994) reported that production of female flowers is frequently less than that of male flowers. In *C. pepo*, Nepi and Pacini (1993) found a 16.5:1 relation between the number of male and female flowers. Temperature and light influence the production of male and female flowers in several of the species (Whitaker and Davis, 1962). More male flowers are produced on long and very hot days, whereas short and cold days induce the development of more female flowers (Robinson and Decker-Walters, 1997). The first flowers on the vine are male, after which three or four female flowers appear. Although female flowers differentiate later in plant development, females develop faster than the males, resulting in near synchronization at anthesis of the flowers of both sexes (Janick and Paull, 2007). Flowers open early in the morning and close around noon of the same day, never to reopen (Nepi and Pacini, 1993). Flowering time both in male and female flowers of *C. pepo* varies depending on the time of year in which the plants develop: male flowers begin to open 15 minutes before the female flowers when the days are longer. On days further along in the year this difference is not significant (Nepi and Pacini, 1993). Scheerens et al. (1987) found similarities on the daily opening time of flowers of *C. foetidissima* of both sexes. Whitaker and Robinson (1986) observed that in some genotypes, a short photoperiod is needed for flowering to begin, and flowers develop only when the days are short.

Flower development in Cucurbitaceae, apart from being regulated by genetic and environmental mechanisms such as temperature and the duration of days, can be modulated by chemical regulators – substances such as gibberellins and ethylene (Rudich, 1990). For example, ethylene is involved in the regulation of fruit ripening and sex expression and in the plant's response to herbivore damage.

Pollen

Cucurbita pollen grains are large and sticky, and well suited to transport by insects. Wind does not pollinate *Cucurbita* species. Ovules are fertile only during the period of flowering, or the day prior. Good fruit and set development requires 500-1 000 live pollen grains on the stigma of the female flower (Stephenson, Devlin and Horton, 1988; Vidal et al., 2010). Pollen viability in a newly opened male flower is about 92%, but by the time it closes that same morning the viability will have dropped to 75%, and by the next day will be only 10% (Nepi and Pacini, 1993). Environmental conditions at the time of anthesis are important. High or low temperature can result in a more rapid decrease in pollen viability. In addition, in windy, dry conditions, pollen can lose viability rapidly.

Fruit

Fruits of *Cucurbita* are of the pepo type: a berry with numerous seeds surrounded by a fleshy wall that does not open at maturity. Fruits have a thin and soft, or rigid and woody, shell that emerges from the outer layer of the ovary (exocarp), whereas the pulp around the seed is derived from the ovarian internal layers (mesocarp and endocarp). In cultivated plants, the fruits are produced in a great variety of shapes, sizes, colours and types of surface, whereas in wild plants they are all relatively small and relatively uniform regarding shape (globous, ovoid or rarely pyriform), surface (generally smooth or without ornaments) and colour (white, yellowish or green with or without spots and/or fringes; Lira, Andres and Nee, 1995). Some of them are among the largest in the plant kingdom.

Production of fruits varies between species. While producing 20-30 male flowers and 8-12 female flowers, cultivated plants of *C. pepo* generally produce 2-6 fruits (Quesada et al., 1991). Lira, Andres and Nee (1995) report that each plant of some domesticated varieties of *C. ficifolia* can produce numerous fruits. The wild species *C. pepo* var. *texana* commonly produces approximately 50 mature fruits by the end of the growing season (Avila-Sakar, Krupnick and Stephenson, 2001).

Flower, fruit and seed production, as well as the offspring's performance can be affected by environmental and genetic factors, and by paternal and maternal conditions. Work on the paternal effects on the offspring of cultivated plants of *Cucurbita pepo* has demonstrated that ovule fertilisation and seed production is non-random and depends on the origin of the paternal genotype (Quesada et al., 1991). Similarly, the strongest offspring are obtained from the stylar region of the fruit, where the ovules are fertilised by the most vigorous pollen grains. From research on the effects of pollen competition on the performance of the offspring using hybrids of cultivated *C. pepo* and *C. pepo* var. *texana*, Quesada, Winsor and Stephenson (1996, 1993), concluded that the offspring resulting from large amounts of pollen reaching styles are more vigorous than those produced when smaller amounts reach the styles. Apparently, competition between pollen grains leads to more successful seeds, progeny and their future flower production. The percentage of success in pollination (experimentally) is highest directly after the flowers have opened, and diminishes gradually as midday approaches (Whitaker and Robinson, 1986).

Increase in the size of the ovaries is noticeable within 24 hours of anthesis. Not all pistillate flowers develop into fruit, however, most often because many more flowers are produced than the plant can support nutritionally. Competition is strongest during the first week after anthesis. *Cucurbita* that are grown for consumption of the young fruit are harvested several days past anthesis. The time from anthesis to a fully mature fruit varies considerably among various *Cucurbita* species. Table 2.4 lists the phenology and life cycle in Mexico of 20 *Cucurbita* taxa.

Plants continue to flower and produce fruits consistently until killed by frost. In some papers, *Cucurbita ficifolia* is considered a perennial species (Dane, 1983), but Lira, Andres and Nee (1995) indicate that *C. ficifolia* is an annual species, which, depending on certain environmental conditions (i.e. not too severe frost) can live longer, giving the impression that it is a short-lived perennial. A similar phenomenon has been seen in *C. lundelliana* and *C. moschata*, which can keep on producing flowers and fruits for an extended period of time given appropriate conditions. On the other hand, because of frost, in some areas the perennial species behave as facultative annuals, dying in their first year (Whitaker and Robinson, 1986).

Fruit dispersal

The routes by which seeds are dispersed is determined largely by the size, shape and character of the seed coat or the persisting structures of the fruit. In the case of the *Cucurbita*, the persisting structure of the mature fruit, i.e. the gourd, can be buoyant in water. Hence, water represents a potential means of *Cucurbita* seed dispersal. In addition, the pepo type fruits may represent an adaptation for dispersal by animals, and animals also represent a means by which *Cucurbita* seeds are dispersed. Generally, this occurs through ingestion of fruits with seeds; with the seeds then being excreted at a distance from the initial point of ingestion. In many areas of the world, *Cucurbita* fruits are used as fodder. For example, in tropical regions, domestic animals such as donkeys and horses will consume *Cucurbita* L. fruits and vines when fodder is scarce at the end of the rainy season (Mariano and Dirzo, 2002).

Seed and germination

The seeds are surrounded by several layers of tissue. The most external layer derives from the internal epidermis of the carpel (endocarp) and generally swells with water; the internal layer derives from the testa (seed coat) and develops from the ovule's integument and nucellus (Zomlefer, 1994).

Table 2.4. **Phenology and life cycles of 20 *Cucurbita* taxa**

	Taxa	Phenological notes in Mexico
Annuals	*C. argyrosperma argyrosperma*	
	C. argyrosperma ssp. *sororia*	Flowers from June to January and begins to fructify in August, but it is more common to find mature fruits from November or December
	C. ficifolia	
	C. maxima	
	C. maxima ssp. *andreana*	Produces fruits in September and from February to April
	C. moschata	
	C. pepo ssp. *pepo*	
	C. pepo ssp. *fraterna*	
	C. pepo var. *texana*	Flowers and fruits between July and November
	C. ecuadorensis	It is possible to find male flowers and fruits between February and July
	C. lundelliana	It is possible to find populations with flowers of both sexes. Mature fruits are more surely found between November and February
	C. okeechobeensis ssp. *okeechobeensis*	Flowers and fruits between May-June and January, and the mature fruits from October onwards
	C. okeechobeensis ssp. *martinezii*	Flowers and fruits between June and January or February, and mature fruits can be found from October onwards
Perennials	*C. digitata*	Populations with flowers and fruits occur all year round
	C. cordata	Populations with flowers and fruits occur all year round
	C. palmata	Populations with flowers and fruits occur all year round
	C. foetidissima	Populations with flowers and fruits occur all year round
	C. pedatifolia	Flowers and fruits between August and November and mature fruits from October onwards
	C. radicans	Flowers and fruits between May-June and December, and the mature fruits from October onwards
	C. scabridifolia	Flowers and fruits from June-July and until December, and the fruits from August or September

Seeds are oval, oval-elliptical or oval-lanceolate, compressed or more or less tumescent or inflated, with a smooth or sometimes scarified or scarred centre which can be white, cream-colored, greenish-grayish-blue or black, with or without marked or differentiated margins, and these of the same or different colour and/or texture as the centre of the seed.

The number of seeds produced per fruit varies among the species. Lira, Andres and Nee (1995) report that some domesticated varieties of *C. ficifolia* have average-sized fruits with more than 500 seeds. *C. argyrosperma* produces more than 250 seeds per fruit (Merrick, 1990). The wild species *C. pepo* var. *texana* also can produce more than 250 seeds per fruit (Avila-Sakar, Krupnick and Stephenson, 2001).

Few studies deal with seed banks, germination and establishment of seedlings; nevertheless, in general terms, germination is high and rapid, and there is no seed bank or it is limited for most species. *Cucurbita* such as *C. argyrosperma* ssp. *sororia* can be opportunists, adapted to rapidly colonise available open spaces at the beginning of the rainy season. The colonisation strategy seems to be based more on the germination speed of the seeds produced during the last season than on the development of a seed bank in the soil. Under experimental conditions, 86-100% of the seeds of *C. argyrosperma* ssp. *sororia* germinate two to six days after they begin to hydrate. This germination is synchronic and begins with the first main rains that can keep the soil damp for more than one day (Mariano, 2001).

Sexual reproduction

Pollination

Among the *Cucurbita*, some agent – usually bees – is necessary to transfer pollen from the male to female flower; as the pollen is large (80 to 150 µm diameter) and sticky, the species of the genera are not wind pollinated. In the Americas, the solitary bees of the genera *Peponapis* and *Xenoglossa* (Hurd, Linsley and Whitaker, 1971; Canto-Aguilar and Parra-Tabla, 2000) have developed a close relationship with wild and cultivated *Cucurbita* plants – both adults and larvae feed almost exclusively on the nectar and pollen of the plants. Indeed, the bees are dependent on pollen and nectar produced by *Cucurbita* flowers for their survival (Hurd, Linsley and Whitaker, 1971), and appear to have co-evolved with the *Cucurbita* (Hurd, Linsley and Whitaker, 1971). These bees display some behaviours that appear to be adaptations to their interaction with the *Cucurbita*, e.g. an ability to fly at low temperatures, with low light intensity and certain modifications that allow for an adequate extraction and transportation of pollen. These bees often fly from flower to flower while still dark to see which flowers are open, apparently oriented by olfactory cues emitted by some of the species, and probably also with the help of visual and/or hearing sensors. Both the *Peponapis* and *Xenoglossa* are very efficient pollinators of the *Cucurbita* (Hurd, Linsley and Whitaker, 1971). The efficiency and specificity of these bees makes them responsible for moving larger amounts of pollen between wild and cultivated *Cucurbita* than any other group of pollinators.

Pollinators collect large amounts of nectar from the female flowers, and pollen and nectar from the male flowers. Nectar is secreted from a ring of tissue surrounding the style and just inside the perianth tube. When a bee forages in a masculine flower in search of nectar, the pollen adheres to the bee's body and will then be transferred to the stigmas when it visits female flowers (Zomlefer, 1994). The most active period for the bees coincides with the beginning of the plant's floral opening, just before daybreak, and this high level of activity is maintained for several hours (Mariano and Dirzo, 2002).

The hind legs of the bees of the genera *Peponapis* and *Xenoglossa* are adapted to the collection and manipulation of the pollen grains of this genus. However, the pollen grains vary in size and structure between the species and the pollen-collecting devices of the bees vary also (Hurd, Linsley and Whitaker, 1971). This variation between the bees has been shown to be species specific (Hurd and Lindsley, 1970), and apparently has profoundly influenced the ability of the different species of bees to collect and utilise pollens of the various *Cucurbita*, both wild and domestic (Hurd, Linsley and Whitaker, 1971; see Table 2.5).

In addition to *Peponapis* and *Xenoglossa* genera, other species of bees can pollinate plants of the genus *Cucurbita*. One of the most frequent pollinators in cultivation systems around the world is the domestic honeybee, *Apis mellifera* (Canto-Aguilar and Parra-Tabla, 2000; Mariano and Dirzo, 2002). While the bees of the genera *Peponapis* and *Xenoglossa* make more contact with the reproductive parts of the flower, work faster and work earlier in the morning, they are no more efficient than honey bees (*Apis mellifera*) at setting fruit (Tepedino, 1981). However, honey bees, in contrast to the solitary bees of the genera *Peponapis* and *Xenoglossa*, are generalists and readily move to any competing bloom that offers richer rewards. Also, early bee activity can be important on hot days when the flowers close early, and bees of the genera *Peponapis* and *Xenoglossa* are adapted to working early in the morning. In general, where *Peponapis* and/or *Xenoglossa* populations are strong, the use of honey bee colonies is superfluous as most pollination is accomplished by *Peponapis* and *Xenoglossa* bees before the honey bees arrive (Tepedino, 1981).

In addition to the bees of the *Peponapis* and *Xenoglossa* genera, bees of the *Bombus* genus, e.g. *Bombus impatiens*, have been identified in the United States as pollinators of *Cucurbita pepo* (Julier and Roulston, 2009).

Table 2.5 indicates the known species of pollinators that have been identified in wild and cultivated *Cucurbita* populations in Mexico and the species they are known to pollinate. *Peponapis* species are found from Ontario, Canada through the United States through Mexico to northern Argentina in South America (Michener, 2007). *Xenoglossa* species are found through the United States through Mesoamerica. The ranges of *Peponapis* and *Xenoglossa* species are similar in tropical regions of the Americas. Some species of *Peponapis* are also capable of surviving in temperate regions (thus their distribution extends from Canada to Argentina). In contrast, species of *Xenoglossa* have a more restricted distribution toward lower latitudes, but are capable of establishing in more desertic environments. *Megalopta* species are found in Mexico through the mid section of South America (Discover Life, 2011). *Melitoma* species are found in the central and eastern United States through Mexico to northern Chile and Argentina (Discover Life, 2011). Although most common in the northern hemisphere, *Bombus* species can be found around the world (Discover Life, 2011).

Hurd (1966) identified several insects other than bees that might play a minor role in pollination of *Cucurbita*: cucumber, scarab and meloid beetles, as well as flies and moths.

Asexual reproduction

The *Cucurbita* species propagate in nature through sexual reproduction as there is essentially no asexual propagation by means of runners or stolons, or apomixes in nature.

Genetics

The basic chromosome number of the *Cucurbita* is 2n = 2x = 40. Karyotypes suggest that these species are of allopolyploid origins. Results from electrophoretic analyses also helped confirm this genus' polyploidy (Kirkpatrick, Decker and Wilson, 1985), or more specifically, allotetraploid origin (Weeden, 1984). Weeden (1984) and Singh (1990) suggested that the *Cucurbita* are ancestral tetraploid, derived from an ancestor with a haploid chromosome number of ten. Although these authors suggest an apparent homogeneity, Weiling (1959) suggested that the genome in *Cucurbita ficifolia* is AACC (each letter refers to a different ancestral plant genome), whereas in the four remaining domesticated species it is AABB. A recent sequence analysis of an intron from the mitochondrial gene *nad1* indicated that *C. ficifolia* was basal to all other taxa in this group (Sanjur et al., 2002). Wilson, Doebley and Duvall (1992) determined that the annual *Cucurbita* species evolved from the perennial species.

Table 2.5. **Bee species pollinating *Cucurbita* species in Mexico**

Pollinators	References	*Cucurbita* species
Apis mellifera Linnaeus	Mariano and Dirzo (2002); Canto-Aguilar and Parra-Tabla (2000)	*C. argyrosperma*, *C. pepo*, *C. moschata*, *C. ficifolia*
Peponapis michelbacherorum Hurd & Linsley	Hurd, Linsley and Whitaker (1971)	
Peponapis utahensis Cockerell	Mariano and Dirzo (2002); Hurd, Linsley and Whitaker (1971)	*C. argyrosperma* ssp. *sororia*, *C. pepo, C. ficifolia*, *C. moschata*
Peponapis melonis Friese	Hurd, Linsley and Whitaker (1971)	
Peponapis fervens Smith	Hurd, Linsley and Whitaker (1971)	
Peponapis citrullina Cockerell	Hurd, Linsley and Whitaker (1971)	
Peponapis limitaris Cockerell	Hurd, Linsley and Whitaker (1971)	*C. argyrosperma*, *C. moschata*
Peponapis pruinosa Say	Hurd, Linsley and Whitaker (1971)	*C. argyrosperma* ssp. *argyrosperma*, *C. argyrosperma* ssp. *sororia*, *C. ficifolia*, *C. pepo*, *C. foetidissima*, *C. lundelliana*, *C. moschata*, *C. maxima*
Peponapis azteca Hurd & Linsley	Hurd, Linsley and Whitaker (1971)	*C. argyrosperma* ssp. *argyrosperma*, *C. argyrosperma* ssp. *sororia, C. pepo*, *C. foetidissima*, *C. ficifolia*, *C. lundelliana*, *C. moschata*, *C. maxima*
Peponapis smithi Hurd & Linsley	Hurd, Linsley and Whitaker (1971)	*C. ficifolia, C. argyrosperma, C. moschata*
Peponapis apiculata Cresson	Hurd, Linsley and Whitaker (1971)	*C. ficifolia*
Peponapis atrata Smith	Hurd, Linsley and Whitaker (1971;) Andres (1990)	*C. argyrosperma* ssp. *argyrosperma*, *C. ficifolia*, *C. pepo*, *C. moschata*, *C. maxima*
Peponapis timberlakei Hurd & Linsley	Hurd, Linsley and Whitaker (1971)	
Peponapis crassidentata Cockerell	Hurd, Linsley and Whitaker (1971)	*C. argyrosperma*, *C. pepo, C. moschata*
Peponapis angelica Cockerell	Hurd, Linsley and Whitaker (1971)	
Xenoglossa kansensis Cockerell	Hurd, Linsley and Whitaker (1971)	
Xenoglossa strenua Cresson	Hurd, Linsley and Whitaker (1971)	*C. pepo*
Xenoglossa angustior Cockerell	Hurd, Linsley and Whitaker (1971)	
Xenoglossa mustelina Fox	Hurd, Linsley and Whitaker (1971)	
Xenoglossa patricia Cockerell	Hurd, Linsley and Whitaker (1971)	*C. argyrosperma* ssp. *argyrosperma, C. digitata*, *C. foetidissima*, *C. pepo*, *C. moschata*, *C. maxima*
Xenoglossa fulva Smith	Hurd, Linsley and Whitaker (1971)	*C. argyrosperma* ssp. *argyrosperma*, *C. ficifolia*, *C. epo*, *C. moschata*, *C. maxima*
Xenoglossa gabbii Cresson	Mariano and Dirzo (2002); Hurd, Linsley and Whitaker (1971)	*C. argyrosperma* ssp. *sororia*, *C. ficifolia*
Megalopta sp.	Mariano and Dirzo (2002)	*C. argyrosperma* ssp. *sororia*
Melitoma marginella Cresson	Mariano and Dirzo (2002)	C. *argyrosperma* ssp. *sororia*

The morphology of the chromosomes is not well characterised as they are small and not easily differentiated (Weeden, 1984; Weeden and Robinson, 1990). Using flow cytometry, Arumuganathan and Earle (1991) determined that the haploid genome of zucchini (*C. pepo* ssp. *pepo*) is approximately 500 million base pairs long. A typical nucleus (2n) contains 1.04-1.08 picograms of DNA. Most morphological traits appear to be unlinked, and many markers are required to adequately map the genome. Havey et al. (1998) used restricted fragment length polymorphisms to study the transmission of the chloroplast and mitochondrial genomes in cucurbits. They concluded that both organelle genomes were maternally transmitted in *Cucurbita*.

Some work on self-incompatibility and inbreeding depression in the genus has been performed. Some authors have seen little evidence of inbreeding depression in members of the genus (Borghi, 1976). Others, however, have observed indications of inbreeding depression. Mahzabin, Parvez and Alam (2008) indicate that *Cucurbita maxima* shows abrupt inbreeding depression after two generations of selfing. Cardoso (2004) observed inbreeding depression affecting certain traits in a *Cucurbita moschata* variety after four successive self-pollination generations. Cardoso (2004) and Hayes, Winsor and Stephenson (2005a, 2005b) have studied inbreeding depression after four successive generations of self-pollination in *Cucurbita pepo* var. *texana*. In general, inbreeding depression seems to be intense, which suggests a level of genetic variation at least as recessive deleterious genes. The selfing rate showed a range from 0.16 to 0.54, but this might vary among characters, years and conditions (Hayes, Winsor and Stephenson, 2005a, 2005b). Whitaker and Robinson (1986) suggest these different observations might represent the response of different species or varieties of *Cucurbita* to inbreeding.

Molecular markers

A number of different genetic markers have been used to analyse the phylogeny of the genus. Wilson, Doebley and Duvall (1992) studied 15 species using chloroplast restricted fragment length polymorphism analysis and analysed the relationships between different cultivars of *C. pepo*. The cultivated species, with the exception of *C. ficifolia*, form a cluster, and the relationships among *C. moschata*, *C. argyrosperma* ssp. *argyrosperma* and *C. argyrosperma* ssp. *sororia* were not resolved. Jobst, King and Hemleben (1998) analysed the internal transcribed spacers of ribosomal DNA for 11 species of the genus, but the alleles between species are shared, possibly because they are species of very recent origin and/or because there is gene flow between species. Using ISSRs (inter-simple sequence repeats), Katzir et al. (2000) analysed *C. pepo* and discovered a clear differentiation between *C. pepo* ssp. *pepo* and *C. pepo* ssp. *ovifera* (as found in other studies) with *C. fraterna* clustering with *C. pepo* ssp. *ovifera*.

King, Jobst and Hemleben (1995) studied nuclear microsatellites in nine species of the genus. They suggested that *Cucurbita* (like most of the Cucurbitaceae) contains a large amount of satellite DNA. In particular, species of the genus *Cucurbita* contain interesting specific satellite DNA with individual variations among some species. Within *Cucurbita*, the genes coding for the ribosomal 18S, 5.8S and 25S rRNA are present in high copy numbers and appear highly methylated (Hemleben et al., 1988; King et al., 1993; Torres-Ruíz and Hemleben, 1994). Mitochondrial DNA is also specially structured and larger than in other angiosperms. Sanjur et al. (2002) analysed 65 individuals from 14 taxa (8 species of *Cucurbita* and 2 outgroups) with a mitochondrial *nad1* gene. They found 16 haplotypes. Four groups can be defined in the phylogenetic analysis: a basal group including *C. ficifolia*; a group composed of *C. foetidissima*; a group formed by *C. maxima*, *C. andreana* and *C. ecuadorensis*; and a large group with *C. okeechobeensis* ssp. *martinezii* at the base, including *C. pepo*, *C. argyrosperma* ssp. *sororia*, *C. argyropserma* ssp. *argyrosperma* and *C. moschata*. Six independent origins of domestication can be inferred based on this phylogeny. Other phylogenetic studies have been carried out, both at wider levels, analysing for instance the relationships of *Cucurbita* with other plant groups (an example within the family is offered by Chung, Decker-Walters and Staub, 2003), and within a given species (as within *C. pepo* as in Paris et al., 2003).

The levels of genetic variation and the differentiation (genetic structure) of *C. argyrosperma* and *C. moschata* and their relatives have been described in various studies. A close relationship between the populations of *C. argyrosperma* ssp. *argyrosperma* (average D (Nei's genetic distance) = 0.02 [range 0.00-0.06]) and *C. argyrosperma* ssp. *sororia* (D = 0.01 [0.00-0.06]) was reported by Decker (1986). Populations of *C. moschata* showed a greater genetic distance (D = 0.24 [0.16-0.32]; Wilson, 1989; Wilson, Doebley and Duvall, 1992). On the other hand, data on the genetic diversity show a close kinship between *C. argyrosperma* ssp. *argyrosperma* and *C. argyrosperma* ssp. *sororia* (average D = 0.03), and a large differentiation between *C. argyrosperma* ssp. *argyrosperma* and *C. moschata* [average D = 0.22] (Wilson, 1989; Merrick, 1991). Another study on the degrees of genetic diversity in *Cucurbita* revealed that *C. moschata* has a greater genetic diversity (mean expected heterozygosity, H = 0.052) than *C. argyrosperma* (0.039), although the number of individuals studied was small in both species (Decker-Walters et al., 1990).

Montes-Hernández and Eguiarte (2002) studied cultivated populations of *Cucurbita argyrosperma* ssp. *argyrosperma and C. moschata*, together with adjacent wild populations of *C. argyrosperma* ssp. *Sororia*, and found similar high degrees of genetic variations in the three taxa (P= 0.96, mean allelic diversity of 2.08, average expected heterozygosity (He) = 0.407) and little genetic differentiation among conspecific populations (D = 0.081: Fst = 0.087; Nm = 5.22). These findings indicate that *Cucurbita* possesses a high pollen dispersal potential, and a UPGMA (unweighted pair group method with arithmetic mean) analysis indicated the existence of at least two distinct groups of populations: one consisting of both subspecies of *C. argyrosperma* and another consisting of *C. moschata*. In *C. moschata* in Africa, Gwanama, Labuschagne and Botha (2000) used 39 random amplified polymorphic DNA (RAPDs) markers, generating 144 fragments, 23% of which were polymorphic; 4 clusters were found to be associated to the geographical origin of the samples. Ferriol et al. (2004), using 156 amplified fragment length polymorphism (AFLP) fragments in *C. moschata*, found 86% to be polymorphic; and using 148 repetitive fragments, found 66% to be polymorphic.

Ferriol, Picó and F. Nuez (2004) analysed genetic variability and differentiation (genetic structure) of *C. maxima* with AFLP, where 55% were polymorphic, and, with sequence-related amplified polymorphism (SRAP) markers where 57% were polymorphic.

In the *C. pepo* complex, genetic diversity and its heterozygosity are moderately high (D = 0.17 and H = 0.089; Decker and Wilson, 1987) and alleles typical of the cultivated species have been found in wild populations (Kirkpatrick and Wilson, 1988). This has been interpreted as evidence of gene flow between wild and cultivated populations (Decker and Wilson, 1987; Kirkpatrick and Wilson, 1988; Wilson, 1990). Decker-Walters et al. (2002) analysed with RAPDs, 37 wild populations and 16 cultivated varieties. Twenty-six primers yielded 70 scorable and variable markers. Their data also suggested gene flow between wild and cultivated populations. The results of Ferriol et al. (2003a), in a study with 69 cultivated variants of *C. pepo*, including the 2 subspecies ssp. *pepo* and ssp. *ovifera*, using AFLP markers comprising 476 fragments, showed 53% were polymorphic, with an average genetic diversity of 0.18; and, with SRAP markers and 88 fragments, found a polymorphism of 73%, with an average gene diversity of 0.25. With the SRAP analyses, the percentage of polymorphic fragments and the gene diversity were higher in ssp. *pepo* than in ssp. *ovifera* (0.19 and 0.16 respectively), and with the AFLP analyses were 0.12 for ssp. *ovifera* and 0.10 for ssp. *pepo*. Kwon et al. (2004) analysed 16 varieties, including *C. maxima*, *C. moschata* *and C. pepo* with RAPDs markers and simple sequence repeats of microsatellites. The degrees of genetic variation were high and these markers permitted the clear identification of the varieties and the species.

In addition, in *C. pepo* different characteristics associated with resistance to different pathogens have been described (Lebeda and Křístová, 1996; Lebeda, Křístková and Doležal, 1999; Paris and Cohen, 2000; Provvidenti and Tricoli, 2002; Cohen, Hanan and Paris, 2003; de Oliveira et al., 2003), as well as the genetic bases of other characteristics, such as the banding patterns and color of fruits (Paris, 2003; 2002; 2000), characteristics of the seed (Teppner, 2000), their yield (Paris, 1997; Mohanty, Mohanty and Mishra, 1999) and fat content (Murkovic, Hillebrand and Winkler, 1996).

Advances in genetic mapping include a study by Brown and Myers (2002) of a cross between *C. pepo* with *C. moschata*, using 148 RAPDs markers found in 28 linkage groups, where quantitative trait loci related to the shape of the fruit and leaves were identified. Using RAPD, AFLP, simple sequence repeats and morphological traits, genetic maps for *C. pepo* have been constructed (Zraidi et al., 2007).

Hybridisation and introgression

A wide range of factors that control the incidence and direction of gene flow and introgression within the *Cucurbita* genus has been identified (Merrick, 1990), including spatial and temporal separation, behaviour of pollinators, genetic compatibility factors, physiological differences and environmental adaptation. Numerous attempts at interspecific hybridisation within *Cucurbita* have been conducted over the years and there has been a wide range of success (Singh, 1990; Lebeda et al., 2006).

In *Cucurbita*, all attempts at crossing the xerophytic species, those adapted to arid environments (*C. digitata*, *C. foetidissima*, *C. pedatifolia* and *C. radicans*), with the mesophytic species, those adapted to moist environments (*C. argyrosperma*, *C. ecuadorensis*, *C. ficifolia*, *C. lundelliana*, *C. maxima*, *C. moschata*, *C. okeechobeensis* and *C. pepo*), have failed to produce fertile hybrids (Lebeda et al., 2006).

The genetic compatibility relations between the five cultivated, and with the other mesophytic species of the genus *Cucurbita*, have been widely studied (Whitaker, 1951; Whitaker and Bemis, 1965; Merrick, 1990; Lira, Andres and Nee, 1995). In general, the cultivated *Cucurbita* species are reproductively isolated from one another. The primary gene pools of each species are represented by their landraces and commercial cultivars as well as by their intraspecific taxa (see Table 2.6). Although experimental interspecific crosses can be made among the cultivated species, these frequently result in hybrids that are only partially fertile, while others result in no fruit set (Merrick, 1995). Spontaneous crosses between the cultivated *Cucurbita* are uncommon, but have been reported occasionally between certain of the various species' landraces, mostly in Mexico (Decker-Walters et al., 1990; Merrick 1991, 1990). Given the experimental results, these are also likely to be hybrids that are only partially fertile or result in no fruit set. Nevertheless, none of the genus' species is completely reproductively isolated from the others in terms of barriers to hybridisation.

Table 2.6 displays the cross-compatibility of the cultivated *Cucurbita* species with regard to the primary gene pool, the secondary gene pool and the tertiary gene pool. The cultivated *Cucurbita* species of interest, i.e. those listed in the leftmost column, cross readily with plants within their primary gene pool. The secondary gene pool includes species that when crossed experimentally with the cultivated species in the leftmost column can yield at least partially fertile F1 on hybridisation. Although genes can be moved in breeding between the cultivated species and plants in their secondary gene pool, the F1 are usually sterile or sparingly fertile. Species listed as being in the tertiary gene pool of the cultivated species represent the outer limit of potential genetic resources for breeding: Pre-zygotic and post-zygotic barriers can cause partial or complete hybridisation failure, inhibiting introgression between the cultivated species and plants in the tertiary gene pool (Lebeda et al., 2006). Crosses between a cultivated *Cucurbita* species and other cultivated species in the secondary or tertiary gene pools (Table 2.6), present a more complicated picture; the use of techniques such as embryo culture, which are used to bypass hybrid sterility barriers, may be required. Hybrids obtained from such crosses are frequently sterile or exhibit reduced fertility (Whitaker and Robinson, 1986). Among the *Cucurbita*, success in crossing frequently depends on the genotypes used as parentals.

C. ficifolia is the least compatible species, not only with the other cultivated species, but with all the remaining species of the genus (Whitaker, 1951; Whitaker and Davis, 1962; Whitaker and Bemis, 1965; Merrick, 1990; Lira, Andres and Nee, 1995; Robinson and Decker-Walters, 1997). Some interspecific hybrids have been obtained from crosses between *C. ficifolia* and *C. pedantifolia*, *C. foetidissima*, or *C. lundelliana*, but they often lack the capacity to produce an F2 generation (Lira, Andres and Nee, 1995).

Among the cultivated species, *C. moschata* has the best crossability. Among the cultivated species, it is easiest to cross *C. moschata* with *C. argyrosperma*. Hybridisation experiments (and some field observations) have revealed that *C. moschata* has the highest degree of compatibility with *C. argyrosperma*, placing *C. argyrosperma* into the *C. moschata* secondary gene pool (Table 2.6; see Lebeda et al., 2006). The *C. moschata* tertiary gene pool is formed by *C. lundelliana* and some taxa of the groups Maxima and Pepo (Lira, Andres and Nee, 1995).

Conversely, hybridisation experiments (and some field observations) place *C. moschata* into the *C. argyrosperma* secondary gene pool. The next level of *C. argyrosperma* cross-compatibility involves the wild and cultivated species of *C. pepo*, some cultivars of *C. maxima*, and the wild perennial species *C. foetidessima*, which collectively represent the *C. argyrosperma* tertiary gene pool (Lebeda et al., 2006).

The primary gene pool of *C. maxima* includes *C. andreana*, which some authors classify as a *C. maxima* subspecies (Systax Database, 2011; see also Annex 2.A1). The secondary gene pool of *C. maxima* is represented by *C. ecuadorensis*; and its tertiary gene pool includes *C. lundelliana*, *C. argyrosperma*, *C. ficifolia* and *C. pepo* (Lira, Andres and Nee, 1995; Lebeda et al., 2006).

The primary gene pool of *C. pepo* is formed by its various edible and ornamental cultivars, as well as populations of the wild taxa, ssp. *fraterna*, and ssp. *ovifera* var. *texana* and var. *ozarkana*; until recently these wild taxa were identified as distinct species (Singh, 1990). There are a great many *C. pepo* cultivars with particular characteristics that, together with local landraces (grown mostly in Mexico), constitute an extraordinary genetic stock. Populations that could be considered as part of the *C. pepo* secondary gene pool are scarce; most attempts at hybridising *C. pepo* with other wild or cultivated *Cucurbita* species have required the use of special techniques such as embryo culture (Lebeda et al., 2006).

The wild mesophytic annual taxa *C. lundelliana, C. okeechobeensis* and *C. ecuadorensis* have shown some possibilities of introgression through breeding hybridisation with cultivated species and/or with one or more of these species' ancestors.

Of the wild species, *C. lundelliana* is generally the most crossable with the other mesophytic species, being in the tertiary gene pool of *C. ficifolia*, *C. maxima*, *C. moschata* and *C. pepo*.

Table 2.6. **Cross-compatibility of cultivated *Cucurbita* species: Gene pools**

Species	Primary gene pool	Secondary gene pool	Tertiary gene pool
C. argyrosperma	*C. argyrosperma* ssp. *soraria* *C. argyrosperma* ssp. *argyrosperma*	*C. moschata*	*C. pepo* *C. maxima* *C. foetidessima*
C. ficifolia	*C. ficifolia*	*C. pedatifolia* *C. foetidissima*	*C. lundelliana* *C. maxima* *C. pepo*
C. maxima	*C. maxima* ssp. *maxima* *C.maxima* ssp. *andreana*	*C. ecuadorensis*	*C. lundelliana* *C. argyrosperma* *C. ficifolia*
C. moschata	*C. moschata*	*C. argyrosperma*	*C. lundelliana* *C. maxima* *C. pepo*
C. pepo	*C. pepo* ssp. *pepo* *C. pepo* ssp. *ovifera* *C. pepo* ssp. *ovifera* var. *texana* *C. pepo* ssp. *ovifera* var. *ozarkana* *C. pepo* ssp. *fraterna*	*C. argyrosperma* *C. okeechobeensis* *C. moschata* *C. ecuadorensis*	*C. lundelliana* *C. ficifolia* *C. maxima*

Sources: Adapted from Lira, Andres and Nee (1995); and Lebeda et al. (2006).

Examples of breeding crosses performed to obtain specific introgressions

Interspecific crosses are an important mechanism for the introduction of valuable traits that are not available, or cannot be found, within the gene pool of a crop species. However, such crosses are often only achieved with difficulty as there are many natural barriers, both pre- and post-fertilisation, that protect the integrity of a species. Even if a cross between the parental plants produces hybrid offspring, the alien gene must introgress into the genome, including successful chromosome pairing in the target species.

Diverse studies have analysed hybridisation in *Cucurbita* (Whitaker and Bohn, 1950; Whitaker and Bemis, 1965; Merrick, 1991, 1990). In spite of hybridisation barriers, desirable traits have been successfully introgressed among species of the *Cucurbita*. In most cases, success in crossing between cultivated species depends on the genotypes used, with some attempts more successful than others (Whitaker and Davis, 1962; Robinson and Decker-Walters, 1997; Lebeda et al., 2006). For example, although *C. moschata* is in the secondary gene pool of *C. argyrosperma* and the hybridisation possibilities between the members of the subspecies of *C. argyrosperma* (i.e. *C. argyrosperma* ssp. *argyrosperma* and ssp. *sororia*) and *C. moschata* are good (Wilson, 1990; Wilson, Doebley and Duvall, 1992), there are reports of a decrease in the level of compatibility when *C. moschata* is used as the female parent (Merrick, 1991, 1990; Wessel-Beaver, 2000a).

Information related to hybridisation among *Cucurbita* species and techniques to overcome crossing barriers and hybrid sterility has been summarised by Lira, Andres and Nee (1995; see also Sisko, Ivancic and Bohanec, 2003). The breeding of *Cucurbita* has primarily focused on improving the production and quality of the fruits by attempting to increase resistance to pathogens and diseases, and by modifying plant architecture and sex expression (Lebeda et al., 2006). Interspecific hybrids have been made to identify diverse resistance sources, primarily to diseases caused by viruses and fungi. Resistance to zucchini yellow mosaic virus (ZYMV) and watermelon mosaic virus (WMV), which *C. moschata* was reported to display, has been incorporated into cultivars of *C. pepo* by crosses with *C. moschata* (Garzón-Tiznado, Montes-Hernández and Becerra, 1993; Gilbert-Albertini et al., 1993). Wild species of *Cucurbita* including *C. ecuadorensis* and *C. foetidissima* have been found to be resistant to a number of viruses (Provvidenti, 1990), and have been used as sources of resistance to these diseases. It is difficult to hybridise *Cucurbita foetidissima* with other members of the genus because it is phylogentically distant from the cultivated species; nevertheless, its virus-resistant alleles can be introduced into the extended *Cucurbita* gene pool for use in genetic improvement of the cultivated species as it is a member of the tertiary gene pool of *C. argyrosperma* (see Table 2.6).

In terms of intraspecific crosses being useful in increasing resistance to pathogens and disease, Lebeda and Widrlechner (2004) published the results of screenings on cultivated *C. pepo*, represented by eight groups of morphotypes, for susceptibility or resistance to the fungi *P. cubensis* or *P. xanthii*. The *C. pepo* morphotypes expressed significant differences in resistance/susceptibility to *P. cubensis* or *P. xanthii*. Generally, there was an inverse relationship detected in resistance to the two fungi. While zucchini, cocozelle and vegetable marrow (ssp. *pepo*) were highly resistant to *P. cubensis*, they had relatively high powdery mildew sporulation. Cultivars with the fruit type acorn, straightneck and ornamental gourd (ssp. *ovifera*) were quite susceptible to *P. cubensis*; however, they were considered resistant to *P. xanthii* in laboratory and field evaluations (Lebeda and Křístová, 2000).

Interspecific hybrids have been made to incorporate the gene responsible for the “bush” phenotype of *C. pepo* into *C. moschata* and *C. argyrosperma*, species that are in the secondary gene pool of *C. pepo*, providing these species with the characteristics of a compact plant (Robinson and Decker-Walters, 1997). Bush plants have a more uniform growth and better response to high-density planting compared to vine plants (Loy and Broderick, 1990).

Hybridisation and introgression in the field

The amount and frequency of gene flow between a cultivated plant and its closest wild relatives are affected by several factors, e.g. the existing mating system, similarities in flowering phenology, ease in which the gametes can move and overlapping ecogeographic distribution. Several authors, including Decker (1986) and Decker-Walters et al. (1990), have presented genetic evidence for introgression in the field among various *Cucurbita*.

As noted earlier in this chapter, the *Cucurbita* with limited exception are monoecious, plants may produce flowers over much of their maturity, and the species are insect pollinated. Kirkpatrick and Wilson (1988) examined the potential for gene flow between cultivated *Cucurbita pepo* and its wild relative *C. pepo* var. *texana* by monitoring flower patterns and gene flow among experimental populations. While flowering patterns and pollinator movements tended to maximise self-pollination and local gene exchange, movement of effective pollen was detected up to a distance of 1 300 metres. Hybridisation rates of 5% have been reported (see also Montes, 2002). Spencer and Snow (2001) compared the fitness component of wild *Cucurbita pepo* from Arkansas (United States) with *C. pepo* wild-crop hybrids. Their results suggest that the F1 generation of the wild-crop cross does not present a strong barrier to introgression of crop genes into free-living *C. pepo* populations. Quesada et al. (1991) and Queseda, Winsor and Stephenson (1996) showed that subsequent generations of offspring of such hybrids are viable. Decker and Wilson (1987) and Kirkpatrick and Wilson (1988) have found alleles typical of the cultivated species in wild populations and this has been interpreted as evidence of gene flow between wild and cultivated populations. Allozyme frequency distributions and distinctive patterns of variation in fruit structure, colour and bitterness within populations of free-living *C. pepo* indicate that past hybridisation events have resulted in introgression between cultivated *C. pepo* L. and free-living *C. pepo* ssp. *ovifera* (Decker and Wilson, 1987; Wilson, 1990).

Similarities in flowering phenology can affect the potential for hybridisation among other species of *Cucurbita*. For example, *C. moschata*, *C. pepo* ssp. *fraterna* and both subspecies of *C. argyrosperma* have a very similar flowering phenology in relation to the day and time of opening of male and female flowers (Wilson, Lira and Rodríguez, 1994). Wilson (1990) and Lira (1991) have reported hybrids between *C. argyrosperma* ssp. *sororia* and *C. moschata* in the state of Chiapas, Mexico. Gene flow and introgression between cultivated populations of *C. argyrosperma* ssp. *argyrosperma* and *C. moschata* with adjacent wild populations of *C. argyrosperma* ssp. *sororia* is attributed partly to the plants flowering at the same time, and partly to pollinators visiting plants in these taxa indiscriminately (Montes-Hernández and Eguiarte, 2002). In addition, Mexican farmers permit wild relatives of cultivated *Cucurbita* to grow in the edges of their plots, and inside the plots they sometimes find bitter fruits which indicate hybridisation (Nabhan, 1984; Merrick and Nabhan, 1985; Montes-Hernández, Merrick and Eguiarte, 2005). Wilson, Lira and Rodríguez (1994) noted that a mixed population of *Cucurbita* in Mexico showed an anomalous pattern of fruit bitterness. Some domesticated plants (*C. argyrosperma* and *C. moschata*) expressed bitterness whereas some sympatric free-living plants (*C. pepo* ssp. *fraterna*) produced non-bitter fruits. Wilson hypothesised that this reversal of typical bitterness expression suggested gene flow between crop and wild plants at the site. Using synthetic hybridisation Wilson, Lira and Rodríguez (1994) showed that F1 hybrids can be produced from crosses involving *C. pepo* ssp. *fraterna* as the pistillate parent and *C. argyrosperma* as the staminate parent.

RAPDs, RFLPs and microsatellites, AFLPs and studies involving nuclear DNA, chloroplast DNA (cpDNA) and mitochondrial DNA (mtDNA) (Ferriol et al., 2004; Ferriol, Picó and Nuez, 2004, 2003b) have been applied to study introgression and gene flow in *Cucurbita*. Morphological and isoenzyme analyses have also been used to study introgression between various members of the *Cucurbita* (Bretting, 1990; Decker, 1988; Decker-Walters et al., 1990; Kirkpatrick and Wilson, 1988; Montes-Hernandez and Eguiarte, 2002; Nee, 1990; Wilson, 1990; and Wilson, Lira and Rodríguez, 1994).

Crop production and use

Production statistics

Originally domesticated in the Americas, now disseminated worldwide, the cultivated *Cucurbita* species play a major role in food-production agriculture, as well as in local home gardening throughout tropical, subtropical and temperate regions of the globe. Collectively, *Cucurbita* species rank among the ten most important vegetable crops worldwide (Ferriol and Picó, 2008).

International statistics on production and trade rarely distinguish between the *Cucurbita* species; it is thus difficult to parse out how much of each species is grown in the various regions of the globe. For example, *C. pepo* is the most important commercial species worldwide (Paris, 2001), and in tropical Africa *C. moschata* and *C. maxima* are known to be more important than other species such as *Cucurbita pepo*; however, production figures simply report on "pumpkins, squash and gourds". In addition, international production statistics do not reflect the use of the *Cucurbita* in home gardens or when grown on a small-scale basis for local consumption. Nonetheless, the FAO gathers production statistics worldwide for commercial production of pumpkins, squash and gourds and these numbers offer some indication of the importance of the *Cucurbita* in commercial agriculture. The FAO Statistical Database reports the 2013 world production of pumpkins, squashes and gourds at 24.6 million metric tonnes (mMT) from almost 1.8 million hectares. The People's Republic of China was by far the main producer with 7.1 mMT, followed by India (4.9 mMT), the Russian Federation (1.1 mMT), Iran (897 293 MT), the United States (796 872 MT) and Ukraine (610 800 MT). For Latin America, the main producer was Mexico (544 998 MT), followed by Cuba (412 028 MT), Argentina (302 324 MT) and Peru (232 888 MT). In tropical Africa, substantial production was reported for Rwanda (239 182 MT) and Cameroon (158 801 MT). Also included in the top 25 producers were Egypt (543 334 MT), Spain (533 200 MT), Italy (530 000 MT), Turkey (388 785 MT), Bangladesh (375 000 MT), Indonesia (372 387 MT), Korea (323 364 MT), Algeria (260 913 MT), Pakistan (257 740 MT), Japan (227 303 MT), Morocco (224 314 MT), the Philippines (223 479 MT), Thailand (207 000 MT) and South Africa (181 315 MT) (FAOSTAT, 2013).

Environmental conditions

All of the cultivated *Cucurbita* are warm season crops adapted to monthly mean temperatures of 18-27ºC, and are killed by frost. Warm temperatures promote growth and are especially beneficial for germination and development of seedlings. *Cucurbita* species are widely adapted to various types of soils, but prefer good drainage and do not tolerate poorly drained soil.

Cucurbita argyrosperma

Cucurbita argyrosperma ssp. *argyrosperma*, within its native range (southwestern United States to Central America), is cultivated in a wide altitudinal range from sea level to 1 800-1 900 metres, generally in regions with warm and slightly dry climate (with irrigation), or in regions with a well-defined rainy season. *C. argyrosperma* does not tolerate very low temperatures well. *C. argyrosperma* can be found in cultivation in Mexico, and some cultivation can be found in Argentina and Peru and the southwestern United States. Some sporadic cultivation may be found elsewhere.

Cucurbita ficifolia

Cucurbita ficifolia is widely distributed under cultivation from 1 000-3 000 metres, on practically all mountain ranges in Latin America. Cultivation at higher altitudes is a feature that distinguishes *C. ficifolia* from other cultivated species of the genus, which, in general, can be managed in a wider interval of ecological conditions. Studies by Andres (1990) and others have shown that *C. ficifolia* is an annual, which, depending on certain ecological conditions (i.e. not too severe frosts), is capable of surviving for a longer period of time than that corresponding to a species with this type of life cycle.

C. ficifolia requires a rich, well-drained, moisture-retentive soil, and a very warm, sunny and sheltered position, but may be able to tolerate poor, wet and badly drained soils in some instances. Plants are not very frost-tolerant, but they can be grown in temperate climate. *C. ficifolia* can only be grown from seed, and can be used as a rootstock for grafts of other *Cucurbita* due to its hardy root system and virus resistance. *C. ficifolia* may be found in cultivation in high elevations from Mexico to northern Chile and Argentina, and in other parts of the world (e.g. France, Germany, Japan and the Philippines).

Cucurbita maxima

Within its native distribution, there are variants or local races of *Cucurbita maxima* cultivated in places within a wide altitudinal range, from 100 metres (in some Brazilian localities) to 3 000 metres (in Bolivia). A frost tender, annual plant, *C. maxima* is primarily cultivated in regions with temperate climate, and very rarely in warm and damp regions (Robinson and Decker-Walters, 1997). *C. maxima* requires a rich, moisture-retentive well-drained soil and a warm, sheltered, sunny position. Many forms require a temperature range of 20-27ºC during the growing season, although there are some forms that tolerate cooler conditions. *C. maxima* is the most tolerant of the cultivated *Cucurbita* of low temperatures. *C. maxima* is cultivated in temperate and subtropical regions worldwide.

Cucurbita moschata

In botanical literature, *C. moschata* is reported as being grown mainly in areas of low altitude with a hot climate and high humidity (Esquinas-Alcazar and Gulick, 1983; Whitaker, 1968). However, while it is true that this species is preferentially grown within these limits, they do not appear to be strictly adhered to, as variants have been found above 2 200 metres, e.g. in Oaxaca, Mexico. For example, Bukasov (1981) fixes 2 200-2 300 metres as the top altitudinal limit for this crop in Colombia and Mexico, and this information has recently been corroborated by means of collections of fruits and seeds of the variants growing above 2 200 metres within the region of the Mixteca Alta in the state of Oaxaca, Mexico (Lira, Andres and Nee, 1995). In general, *C. moschata* is the cultivated *Cucurbita* least tolerant of low temperatures, but is relatively drought tolerant. *C. moschata* is cultivated in subtropical and tropical regions worldwide, but can also be cultivated sporadically elsewhere.

Cucurbita pepo

C. pepo can grow in a variety of ecological conditions. *C. pepo* tolerates a fairly wide range of altitudes ranging from 8-2 300 metres. This species includes variants which are cultivated at altitudes above 2 000 metres (during the rainy season or even during the dry season on land that remains wet), and still others can grow near the sea and in even more extreme conditions (i.e. those found on the Yucatan Peninsula). For example, in Mexico there are native varieties that grow close to sea level in semi-dry climates and limestone soil (i.e. the "*tsol*" in the Yucatan Peninsula), while others are managed at altitudes above 2 000 metres, with colder climatic conditions and sometimes highly eroded soil (i.e. the "*güiches*" in the state of Oaxaca) (Lira, 1991; 1988; 1985). In Guatemala the varieties or native races commonly called "*güicoy*" are grown above 1 800 metres, while those called "*tsol*" are managed in the low and warm-humid areas of the Petén, below 500 metres (Azurdia-Pérez and González-Salán, 1986). *C. pepo* grows best when day temperatures are between 24°C and 28ºC and night temperatures between 16°C and 24ºC, although it can tolerate monthly average day temperatures of 18-28ºC. It needs six to eight hours of sunlight a day and has some level of drought tolerance. Many of the commercial cultivars are widely spread around the world, demonstrating the ability of varieties to adapt to different environments. *Cucurbita pepo* may be grown in temperate, subtropical and tropical regions worldwide.

Agricultural practices

The cultivated *Cucurbita* are frost sensitive and need frost-free growing periods of four to five months. Temperatures of 20-35°C are ideal for growth. The *Curcurbita* can be grown on a wide range of soil types. They prefer a soil pH between 6.0 and 6.5, although they will tolerate both slightly acidic and slightly alkaline soils. As roots can penetrate up to a metre into the soil, a well-drained soil is preferred. *Cucurbita* also have feeder roots close to the surface. Roots can grow to about the same spread as the vines. The *Cucurbita* are sensitive to soil salinity. They are also susceptible to herbicide damage, and this susceptibility would suggest that care should be taken with herbicide use, or that herbicides can be used for control. The cultivated *Cucurbita* are usually established by direct sowing of seed, although seeds can be sprouted in containers and seedlings transplanted to the field when about 10 cm high. Seedling transplant is particularly indicated if the growing season is short. *Cucurbita* are insect pollinated and require bees for pollination. Inadequate pollination results in poor fruit shape and blossom drop.

Cucurbita fruit develop rapidly after the flower closes, and fruit eaten at the immature stage (e.g. zucchini) must be harvested before the rind begins to harden. For those types that are eaten after the fruit fully matures (e.g. pumpkin), three to four months are generally required to mature a crop to this stage. At this stage the fruit is hard and imperious to scratching; the fruit is removed from the vine with a portion of the stem attached. The mature fruit can be kept in long-term storage (e.g. four to six months) if the fruit is properly ripened and cured. Curing hardens the shell, heals superficial wounds, reduces the water content of the fruit and improves the quality of the flesh. Fruits can be cured by leaving them in the field in warm and dry conditions for ten days to two weeks or by keeping them inside at room temperature for a month (OMAFRA, 2011). Table 2.4 offered phenological notes on the various *Cucurbita* species, including the cultivated species, in Mexico.

Cucurbita species can express highly oxygenated, triterpene compounds called cucurbitacins, which taste bitter to humans and can be toxic (US Environmental Protection Agency, 1999). Cultivated *Cucurbita* varieties intended for consumption by humans or domesticated animals have been bred to express low levels of cucurbitacins. However, plants in wild populations express high levels of these substances and if a cultivated plant is visited by bees carrying pollen from plants in a wild population, higher levels of the toxicant can be produced in the fruit. Any resulting seeds would produce plants with bitter fruit as bitterness is a dominant characteristic. Higher cucurbitacin levels can also be expressed by the plant in response to stresses such as drought, high temperatures, low soil fertility and low soil pH. Higher levels can also be expressed in the newly emergent seedling, and by improperly cared for, harvested fruit. In addition to producing inedible fruit, plants producing higher level of cucurbitacins can attract phytophagous Chrysomelidae beetles and attendant pest management problems (see below for additional information on the cucurbitacins and Chrysomelidae beetles).

Cucurbita argyrosperma

The cultivated varieties of *Cucurbita argyrosperma* are used in the traditional heavy rain agricultural systems and are sown at the start of the rainy period (May-June in the northern hemisphere) from 1 000-3 000 metres. Growth of these varieties lasts five to seven months; the young fruit for vegetables is harvested approximately three months after being sown, while the ripe fruit for seed is harvested between October and

December. Unlike other cultivated species of the genus, it is less frequent for varieties of the *argyrosperma* complex to be found in vegetable gardens, plots or in small agricultural holdings, or to be associated with other species (Lira-Saade and Montes-Hernández, 1992). In some areas its rapid growth is used to provide ground cover with the aim of preventing weeds from developing in the field.

Cucurbita ficifolia

Cucurbita ficifolia is a crop grown mainly in traditional heavy rain agricultural systems. It is typically sowed at the beginning of the rainy season, and harvested from the end of September (young fruit and flowers for vegetables) to December or January (ripe fruit for seeds and pulp) in the northern hemisphere. The only form of propagation is the sowing of seed, together with one of the traditional crops of this type of agriculture (maize, bean and other species of *Cucurbita*) or else cultivation in vegetable gardens along with other species or by itself. The ripe fruit is harvested and selected for seed. It can be stored for long periods (18-20 months) and it is frequently seen drying on the roofs of farmers' houses (Lira-Saade and Montes-Hernández, 1992).

Cucurbita maxima

Cucurbita maxima prefers light (sandy), medium (loamy) or heavy soil (clay) which is well-drained. The plant prefers acidic and neutral soils. It can grow in semi-shade or no shade. Dry periods with a relatively low humidity favour the best growth. A frost-sensitive annual plant, it is widely cultivated in the tropical and temperate zones. It is one of the species used in large-scale production agriculture.

Cucurbita moschata

C. moschata variants are grown under traditional, heavy rain agricultural systems. It is possible to find varieties grown in maize fields together with maize, beans and one or two other *Cucurbita*, or in vegetable gardens and other more intensively managed farmland where they are grown alone or with other species. There are some old references to a considerable variation in Colombia, but that has yet to be properly documented and evaluated (Lira-Saade and Montes-Hernández, 1992). The greatest diversity lies in the neotropics where the vines are grown under a wide range of ecological conditions, including under hotter conditions than are tolerated by the other *Cucurbita* species (Andres, 2004). This species is used in large-scale production agriculture.

Cucurbita pepo

In its native area of distribution, *C. pepo* is grown both in maize fields and vegetable gardens as well as in other more intensive systems. In the former case, it is combined with maize, beans and/or with one to three of the other cultivated species of *Cucurbita*, while in the latter system it may be found growing on plots or in small groups, generally combined with other vegetables. Where it is grown commercially, it is generally found as the sole crop, occupying areas of varying size (Lira-Saade and Montes-Hernández, 1992). Although *C. pepo* is grown in several different commercial cropping systems, there may be as much grown in home gardens as grown commercially for sale in local or distant markets, and this may be true even in countries such as the United States where it is frequently grown in larger scale production systems (National Gardening Association, 2009). *C. pepo* is the most important *Cucurbita* species economically. In North America cultivars of both ssp. *pepo* and ssp. *ovifera* are grown. Elsewhere in the world, ssp. *pepo* is the more economically important subspecies.

Management issues

Amongst the *Cucurbita*, *C. pepo* can present a weed problem in certain agricultural settings; these problems are associated with free-living members of the species in North America. *C. pepo* var. *ozarkana* is considered a weed in the states of Arkansas, Louisiana and Mississippi in the United States in soybean and cotton fields (Boyette, Templeton and Oliver, 1984; Oliver, Harrison and McClelland, 1983). While a perennial problem in Arkansas, reports from Louisiana and Mississippi are based on "outbreaks" that are evidently linked to sporadic flooding events and associated fruit dispersal into cultivated fields. Whereas in wild habitats (i.e. those not directly influenced by human activity), individual plants or small groups of plants are widely dispersed along flood plain corridors, in weedy habitats (i.e. disturbed habitats created by human activities), populations can be very dense and cover agricultural fields. Neither *Cucurbita pepo* var. *texana* nor var. *ozarkana* are found on the United States Department of Agriculture's Federal Noxious Weeds List (USDA, 2011b).

Morphological and isozymic evidence suggests that some free-living *C. pepo* populations in Illinois (Decker and Wilson, 1987; Wilson, 1990), Kentucky (Cowan and Smith, 1993; Decker-Walters et al., 1993) and possibly elsewhere (Asch and Asch, 1992) may have evolved purely as escapes of ornamental gourds, which may or may not have experienced subsequent introgression with other nearby cultivated, weedy or wild material of *C. pepo*. Such wild-habitat populations in northeastern Mexico, Texas and many parts of the Mississippi Valley in the United States have long histories of occupation in their general areas, however, and have been accepted as indigenous (e.g. Smith, Cowan and Hoffman, 1992).

Unlike the wild *C. pepo* which wards off predation by producing small, hard-shelled, tough-pericarped, bitter-fleshed gourds, the edible cultivars under human selection have yielded characteristics that hinder the cultivars' ability to persist in the wild, e.g. large, fleshy, non-bitter fruit. The edible cultivars consequently do not survive as long-lived escaped populations in wild or weedy habitats. *C. moschata*, *C. maxima* and *C. ficifolia* are known to grow outside of cultivation in the United States. The species have been collected from various habitats outside of cultivation: oak-pine woods, agricultural fields, brush and trash heaps, roadsides, ditch banks, vacant lots and disturbed sites. In addition to the US localities, *C. moschata* has been reported as naturalised in the West Indies, Central America (Belize) and South America (Galapagos, Guyana, French Guiana, Surinam). In most cases, these plants are most accurately described as "waifs" as they apparently do not maintain themselves in persistent populations (Nesom, 2011).

The edible cultivars can occur as volunteers in fields and thus present certain management considerations. Because of their rapid germination and large canopy, certain of the *Cucurbita* are used in weed control strategies, e.g. *C. argyrosperma* in traditional growth systems in smaller agricultural holdings (Anaya et al., 1987; Anaya, Ortega and Nava Rodriguez, 1992). Rapid vine growth and large leaves make the *Cucurbita* relatively weed tolerant and these characteristics can be used to reduce weed pressure as seen in traditional native agriculture (Anaya et al., 1987; Anaya, Ortega and Nava Rodriguez, 1992; Radovich, 2011).

General interactions with other organisms (ecology)

This section highlights several interesting interactions of note between the *Cucurbita* and other organisms. It does not attempt to create an exhaustive list of interactions.

Cucurbitacin mediated interactions

Species in the family Cucurbitaceae are characterised by their biosynthesis of a group of secondary compounds that are thought to function as chemical defense compounds (Bar-Nun and Mayer, 1990; Tallamy et al., 1998a) against insects, fungi and herbivores. These compounds are known as cucurbitacins (Rehm et al., 1957) and are responsible for the bitter taste found most obviously in the wild Cucurbitaceae. The cucurbitacins are highly oxygenated tetracyclic triterpene compounds (tetracyclid triterpenoids). These non-volatile compounds possess cytotoxic properties. For example, one form of cucurbitacin antagonises insect steroid responses (Dinan et al., 1997). There are 17 identified cucurbitacin compounds, generally named alphabetically, e.g. A, B, C, D, E, F, I, J, K and L. These compounds are based on the unusual amino acid (-)-3-amino-3-carboxypyrrolidine, and can occur both free and in glycosidic combination. The 17 different members of the cucurbitacin class of natural toxicants can be found as naturally occurring mixtures in species of the *Cucurbita*, primarily in the leaves and seeds. Although originally isolated from species in the Cucurbitaceae, cucurbitacins occur in a variety of plant families (e.g. Brassicaceae, Begoniaceae, Rosaceae) as well as in some mushrooms (e.g. *Russula* and *Hebeloma*). The ability of the *Cucurbita* to produce cucurbitacins influences several aspects of their ecology.

Animals

Humans find almost all the cucurbitacins contained within the fruit of the wild *Cucurbita* to be extremely bitter and the compounds have been found to be toxic to a number of animal species. The most toxic cucurbitacin has an LD_{50} of 5 mg/kg body weight in the mouse. The least toxic has an LD_{50} of 650 mg/kg body weight in the mouse (US Environmental Protection Agency, 1999). In spite of the bitter taste and toxicity which appears to deter most animals, some animals can tolerate at least some of the pulp of wild *Cucurbita*; e.g. coyotes (*Canis latrans*) and porcupines (*Erethizontidae* spp.) eat seeds tainted by the pulp of xerophytic *Cucurbita digitata* (Sowls, 1997). Javelina (*Pecari tajacu*) appears to have even greater tolerance as they have been reported to dig up and eat the bitter tuberous roots of *C. foetidissima* and *C. digitata* (Sowls, 1997).

Phytophagous insects

In general, the cucurbitacins produced by the *Cucurbita* are thought to defend against phytophagous insects (Tallamy et al., 1998a). However, for a group of Chrysomelidae beetles of the tribe Luperini, cucurbitacins act as arrestants and feeding stimulants (Metcalf et al., 1982). The beetles belong to the subtribes Diabroticina (about 900 species distributed in the American continent) and Aulacophorina (about 480 species found in Asia). Diabroticina beetles can detect these compounds in plant tissues and inert substances like silica gel or filter paper at quantities as low as 0.1 ng (Metcalf, Metcalf and Rhodes, 1980). When the beetles encounter bitter plant tissues they compulsively ingest them. Furthermore, they sequester cucurbitacins in hemolymph and elytra as chemical defense against natural enemies and transfer the compounds to their eggs (Ferguson and Metcalf, 1985; Brust and Barbercheck, 1992; Tallamy et al., 1998b). A paper by Nishida, Yokoyama and Fukami (1992) showed, for several members of the

Luperini tribe, that these sequestered cucurbitacins deterred feeding by a bird predator, indicating an allomomal role for these compounds. Interestingly enough, some beetle species which do not rely on cucurbits as a food source still show this behaviour, known as pharmacophagy (Fukami and Nishida, 1990; Eben, Barbercheck and Aluja, 1997). An example of such behaviour is displayed by *Diabrotica virgifera virgifera* which is a specialist on plants of the Poaceae. When it reaches maturity, this beetle leaves the nutritious and toxin-free *Zea maize* in search of cucurbitacin enriched plants (Tallamy et al., 2005). Metcalf (1986) proposed that this behaviour is a relict of a coevolutionary association with cucurbits. Gillespie et al. (2003) argued that phylogenetic analysis within the Luperini tribe supports the theory that this behaviour represents convergent evolution of cucurbitacin feeding. Whatever the origin of the behaviour, compulsive feeding is such a strong and reliable characteristic of Diabroticina beetles that cucurbitacins are used as bait in insecticidal preparations for the control of several pest species within the Diabroticina (Lance and Sutter, 1990).

Micro-organisms

As with many other members of the plant kingdom, *Cucurbita* are attacked by a number of microbial pathogens. The next section provides a listing of those pathogens most commonly found on *Cucurbita* species. The largest diversity of disease-producing organisms on species of *Cucurbita* is found among the fungi (Blancard et al., 1994; Zitter, Hopkins and Thomas, 1996; Davis et al., 2008). The fungi causing the largest economic losses in the *Cucurbita* are those that cause powdery mildew (*Podosphaera xanthii*, *Erysiphe cichoracearum*). Some research (Bar-Nun and Mayer, 1990) has shown that application of cucurbitacins to plant tissue can reduce the infection rate of a fungus, *Botrytis cinerea*, supporting the hypothesis that cucurbitacins can act as defense compounds against at least some fungi.

One bacterial pathogen, *Erwinia tracheiphila*, is particularly problematic in the *Cucurbita*. It is transmitted to the plant by chrysomelid beetles and, as noted above, these beetles are attracted to plants expressing cucurbitacins.

Other interactions

Insect pollinators

As discussed above, the *Cucurbita* are primarily pollinated by bees, and the most efficient pollinators of the *Cucurbita* are the solitary bees of the genera *Peponapis* and *Xenoglossa*. A coevolutionary relationship exists between the bees of the genera *Peponapis* and *Xenoglossa* and the *Cucurbita*. To the bees, it is a relationship on which their survival depends (Hurd, Linsley and Whitaker, 1971). It also seems to be the chief parameter of the bees' evolution (Hurd, Linsley and Whitaker, 1971). A number of coevolutionary adaptations exist between the bees of the genera *Peponapis* and *Xenoglossa* and the *Cucurbita*. For example, these bees are adapted to collect the large (80-150 µm diameter) and spiny pollen grains and to drink the nectar of *Cucurbita* from which the bees derive the majority of their food (Hurd, Linsley and Whitaker, 1971). Although other plants are occasionally visited, adult females rely solely on plants of the *Cucurbita* for the pollen food used to rear offspring (Hurd and Linsley, 1964). It has been hypothesised that the original ranges of the bees were affected by the spread by humans of *Cucurbita* species through the Americas, with the bees extending their ranges using "pollen avenues" established by these cultivated *Cucurbita* in a coevolutionary facilitation (Hurd, Linsley and Whitaker, 1971). Other bees, e.g. the honey bee (*Apis mellifera*), also pollinate *Cucurbita*.

Phytophagous insects

In general, cultivated plant species are used as a food source by a large number of phytophagous insects (e.g. Hodgekinson and Hughes, 1982; Hendrix, 1988), and the *Cucurbita* are no exception, particularly in an agricultural setting. In addition to chrosomalid beetles, other insects are known as pests of the cultivated *Cucurbita* species; some of these have also been seen feeding from wild plants. These include *Epilachna* spp. (Coleoptera: Coccinellidae) and *Diaphania hyalinata* and *Diaphania nitidalis* (Lepidoptera: Pyralidae) (Mariano and Dirzo, 2002). See below for additional information on common insect pests.

Plants in the genus *Cucurbita* have been shown to respond to herbivory in a number of ways, e.g. in the production of flowers, fruits, pollen and pollen performance. Mariano (2001) has observed such effects in *C. argyrosperma* ssp. *sororia* and *C. pepo* var. *texana*. Ávila-Sakar, Krupnick and Stephenson (2001) have shown that the plants of *Cucurbita pepo* var. *texana* are capable of reassigning resources destined for the production of fruits and seeds to growth and production of staminate flowers as a response to the removal of female flowers. Further, Avila-Sakar, Leist and Stephenson (2003) have shown that *C. pepo* var. *texana* has a high tolerance of simulated herbivory; low to moderate levels of foliar damage significantly affected very few traits. Finally, Theis, Kesler and Adler (2009) in *Cucurbita pepo* var. *texana* showed that simulated leaf damage increased fragrance production in male flowers. Female flowers which were bigger and produced more fragrance than males flowers were unaffected by leaf damage. These results suggest that changes in fragrance following herbivory may mediate interactions between plants, herbivores and pollinators.

Plants

Anaya et al. (1987) and Anaya, Ortega and Nava Rodriguez (1992) suggest that the effectiveness of *Cucurbita* species in weed suppression in traditional American polyculture is due to a combination of competition for light and allelopathy. Qasem and Issa (2005) reported that volatiles from *C. pepo* shoots may be phytotoxic: soil-incorporated *C. pepo* residues prevented seed germination of *P. oleracea* and arrested growth of other weed species tested (Qasem and Issa, 2005). In 2007, Fujiyoshi, Gliessman and Langenheim examined the weed-suppressive properties of *Cucurbita* interplanted with corn (*Zea maize*) by comparing different planting and weeding regimes, and measuring weed biomass, light interception by crop canopy and yield. Shading by the *Cucurbita* appeared to be the major mechanism of weed suppression, but the analysis suggested that other factors, such as allelopathy, might also contribute.

Micro-organisms

Several types of viruses are known to attack the *Cucurbita*. The Mosaic viruses (cucumber mosaic – CMV, watermelon mosaic – WMV, zucchini yellow mosaic virus – ZYMV, and squash mosaic virus – SqMV) are the types most commonly observed in the *Cucurbita*. These viruses are transmitted primarily by insect vectors (aphids) and the primary approach to controlling the incidence of viral disease in cultivated *Cucurbita* is control of the vector. The next section discusses the viruses known to infect the *Cucurbita* in greater detail. The following section then briefly describes newer biotechnological approaches to addressing the economic losses associated with certain of the viruses causing disease in *Cucurbita*.

Animals

Cultivated *Cucurbita* are bred to express only very low levels of cucurbitacins, and are far more palatable to humans and other animals than wild *Cucurbita*. In many regions of the world, for example, fruits of the cultivated *Cucurbita* are used as fodder. In tropical regions, domesticated animals such as donkeys and horses will consume *Cucurbita* fruits and vines when fodder is scarce at the end of the rainy season (Mariano and Dirzo, 2002).

Common pests and pathogens

This section lists some of the common pests and pathogens of *Cucurbita*. It is not an exhaustive list.

Viruses

Although only a dozen problem viral variants have been identified, these variants are serious problems for the crops due to the rate of disease spread, the severity of infection, the potential for large economic losses and the difficulty in controlling the diseases. These viral diseases are particularly important due to the susceptibility of the plants to attacks by virus-transmitting insect vectors such as whiteflies, aphids and chrysomelid beetles.

Cucumber mosaic virus (CMV)

This Cucumovirus has worldwide distribution and the widest host range of any plant virus, including more than 1 200 species in over 100 families of dicotyledonous and monocotyledonous angiosperms. The host range includes cereals, forages, woody and herbaceous ornamental, vegetable and fruit crops such as squash, melons, peppers, beans, tomatoes, carrots, celery, lettuce, spinach and beets, various weeds and many ornamentals and bedding plants. Symptoms seen in infections of the virus include leaf mosaic or mottling, yellowing, ringspots, stunting and leaf, flower and fruit distortion.

CMV can be vectored by 60-80 different aphid species in a non-persistent manner from plant to plant in a stylet-borne fashion. The peach (*Myzus persicae*) and melon (*Aphis gossypii*) aphids are the primary CMV vectors. CMV can also be transmitted in seeds, and by the parasitic weeds, *Cuscuta sp.*, as well as mechanically by humans cultivating or touching healthy plants after touching infected plants. It can also be carried by the striped and 12-spotted cucumber beetles but the transmission success rate under field conditions makes these insects minor contributors to CMV infection. Many variants of the virus occur, and it is difficult to identify CMV from symptoms alone. CMV produces a systemic infection in most host plants. Older tissues and organs that developed prior to infection usually are not affected by the virus, but newer cells and tissues that develop after infection may be affected with varying severity. Leaves of infected plants become mottled and vines are stunted. The concentration of the virus increases for several days following inoculation, then decreases until it levels off or the plant dies (Agrios, 1997). The virus can overwinter in perennial weeds, flower and food crops by surviving in the roots.

Papaya ringspot virus Type W (PRSV)

This Potyvirus is distributed worldwide. PRSV is transmitted in a non-persistent manner by various aphids such as the peach aphid *Myzus persicae* (Brunt et al., 1996). It can also be transmitted mechanically by humans. It is not seed transmitted (Brunt et al., 1996). This virus was originally called water melon mosaic virus 1 (WMV1) but today is considered to be the W strain of PRSV. PRSV-W should not be confused with what had been called watermelon mosaic virus 2 (WMV2) but is now simply WMV (Lecoq and Desblez, 2009). PSRV has a different host range, different serological properties and no sequence homology with WMV. As with other mosaic viruses, leaves of infected plants become mottled and vines are stunted (Brunt et al., 1996).

Squash mosaic virus (SqMV)

SqMV is a Comovirus and was first reported in California in 1956 (Brunt et al., 1996). SqMV is probably distributed worldwide. This virus can infect and produce symptoms on several commercially grown cucurbits, including *C. maxima*, *C. moschata* and *C. pepo*. It can also infect some plants in the Leguminosae and the Chenopodiaceae. The virus is insect-transmitted in a non-persistent fashion by several insects (*Acalymma vitatta*, *Acalymma thiemei*, *Diabrotica undecimpunctata*, *Diabrotica bivittula*, *Epilachna chrysomalina*, *Epilachna paenulata*) (Brunt et al., 1996). In nature it is spread principally by the spotted cucumber beetle (*Diabrotica undecipunctata*) and striped cucumber beetle (*Acalymma vittata*). The virus can also be transmitted by seed and by mechanical inoculation.

Watermelon mosaic virus (WMV)

In the 1990s, this Potyvirus was referred to as WMV2 to distinguish it from WMV1. Today, WMV1 is considered to be the W strain of papaya ringspot virus (PRSV), while WMV2 is referred to as WMV (Lecoq and Desblez, 2009). WMV has worldwide distribution and is a major viral pathogen of cucurbit crops (Adlerz et al., 1983; Provvidenti, Gonsalves and Humaydan, 1984; Davis and Mizuki, 1987; Chala, Harrison and Halliwell, 1987). This virus can infect and produce symptoms on all commercially grown cucurbits. It can also infect several leguminous and malvaceous species. The virus is aphid-transmitted in a non-persistent fashion. As the host range for WMV is not limited to cucurbits, overwintering of this virus in several leguminous species such as clover can occur. Mixed infections of cucurbits with CMV and WMV are common. WMV causes mosaic and mottle diseases of cantaloupe, cucumber, pumpkin, squash and watermelon and reduces fruit production and quality in squash and other cucurbits (Thomas, 1971; Greber, 1978). Leaves of infected plants become mottled and vines are stunted.

Zucchini yellow mosaic virus *(ZYMV)*

This Potyvirus is a recently described virus disease of cucurbits, first identified in Europe in 1981. The virus is serologically related to, and has characteristics very similar to, WMV (Brunt et al., 1996). ZYMV is also serologically related to bean yellow mosaic virus (Brunt et al., 1996). Like WMV, the ZYMV host range is not limited to cucurbits. The known host range of ZYMV includes *Cucurbita pepo*, *Cucumis melo*, *Cucumis sativus* and *Citrullus lanatus* (ANU, 2005). ZYMV is transmitted in a non-persistent manner by aphid transmission (Lecoq, Pitrat and Clement, 1981; Lisa et al., 1981; Adlerz et al., 1983; Purcifull et al., 1984; Dodds et al., 1984; Adlerz, 1987). It can also be transmitted vertically through seed. Its effects are severe leaf mosaic, yellowing and eventually shoestring symptoms in the leaves. The fruits are stunted, twisted and deformed by raised protuberances. In cultivated crops, plants cease producing marketable fruits within a week or two of infection. On a given cucurbit host, ZYMV usually causes more severe symptoms than WMV, and there is some indication that WMV may make the plant more susceptible to ZYMV (Xu et al., 2004). Leaves of infected plants become mottled and vines are stunted.

Tobacco ringspot virus (TRSV)

TRSV is a Nepovirus and considered a minor cucurbit virus. It is primarily nematode transmitted (*Xiphinema americanun*) but can also be transmitted nonspecifically by insects such as aphids (*Aphis gossypii*) and mites (*Tetranychus* ssp). Melons and cucumbers are the cucurbits most commonly affected by this virus, but it has been found in the *Cucurbita* (Jossey and Badadoost, 2006). It has been reported to spread in North America and China, and has been reported in Australia, Germany, New Zealand and the United Kingdom (Brunt et al., 1996).

Tomato ringspot virus (ToRSV)

ToRSV is a Nepovirus and is considered a minor cucurbit virus. It causes severe damage to summer and winter squash, but shows only mild symptoms in the other cultivated cucurbits. Like TRSV, ToRSV is nematode transmitted (*Xiphinema americanun*) and can overwinter on many weed species without expressing symptoms (Brunt et al., 1996). It has been reported in Australia, Bulgaria, Chile, China, Germany, Italy, Japan, Korea, New Zealand, North America, Peru, Puerto Rico, Turkey and the former Soviet Union (Brunt et al., 1996).

Clover yellow vein virus (CYVV)

CYVV is a Potyvirus and considered a minor cucurbit virus. It is aphid-transmitted in a non-persistent manner and can infect summer squash. Infected plants mostly show chlorotic or necrotic local lesions. It is probably distributed worldwide (wherever white clover occurs). It was previously considered to be the severe strain of bean yellow mosaic virus (Brunt et al, 1996).

Fungi

The most economically important fungal diseases of the *Cucurbita* are the powdery mildews (OMAFRA, 2011).

Cladosporium cucumerinum

C. cucumerinum causes a disease known as scab or gummosis. The fungus can attack any aboveground portion of the plant, including the leaves, petioles, stems and fruits. Scab produces its greatest damage when infection occurs on the fruit. Infected fruit appears to have small spots or sunken areas similar to insect stings. A sticky substance may ooze from the infected area, especially on fleshy fruit. Soft-rotting bacteria may invade these lesions resulting in foul-smelling decay (Strider and Konsler, 1965; Agrios, 1997; American Phytopathological Society, 2011; OMAFRA, 2011).

Choanephora cucurbitarum

This fungus causes a whisker-like fungal growth that causes blossoms and fruits to rot. The disease is commonly referred to as blossom blight or wet rot (Agrios, 1997; American Phytopathological Society, 2011; OMAFRA, 2011).

Erysiphe cichoracearum

E. cichoracearum causes a disease known as powdery mildew. Whitish, talcum-like, powdery fungal growth develops on both upper and lower leaf surfaces and on petioles and stems. Symptoms usually develop first on older leaves, on shaded lower leaves and on upper leaf surface. Infected leaves usually die, and plants senesce prematurely reducing photosynthesis, thereby reducing yield (Agrios, 1997; Jahn, Munger and McCreight, 2002; American Phytopathological Society, 2011; OMAFRA, 2011).

Fusarium oxysporum

F. oxysporum is soil borne and causes a damping-off disease; i.e. it causes young seedlings to wilt and die or not emerge at all. It is occasionally found in cucurbits (Agrios, 1997; American Phytopathological Society, 2011; OMAFRA, 2011).

Phytophthora capsici

P. capcisi causes a blight resulting in leaf spots and fruit rot, seedling damping-off and possible total crop loss. Stem and leaf petiole lesions appear as light to dark brown, water-soaked and irregular in shape, eventually becoming dry, brittle and papery. Older plants with root infections may suddenly wilt. In fruit, the symptoms begin as small water-soaked lesions in the rind, which enlarge quickly and become a soft sunken area covered with white fungal growth (Agrios, 1997; Lopez, Brune and Henz, 1999; American Phytopathological Society, 2011; OMAFRA 2011).

Plectosporium tabacinum

P. tabacinum, also known as *Microdochium tabinum*, causes a blight characterised by the production of light tan to "bleached" sunken, spindle-shaped lesions, primarily on the main stems, petioles main leaf veins and peduncles and sometimes on leaf blades. On fruit, the fungus causes white, tan or silver russeting on the upper surface. Lesions often coalesce to form a continuous dry, scabby surface (Agrios, 1997; American Phytopathological Society, 2011; OMAFRA, 2011).

Podosphaera xanthii

P. xanthii, also known as *Podosphaera fusca*, is the main causal agent of cucurbit powdery mildew and one of the most important limiting factors for cucurbit production worldwide. Although great efforts have been invested in disease control, many basic aspects of the biology of this pathogen remain unknown. Powdery mildews are characterised by spots or patches of white to grayish, talcum powder-like growth. The disease is most commonly observed on the upper sides of the leaves. It also affects the bottom sides of the leaves, buds, stems, flowers and young fruit. Infected leaves may become distorted, turn yellow with small patches of green, and fall prematurely. Infected buds may fail to open (Agrios, 1997; Jahn, Munger and McCreight, 2002; American Phytopathological Society, 2011; OMAFRA, 2011).

Pseudoperonospora cubensis

The symptoms caused by *P. cubensis* are almost exclusively confined to the leaves, although there are rare reports of sporulation on fruits and floral parts. The first evidence of infection is small, slightly chlorotic to bright yellow areas on the upper leaf surface; the colour is less vivid on the lower leaf surface. As lesions expand, they often coalesce, resulting in necrosis of the infected leaves so that in a few days the entire leaf is dead. This disease is commonly referred to as downy mildew (Agrios, 1997; Lebeda and Wedrlechner, 2004; American Phytopathological Society, 2011; OMAFRA, 2011).

Pythium spp.

These soil-borne micro-organisms can cause damping-off, with young seedlings wilting or not emerging at all (Agrios, 1997; American Phytopathological Society, 2011; OMAFRA, 2011).

Sphaerotheca fuliginea

S. fuliginea causes a powdery mildew wherein whitish, talcum-like, powdery fungal growth develops on both upper and lower leaf surfaces and on petioles and stems. Symptoms usually develop first on older leaves, on shaded lower leaves and on the upper leaf surface. Infected leaves usually die, and plants senesce prematurely reducing photosynthesis, thereby reducing yield (Agrios, 1997; American Phytopathological Society, 2011; OMAFRA, 2011).

Bacteria

Erwinia tracheiphila causes bacterial wilt. It is spread by the stripped cucumber beetle, *Diabrotica undecipunctata*, and the spotted cucumber beetle, *Acalymma vittata*, and controlled by eliminating cucumber beetles. The bacteria live in the digestive tract of the striped and spotted cucumber beetles. The beetles defecate frass as they feed and *E. tracheiphila* invades the plant through the wounds caused by the feeding beetles (Sasu et al., 2010).

Insects

A number of insects can attack *Cucurbita* species. Some of the insects listed below are cosmopolitan and have a worldwide distribution, e.g. *Myzus persicae* and *Aphis gossypii*, while others are more limited in their distribution, e.g. *Anasa tristis*.

Aphididae

Aphid species most commonly found on *Cucurbita* include: *Aphis gossypii*, the melon aphid; *Myzus persicae*, the peach aphid; *Aphis fabae*, the bean aphid; and *Aphis craccivora*, the cowpea aphid.

Aphids extract sap from the terminal leaves and stems of plants. They may also feed on developing pods causing them to shrink or become malformed. Their feeding can result in deformation, wilting or death of the plant depending on populations and size of the plant. Saliva injected during feeding can also cause deformation of plant tissue. While aphids can cause significant damage on their own, they frequently present another concern: the transmission of several plant viruses.

Coleoptera

Beetle species most commonly found on *Cucurbita* species include: the stripped cucumber beetle, *Diabrotica undecipunctata*, and the spotted cucumber beetle, *Acalymma vittata*. Beetles such as the palestriped flea beetle, *Systena blanda*, can also attack plants of the *Cucurbita.*

Cucumber beetles (the stripped cucumber beetle, *Diabrotica undecipunctata*, and the spotted cucumber beetle, *Acalymma vittata*) are common pests on various members of the Cucurbitaceae. The name stems from the tendency of these beetles to be found on cucurbits. These coleopterans are among the first insects to attack cucurbits as the plants emerge. The spotted cucumber beetle is about 0.25 inches long, yellow to greenish-yellow with 12 black spots on its back and a black head. They overwinter in the adult stage near plants and in debris. Some migrate south and have been known to travel 500 miles in 3-4 days. The larvae are yellowish-white with a brown head and a brownish patch on top of the last body segment. The larvae feed on plant roots. When there is ample moisture, they will feed on the flesh of the fruit, especially fruits lying on the soil surface. Whereas larvae are root feeders, adults are primarily pollen feeders and do not damage the leaves of cucurbits to a significant extent (Krysan and Smith, 1987; Eben and Barbercheck, 1996; Gámez-Virués and Eben, 2005). The striped cucumber beetle is pale white-yellow to orange with a black head. Its wings have three black stripes running their entire length. Other than immediate stand loss, and damage to leaves, stems, blossoms and fruit, damage is incurred from the beetles' ability to carry the pathogen *Erwinia tracheiphila*, which is carried in the insects' body and transmitted to the plant as the beetles feed (OMAFRA, 2011).

The palestriped flea beetle (*Systena blanda*) is a general feeder attacking a multitude of plants. Larvae can be found feeding on roots. Adults attack the foliage of plants leaving small round holes.

The squash-ladybird (*Epilachna borealis*) is a black-spotted, yellow hemispherical species of wide geographical distribution. The adult beetles hibernate and lay their eggs on leaves in the spring. The yellow, spiny larvae chew circular holes in the leaves. A closely related species is *Epilachna varvestis*, the Mexican bean beetle. The Mexican bean beetle resembles the ladybird; it is coppery coloured with 16 black dots in 3 rows down its back. Its larvae are orange or yellow, humped-backed and fuzzy. Both feed on the lower surface of leaves, skeletonise the leaf.

Lepidoptera

The term "cutworm" applies to the larvae of various moth species in the Noctuidae family. Cutworms are general feeders and attack a wide range of plants, including the cucurbits. These cucurbit pests include the black cutworm (*Agrotis ipsilon*), the granulate cutworm (*Feltia subterranea*) and the spotted cutworm (*Amathes c-nigrum*). These lepidopterans may injure many types of vegetables and sometimes cereals. Larvae hide under clods or in tracks of the soil by day and feed at night, cutting young plants near the ground or feeding on the foliage. They cause greatest damage to seedlings and newly set plants, resulting in stand loss. Cutworms overwinter as larvae or pupae, depending on the species.

"Melonworm" and "pickleworm" are the common names of the larvae of two moth species in the family Pyralidae, with the name melonworm applying to the species *Diaphania hyalinata* and the name pickleworm applying to the species

Diaphania nitidalis. The larvae of these lepidopterans are restricted to feeding on the cucurbits, with both summer and winter squash being particularly favoured hosts. Melonworms feed mainly on the foliage, being primarily a leaf feeder which seldom feeds on the fruits. The pickleworm, in contrast, does feed on the fruits of squash, and can cause serious damage. Early in the season, pickleworms bore into the stems and terminal buds. Later in the season, pickleworms bore into the fruit from the side next to the ground. After feeding for about two weeks, the larva moves out of the fruit to the leaves, where it will spend seven to ten days as a pupa inside a cocoon. Pickleworm is highly dispersive, e.g. in the United States it overwinters in south Florida, spreading northward each spring. The pickleworm has been reported from Canada southward to South America.

"Squash vine borer" (*Melitta satyriniformis*) is a diurnal species of sesiid moth that attacks wild and cultivated varieties of *Cucurbita*. The moth of this lepidopteran resembles a large wasp without the stinging apparatus. Females deposit eggs near the base of the plant about the time the first planting begins to emerge until bloom. A small larva emerges and enters the stem of the plant. The larva then feeds inside the stem and eventually causes it to die. As the worm feeds, it pushes its excrement out of the entrance hole. The worm will eventually exit the stem and enter the soil to pupate (OMAFRA, 2011).

Hemiptera

"Squash bugs" (*Anasa tristis*) are Hemiptera and colloquially called "squash bugs" in North America because some of the species are pests of squash plants and other cucurbits. Squash bugs are quite mobile and can move easily among plants within a field and later move to late planted fields. The insects spend most of their time within the plant canopy, mainly around the stems and on the underside of the leaves. Both nymphs and adults feed by sucking sap from the plant. The adults often congregate near the base of the plant and young nymphs concentrate on the leaf where they hatch and then migrate to other plant parts. Squash bugs can increase in numbers very rapidly and, in high numbers, can cause plant wilting. This insect injects a toxin into the plant while feeding and this toxin results in wilting (OMAFRA, 2011).

Whitefly (*Bemisia tabaci*) is reported on all continents except Antarctica. Over 900 plant hosts are recorded and it reportedly transmits 111 virus species. Most of these whitefly transmitted diseases are begomoviruses, although whiteflies are also vectors of criniviruses, ipomoviruses (Adkins et al., 2006), potyvirus, torradoviruses and carlaviruses (Markham et al., 1994; Navas-Castillo, Fiallo-Olive and Sanchez-Campos, 2011). Its small size belies its ability to move large distances (Ellsworth and Martinez-Carillo, 2001; ISSG *Global Invasive Species Database*, 2011). *B. tabaci* is phytophagous and has been reported to produce silvering of leaves in *Cucurbita* (Schuster, Kring and Price, 1991).

Diptera

Vegetable leafminer (*Liriomyza* spp): Adult leafminers are small flies with a small wing length. Adult females puncture the upper surfaces of leaves with the ovipositor for feeding and egg laying. Adults feed on fluids that exude from the wounds. Eggs are laid singly in separate leaf punctures and hatch within two to seven days. Larvae feed on the leaf mesophyll for 6-12 days. Full-grown larvae slit the leaf epidermis, exit the leaf, fall to the ground and pupate in the soil. Losses in cucurbits due to these dipterans are difficult to quantify. The mining activity of these insects may cause photosynthetic reduction. High populations of leafminers can cause leaf distortion and premature leaf abscission. Infestation may also predispose the plant to other foliar diseases. Adult leafminers may be able to transmit viruses, because of their feeding habits.

Spider mite

Spider mites (*Tetranychus urticae*) are arachnids. Spider mites feed by sucking the contents from individual leaf cells. The feeding of one mite is not damaging but mites are usually present in huge numbers. Mite populations explode during hot, dry weather as they reproduce very rapidly. A female lays an average of 100 eggs and most eggs hatch within 3 days. Mites can complete a life cycle in 5 days when the temperature is 75°F or above.

Biotechnological developments

Genetic modification

As noted earlier in this chapter, the cultivated *Cucurbita* species are important food sources worldwide. Although some of the wild *Cucurbita* species have been reported to display resistance to viral disease, the cultivated *Cucurbita* display far lower levels of resistance. This is particularly true of the most economically important of the *Cucurbita*, *C. pepo*, and diseases caused by viruses can result in large economic losses (Provvidenti, 1990). The presence of these viruses has been reported in nearly all countries and territories where commercial crops of *C. pepo* are produced: Algeria, Australia, Brazil, Bulgaria, Canada, China, Costa Rica, the Czech Republic, the Dominican Republic, Egypt, England, France, Germany, Greece, Guadeloupe, Guam, Japan, Bailiwick of Jersey, Jordan, Honduras, Islamic Republic of Iran, Israel, Italy, Lebanon, Madagascar, Malaysia, Martinique, Mauritius, Mayotte, Mexico, Morocco, Nepal, the Netherlands, New Caledonia, New Zealand, Nigeria, Pakistan, Portugal, Puerto Rico, Saudi Arabia, Singapore, Spain, Sudan, Swaziland, Syrian Arab Republic, Chinese Taipei, Tunisia, Turkey, the United States, Bolivarian Republic of Venezuela and Yemen (Desbiez and Lecoq, 1997).

The primary means of controlling these diseases is control of the insect vectors, a methodology presenting a less than perfect solution. Due to the importance of the cultivated species affected by these viruses, and the difficulty in controlling spread of the viruses, the use of biotechnological techniques to develop resistant varieties has offered an alternative, successful approach. *Cucurbita pepo* cultivars containing the transgenes ZW20 (OECD Unique Identifier SEM-0ZW20-7) and CZW3 (OECD Unique Identifier SEM-0CZW3-2), have been commercially available since the mid-1990s in the United States. The ZW20 transgene confers resistance to the zucchini yellow mosaic virus (ZYMV) and the watermelon mosaic virus (WMV), both members of the potyvirus group. The CZW3 transgene confers resistance to ZYMV and WMV and to the cucumber mosaic virus (CMV), the type member of the cucumovirus group. Protection against these viruses is provided by insertion of DNA sequences encoding the coat protein gene of the various viruses into the *C. pepo* genome. Analysis shows that for both ZW20 and CZW3, a single copy of the transgene has inserted at a single site in the *C. pepo* genome (USDA, 1994). Although it is now known that protection occurs through interfering RNA mechanism (RNAi), expression of the transgenes was specifically engineered into the *C. pepo* cultivars and is controlled by the 35S promoter of the cauliflower mosaic virus (CaMV) to allow constitutive expression of the various coat proteins.

Other studies involving Cucurbita

Several species of *Cucurbita* have been used in classic studies of plant biochemistry (Frisse, Pimenta and Lange, 2003). *Cucurbita pepo* has long been used in studies of purine synthesis (Lovatt, 1983), amino acid transport and beta oxidation of fatty acids (Bush and Langston-Unkefer, 1988). This type of research has continued and, with use of molecular tools, the expression of the ascorbic acid oxidase has been studied (Lin and Varner, 1991), and cDNA from an anionic peroxidase has been obtained and its expression analysed in different kinds of tissues (Carpin et al., 1999). A chromosomal homologue to the aminocyclopropane-carboxylate synthase has also been cloned and sequenced (Huang et al., 1991).

Modern biotechnology has supported an in-depth study of infection resistance mechanisms by CMV (Havelda and Maule, 2000), and identified the genes that are systemically induced by attacks of the white flies *Bemisia argentifolii* and *B. tabaci* (van de Ven et al., 2000).

In addition, recent research has shown promising results for the use of the certain cucurbitacins or cucurbitacin analogues to arrest the cell cycle in tumor cells and induce apoptosis (Sun et al., 2005; Zhang et al., 2010; Boykin et al., 2011).

References

Adkins, S. et al. (2006), “A novel whitefly transmitted potyvirus isolated from cucurbits in Florida”, *Phytopathology*, Vol. 97, S3, pp. 145-154.

Adlerz, W.C. (1987), “Cucurbit potyvirus transmission by alate aphids (Homoptera: Aphididae) trapped alive”, *Journal of Economic Entomology*, Vol. 80, No. 1, pp. 87-92, *http://dx.doi.org/10.1093/jee/80.1.87*.

Adlerz, W.C. et al. (1983), “Zucchini yellow mosaic virus: A pathogen of squash and other cucurbits in Florida”, *Proceedings of the Florida State Horticultural Society*, Vol. 96, pp. 72-74, *http://fshs.org/proceedings-o/1983-vol-96/72-74%20(ADLERZ).pdf.*

Agrios, G.N. (1997), *Plant Pathology, 4th edition*, Academic Press, New York, New York.

Aliu, S. et al. (2011), “Morphological and nutritive variation in a collection of *Cucurbita pepo* L. growing in Kosovo”, *Notulae Scientia Biologicae*, Vol. 3, No. 2, pp. 119-122, *http://notulaebiologicae.ro/index.php/nsb/article/view/6066/5536*.

American Phytopathological Society (2011), APSnet, *www.apsnet.org/Pages/default.aspx* (accessed October 2011).

Anaya, A.L., R.C. Ortega and V. Nava Rodriguez (1992), “Impact of allelopathy in the traditional management of agroecosystems in Mexico”, Chapter 17, in: Rizvi, S.J.H. and V. Rizvi (eds), *Allelopathy: Basic and Applied Aspects*, Chapman and Hall, London, pp. 271-301.

Anaya, A.L. et al. (1987), “Perspectives on allelopathy in Mexican traditional agor ecosystems: A case study in Tlaxcala”, *Journal of Chemical Ecology*, Vol. 13, No. 11, pp. 2 083-2 101, November, *http://dx.doi.org/10.1007/BF01012873*.

Andrade-Cetto, A. and M. Heinrich (2005), “Mexican plants with hypoglycaemic effects used in the treatment of diabetes”, *Journal of Ethnopharmacology*, Vol. 99, No. 3, pp. 325-348, July.

Andres, T.C. (2004), “Progress in cucurbit genetics and breeding research”, pp 113-118, in: *Proceedings of Cucurbitaceae 2004*, the 8th EUCARPIA Meeting on Cucurbit Genetics and Breeding, Olomouc, Czech Republic, 12-17 July 2004.

Andres, T.C. (1990), “Biosystematics, theories on the origin, and breeding potential of *Cucurbita ficifolia* (Cucurbitaceae)”, in: Bates, D.M., R.W. Robinson and C. Jeffrey, (eds.), *Biology and Utilization of the Cucurbitaceae*, Cornell University Press, Ithaca, New York, pp. 102-118.

Andres, T.C. (1987a), “*Cucurbita fraterna*, the closest wild relative and progenitor of *C. pepo*”, *Cucurbit Genetics Cooperative Report*, Vol. 10, Article 36, pp. 69-71, *http://cuke.hort.ncsu.edu/cgc/cgc10/cgc10-36.html.*

Andres, T.C. (1987b), “Hybridization of *Cucurbita foetidissima* with *C. pedatifolia*, *C. radicans*, and *C. ficifolia*”, *Cucurbit Genetics Cooperative Report*, Vol. 10, Article 37, pp. 72-73, *http://cuke.hort.ncsu.edu/cgc/cgc10/cgc10-37.html.*

Andres, T.C. (1987c), “Relationship of *Cucurbita scabridifolia* to *C. foetidissima* and *C. pedatifolia*: A case of natural interspecific hybridization”, *Cucurbit Genetics Cooperative Report*, Vol. 10, Article 38, pp. 74-75, *http://cuke.hort.ncsu.edu/cgc/cgc10/cgc10-38.html.*

ANU (2005), Research School of Biological Sciences, Australian National University, *http://life.anu.edu.au./viruses/ICTVdB/57010077.htm* (accessed July 2005).

Argueta, A. (1994), *Atlas de las Plantas de la Medicina Tradicional Mexicana. 3 Volumes*, Instituto Nacional Indigenista, Mexico City, Mexico.

Arumuganathan, K. and E.D. Earle (1991), “Nuclear DNA content of some important plant species”, *Plant Molecular Biology Reporter*, Vol. 9, No. 3, pp. 208-218.

Asch, D.L. and N.B. Asch (1992), “Archeaobotany”, in: Stafford, R. (ed.), *Geoarchaeology of the Ambrose Flick Site*, Res. Series 10, Center for American Archaeology, Kampsville, Illinois.

Asch, D.L. and N.A. Sidell (1992), “Archeobotany”, in: Stafford, C.R. (ed.), *Early Woodland Occupations at the Ambrose Flick Site in the Northern Syn Bottom of West Central Illinois*, Research Series 10, Center for American Achaeology, Kampsville, Illinois, pp. 167-263.

Avila-Sakar, G., G.A. Krupnick and A.G. Stephenson (2001), “Growth and resource allocation in *Cucurbita pepo* ssp. *texana*: Effects of fruit removal”, *International Journal of Plant Sciences*, Vol. 162, No. 5, pp. 1 089-1 095, *http://dx.doi.org/10.1086/322879*.

Avila-Sakar, G., L.L Leist and A.G. Stephenson (2003), “Effects of the spatial pattern of leaf damage on growth and reproduction: Nodes and branches”, *Journal of Ecology*, Vol. 91, No. 5, pp. 867-879, October, *www.jstor.org/stable/3599710*.

Azurdia-Pérez, C.A. and M. González-Salán (1986), *Informe Final del Proyecto de Recolección de Algunos Cultivos Nativos de Guatemala*, Facultad de Agronomía, Universidad de San Carlos de Guatemala (USAC), Instituto de Ciencia y Technología Agrícolas (ICTA) and Consejo Internacional de Recursos Fitogenéticos (CIRF), IBPGR, Guatemala City, pp. 256.

Bailey, L.H. (1948), “Jottings in the cucurbitas”, *Gentes Herbarum 7*, pp. 447-477.

Bailey, L.H. (1943), “Species of *Cucurbita*”, *Gentes Herbarum 6*, pp. 265-322.

Bailey, L.H. (1929), “The domesticated cucurbitas. I”, *Gentes Herbarum 2*, pp. 63-115.

Bar-Nun, N. and A.M. Mayer (1990), “Cucurbitacins protect cucumber tissue against *Botrytis cinerea*”, *Phytochem.* Vol. 29 No. 3, pp. 787-791, *http://dx.doi.org/10.1016/0031-9422(90)80019-D*.

Bisognin, A.D. (2002), “Origin and evolution of cultivated Cucurbits”, *Ciencia Rural, Santa Maria*, Vol. 32, No. 5, pp. 715-713, *www.scielo.br/pdf/cr/v32n4/a28v32n4.pdf*.

Blancard, D., H. Lecoq and M. Pitrat with M. Javoy (1994), *A Colour Atlas of Cucurbit Diseases: Observation, Identification and Control*, Manson Publishing, London, and Wiley & Sons, N.Y.

Borghi, B. (1976), "Evaluation of necrosis in Cucurbita pepo L.", in: *Heterosis in Plant Breeding*, Proceedings 7th Congress, Eucarpia, Elsevier, Amsterdam, Netherlands.

Boyette, G., E. Templeton and L.R. Oliver (1984), "Texas gourd (*Cucurbita texana*) control", *Weed Science*, Vol. 32, No. 5, pp. 649-655, September, *www.jstor.org/stable/4043984*.

Boykin, C. et al. (2011), "Cucurbitacin IIa: A novel class of anti-drug inducing non-reversible actin aggregation and inhibiting survivin independent of JAK2/STAT3 phosphorylation", *British J. of Cancer*, Vol. 104, No. 5, pp. 781-789, March, *http://dx.doi.org/10.1038/bjc.2011.10*.

Bretting, P.K. (1990), "New perspectives on the origin and evolution of New World domesticated plants: Introduction", *Economic Botany*, Vol. 44, No. 3, Supplement: New Perspectives on the Origin and Evolution of New World Domesticated Plants, pp. 1-5, *www.jstor.org/stable/4255267*.

Brown, R.N. and J.R. Myers (2002), "A genetic map of squash (*Cucurbita* sp.) with randomly amplified polymorphic DNA markers and morphological markers", *J Amer. Soc. for Hort. Science*, Vol. 127 No. 4, pp. 568-575, *http://journal.ashspublications.org/content/127/4/568.full.pdf*.

Brunt, A.A. et al. (eds.) (1996), "Plant viruses online: Descriptions and lists from the VIDE Database", C.A.B. International, U.K., *http://pvo.bio-mirror.cn/refs.htm#vide96*.

Brust, G.E. and M.E. Barbercheck (1992), "Effect of dietary cucurbitacin C on southern corn rootworm (Coleoptera: Chrysomelidae) egg survival", *Environmental Entomology*, Vol. 21, No. 6, pp. 1 466-1 471, *http://dx.doi.org/10.1093/ee/21.6.1466*.

Bukasov, S.M. (1981), *Las Plantas Cultivadas de México, Guatemala y Colombia*, Proyecto CATIE-GTZ de Recursos Geneticos, Turrialba, Costa Rica.

Bush, D.R. and P.J. Langston-Unkefer (1988), "Amino acid transport into membrane vesicles isolated from zucchini", *Plant Physiology*, Vol. 88, No. 2, pp. 487-490, October.

Canto-Aguilar, M.A. and V. Parra-Tabla (2000), "Importance of conserving alternative pollinators: Assessing the pollination efficiency of the squash bee, *Peponapis moschata* (Cucurbitaceae)", *Journal of Insect Conservation*, Vol. 4, No. 3, pp. 203-210, September.

Cárdenas, M. (1944), "Las cucurbitas cultivadas de Bolivia", *Revista Agricola* (*Cochabamba*), Vol. 2, pp. 3-12.

Cardoso, A. (2004), "Depression by inbreeding after four successive self-pollination squash generations", *Scientia Agricola*, Vol. 61, pp. 224-227.

Carpin, S. et al. (1999), "Molecular cloning and tissue-specific expression of an anionic peroxidase in zucchini", *Plant Physiology*, Vol. 120, No. 3, pp. 799-810, July.

Castetter, E.F. (1925), "Horticultural groups of cucurbits", *Proceedings of the American Society for Horticultural Science*, Vol. 22, pp. 338-340.

Chala, V.H., C.W. Harrison and R.S. Halliwell (1987), "Identification of two distinct strains of watermelon mosaic virus 2 affecting cucurbits in Texas", *Plant Disease*, Vol. 71, No. 8, pp. 750-752, *http://dx.doi.org/10.1094/PD-71-0750*.

Chiej, R. (1984), *Encyclopaedia of Medicinal Plants (MacDonald Encyclopedias)*, Little Brown and Company, London.

Chopra, R.N., N. Nayar and I.C. Chopra (1956), *Glossary of Indian Medicinal Plants*, Council of Scientific and Industrial Research, New Delhi, India.

Chou, H.C. and M. Huangfu (1960), "Pumpkin seed (*Cucurbita moschata*) in the treatment of acute schistosomiasis", *Chinese Medical Journal*, Vol. 80, No. 2, pp. 115-120, February.

Chung, S.M., D.S. Decker-Walters and J.E. Staub (2003), "Genetic relationships within the Cucurbitaceae as assessed by consensus chloroplast simple sequence repeats (ccSSR) marker and sequ. analyses", *Can. J. Botany* Vol.81 No.8 pp. 814-832, *http://dx.doi.org/10.1139/b03-074.*

Cohen, R., A. Hanan and H.S. Paris (2003), "Single-gene resistance to powdery mildew in zucchini squash (*Cucurbita pepo*)", *Euphytica*, Vol. 130, No. 3, pp. 433-441, April.

Cowan, C.W. and B.D. Smith (1993), "New perspectives on a wild gourd in eastern North America", *Journal of Ethnobiology*, Vol. 13, No. 1, pp. 17-54, Summer, available at: *https://ethnobiology.org/sites/default/files/pdfs/JoE/13-1/CowanSmith.pdf.*

Cutler, H.C. and T.W. Whitaker (1969), "A new species of *Cucurbita* from Ecuador", *Annals of the Missouri Botanical Garden*, Vol. 55, No. 3, pp. 392-396, *http://dx.doi.org/10.2307/2395132.*

Cutler, H.C. and T.W. Whitaker (1961), "History and distribution of the cultivated cucurbits in the Americas", *American Antiquity* Vol. 26 No. 4, pp. 469-485, *http://dx.doi.org/10.2307/278735.*

Dane, F. (1983), "Cucurbits", in: Tanksley, S.D. and T.J. Orton (eds.), *Isozymes in Plant Genetics and Breeding*, Part B, Elsevier Science Publishers, Amsterdam, Netherlands.

Davis, R.F. and M.K. Mizuki (1987), "Detection of cucurbit viruses in New Jersey", *Plant Disease*, Vol. 71, No. 1, pp. 40-44, *www.apsnet.org/publications/plantdisease/backissues/Documents/1987Articles/PlantDisease71n01_40.pdf.*

Davis, R.M. et al. (2008), "Diseases", in: *UC IPM Pest Management Guidelines: Cucurbits*, University of California, Agriculture and Natural Resources Publication 3445, pp. 45-65, *www.ipm.ucdavis.edu/PMG/selectnewpest.cucurbits.html* (accessed November 2009).

de Oliveira, A.C.B. et al. (2003), "Resistance to papaya ringspot virus in summer squash *Cucurbita pepo* L. introgressed from an interspecific *C. pepo* × *C. moschata* cross", *Euphytica*, Vol. 132, No. 2, pp. 211-215, July.

Decker, D.S. (1988), "Origin(s), evolution, and systematics of *Cucurbita pepo*", *Economic Botany*, Vol. 42, No. 1, pp. 4-15, January-March, *www.jstor.org/stable/4255033.*

Decker, D.S. (1986), "A biosystematic study of *Cucurbita pepo*", Ph.D. Thesis, Texas A&M University, College Station.

Decker, D.S. (1985), "Numerical analysis of allozyme variationin *Cucurbita pepo* L.", *Economic Botany*, Vol. 39, No. 3, pp. 300-309, July.

Decker, D.S. and H.D. Wilson (1987), "Allozyme variation in the *Cucurbita pepo* complex: *C. pepo* var. *ovifera* vs. *C. texana*", *Systematic Botany*, Vol. 12, No. 2, pp. 263-273, April-June, *www.jstor.org/stable/2419320.*

Decker-Walters, D.S. and T.W. Walters (2000), "Squash", in: Kiple, K.F. and K.C. Ornelas (eds.), *The Cambridge World History of Food*, Cambridge University Press, pp. 335-351.

Decker-Walters, D.S. et al. (2002), "Diversity in free-living populations of *Cucurbita pepo* (Cucurbitaceae) as assessed by random amplified polymorphic DNA", *Systematic Botany*, Vol. 27, No. 1, pp. 19-28, January-March, *www.jstor.org/stable/3093892.*

Decker-Walters, D.S. et al. (1993), "Isozymic chacterization of wild populations of *Cucurbita pepo*", *Journal of Ethnobiology*, Vol. 13, No. 1, pp. 55-72, Summer, available at: *https://ethnobiology.org/sites/default/files/pdfs/JoE/13-1/Decker-Walters.et.al.pdf.*

Decker-Walters, D.S. et al. (1990), "Genealogy and gene flow among annual domesticated species of *Cucurbita*", *Can. J. of Botany*, Vol. 68, No. 4, pp. 782-789, *http://dx.doi.org/10.1139/b90-104.*

Desbiez, C. and H. Lecoq (1997), "Zucchini yellow mosaic virus", *Plant Pathology*, Vol. 46, pp. 809-829, *http://onlinelibrary.wiley.com/doi/10.1046/j.1365-3059.1997.d01-87.x/pdf.*

Dinan, L. et al. (1997), "Cucurbitacins are insect steroid hormone antagonists acting at the ecdysteroid receptor", *Biochemical Journal*, Vol. 327, Pt. 3, pp. 643-650, November.

Discover Life (2011), Interactive encyclopedia about the taxonomy, natural history, distribution, abundance and ecology of species, at: *www.discoverlife.org* (accessed September 2011).

Dodds, J.A. et al. (1984), "Aphid- and whitefly-transmitted cucurbit viruses in Imperial County, California", *Phytopathology*, Vol. 72, No. 2, pp. 221-225, *http://dx.doi.org/10.1094/Phyto-74-221.*

Du, X. et al. (2011), "Genetic divergence among inbred lines of *Cucurbita moschata* from China", *Scientia Horticulturae* Vol. 127 No. 3, pp. 207-213, *http://dx.doi.org/10.1016/j.scienta.2010.10.018.*

Duke, J.A. and E.S. Ayensu (1985), *Medicinal Plants of China*, Reference Publications, Inc., Missouri, United States.

Eben, A. and M.E. Barbercheck (1996), "Field observations on host plant associations and natural enemies of diabroticite beetles (Chrysomelidae: Luperini) in Veracruz, Mexico", *Acta Zoológica Mexicana*, Vol. 67, pp. 47-65.

Eben, A., M.E. Barbercheck and M. Aluja (1997), "Mexican diabroticite beetles (Chrysomelidae: Galerucinae): II. Laboratory tests for the preference of cucurbitacins", *Entomologia Experimentalis et Applicata*, Vol. 82, No. 1, pp. 63-72, January, *http://dx.doi.org/10.1046/j.1570-7458.1997.00113.x.*

Ellsworth, P.C. and J.L. Martinez-Carrillo (2001), "IPM for *Bemisia tabaci*: A case study from North America", *Crop Protection*, Vol. 20, pp. 853-869, *www.issg.org/database/species/reference_files/bemtab/Ellsworth%20and%20Martinez-Carrillo,%202001.pdf.*

Emshwiller, E. (2006), "Genetic data and plant domestication", Chapter 8, in: Zeder, M.A. et al. (eds.), *Documenting Domestication: New Genetic and Archaeological Paradigms*, University of California Press, Berkeley and Los Angeles, California, pp. 99-122, *www.botany.wisc.edu/courses/botany_940/06CropEvol/papers/Emshwiller06.pdf.*

Esquinas-Alcazar, J.T. and P.J. Gulick (1983), *Genetic Resources of Cucurbitaceae: A Global Report*, IBPGR, Rome.

Esteras, C. et al. (2008), "Diversity of Spanish landraces of Cucumis Sativus and Cucurbita ssp.", in: Pitrat, M. (ed.), *Cucurbitaceae 2008*, Proceedings of the IX EUCARPIA Meetings on Genetics and Breeding of Cucurbitaceae, INRA, Avignon, France, 21-24 May 2008.

Facciola, S. (1990), *Cornucopia: A Source Book of Edible Plants*, Kampong Publications, Vista, California.

FAOSTAT (2013), FAO Statistics online database, "Production / Crops, – pumpkins, squash and gourds, Year 2013", Food and Agriculture Organization of the United Nations, *http://faostat3.fao.org/home/E* (accessed 5 January 2016).

Ferguson, J.E. and R.L. Metcalf (1985), "Cucurbitacins: Plant derived defense compounds for *Diabroticites* (Coleoptera: Chrysomelidae)", *Journal of Chemical Ecology*, Vol. 11, No. 3, pp. 311-318, March, *http://dx.doi.org/10.1007/BF01411417.*

Ferriol, M. and B. Picó (2008), "Pumpkin and winter squash", in: Prohens-Tomas, J., F. Nuez and M.J. Carena (eds.), *Handbook of Vegetable Breeding*, Springer, Berlin, pp 317-349.

Ferriol, M., B. Picó and F. Nuez (2004), "Morphological and molecular diversity of a collection of *Cucurbita maxima* landraces", *Journal of the American Society for Horticultural Science*, Vol. 129, No. 1, pp. 60-69, January.

Ferriol, M., B. Picó and F. Nuez (2003a), "Genetic diversity of a germplasm collection of *Cucurbita pepo* using SRAP and AFLP markers", *Theoretical and Applied Genetics*, Vol. 107, No. 2, pp. 271-282, July.

Ferriol, M., B. Picó and F. Nuez (2003b), "Genetic diversity of some accessions of *Cucurbita maxima* from Spain using RAPD and SBAP markers", *Genetic Resources and Crop Evolution*, Vol. 50, No. 3, pp. 227-238, May.

Ferriol, M. et al. (2004), "Molecular diversity of a germplasm collection of squash (*Cucurbita moschata*) determined by SRAP and AFLP markers", *Crop Science*, Vol. 44, No. 2, pp. 653-664, *http://dx.doi.org/10.2135/cropsci2004.6530.*

Filov, A.I. (1966), "Ekologija i klassifikatzija tykuy", *Bjulleten Glavnogo Botaniceskogo Sada*, Vol. 63, pp. 33-41 (in Russian).

Frisse, A., M.J. Pimenta and T. Lange (2003), "Expression studies of gibberellin oxidases in developing pumpkin seeds", *Plant Physiology*, Vol. 131, No. 3, pp. 1 220-1 227, March, *http://dx.doi.org/10.1104/pp.015206.*

Fujiyoshi, P.T., S.R. Gliessman and J.H. Langenheim (2007), "Factors in the suppression of weeds by squash interplanted with corn", *Weed Biology and Management*, Vol. 7, No. 2, pp. 105-114, June, *http://dx.doi.org/10.1111/j.1445-6664.2007.00242.x.*

Fukami, H. and R. Nishida (1990), "Sequestration of distasteful compounds by some pharmacophagous insects", *Journal of Chemical Ecology*, Vol. 16, No. 1, pp. 151-164, January, *http://dx.doi.org/10.1007/BF01021276.*

Fursa, T.B. and A.I. Filov (1982), "Cucurbitaceae", in: Korovina, O.N. and T.B. Fursa (eds), *Flora of Cultivated Plants*, Kolos, Moscow, pp. 102-132.

Gallegos, J.J.G. (1990), "Avance generacional de genotipos de calabacita con resistencia a virus mosaico del pepino y de sandía 1 y 2", in : *Informe de Investigación, Ciclo 1989-90*, Proyecto: Estudio y Control de las Enfermedades Virales en el Cultivo de la Calabacita, INIFAP-SARH, Mexico, pp. 1-6.

Gámez-Virués, S. and A. Eben (2005), "Comparison of beetle diversity and incidence of parasitism in Diabroticina (Coleoptera: Chrysomelidae) species collected on cucurbits", *Florida Entomol.* Vol. 88 No. 1 pp. 72-76, *http://journals.fcla.edu/flaent/article/view/75391/73049.*

Garzón-Tiznado, J.A., S. Montes-Hernández and F.A. Becerra (1993), "Fuentes de resistencia a los virus mosaico del pepino y de la sandía-2, en calabaza (*Cucurbita moschata*) en México", *Revista Mexicana de Fitopatología*, Vol. 11, pp. 167-171.

Gilbert-Albertini, F. et al. (1993), "Resistance of *Cucurbita moschata* to watermelon mosaic virus type 2 and its genetic relation to resistance to zucchini yellow mosaic virus", *Euphytica*, Vol. 69, No. 3, pp. 231-237, January.

Gillespie, J.J. et al. (2003), "Convergent evolution of cucurbitacin feeding in spatially isolated rootworm taxa (Coleoptera: Chrysomelidae; Galerucinae, Luperini)", *Molecular Phylogenetics and Evolution*, Vol. 29, No. 1, pp. 161-175, October.

Gong, L. et al. (2012), "Genetic relationships and evolution in *Cucurbita pepo* (pumpkin, squash, gourd) as revealed by simple sequence repeat polymorphisms", *Theoretical and Applied Genetics*, Vol. 124, No. 5, pp. 875-891, March, *http://dx.doi.org/10.1007/s00122-011-1752-z*.

Gossell-Williams, M., A. Davis and N. O'Connor (2006), "Inhibition of testosterone-induced hyperplasia of the prostate of sprague-dawley rats by pumpkin seed oil", *Journal of Medicinal Food*, Vol. 9, No. 2, pp. 284-286, Summer.

Gray, A. (1850), "Cucurbitaceae *Cucurbita texana*", *Boston Journal of Natural History*, Vol. 6. See also: *www.theplantlist.org/tpl/record/kew-2747227.*

Greber, R.S. (1978), "Watermelon mosaic virus 1 and 2 in Queensland cucurbit crops", *Australian Journal of Agricultural Research*, Vol. 29, No. 6, pp. 1 235-1 245, *http://dx.doi.org/10.1071/AR9781235.*

Grubben, G.L.H. (2004), *Plant Resources of Tropical Africa 2: Vegetables*, PROTA Foundation/Backhuys Publishers/CTA Wageningen, Netherlands, *www.ebookdb.org/reading/53283D1E3E6535243D407369/Plant-Resources-Of-Tropical-Africa--Vegetables*.

Gwanama, C., M.T. Labuschagne and A.M. Botha (2000), "Analysis of genetic variation in *Cucurbita moschata* by random amplified polymorphic DNA (RAPD) markers", *Euphytica*, Vol. 113, No. 1, pp. 19-24, May.

Hart, J.P., R.A. Daniels and C.J. Sheviak (2004), "Do *Cucurbita* gourds float fishnets?", *American Antiquity*, Vol. 69, No. 1, pp. 141-148, January, *http://dx.doi.org/10.2307/4128352*.

Havelda, Z. and A.J. Maule (2000), "Complex spatial responses to cucumber mosaic virus infection in susceptible *Cucurbita pepo* cotyledons", *The Plant Cell*, Vol. 12, No. 10, pp. 1 975-1 985, October.

Havey, M.J. et al. (1998), "Differential transmission of the *Cucumis* organellar genomes", *Theoretical Applied Genetics*, Vol. 97, No. 1, pp. 122-128, July.

Hayes, C.N., J.A. Winsor and A.G. Stephenson (2005a), "Environmental variation influences the magnitude of inbreeding depression in *Cucurbita pepo* ssp. *texana* (Cucurbitaceae)", *Journal of Evolutionary Biology*, Vol. 18, No. 1, pp. 147-155, January.

Hayes, C.N., J.A. Winsor and A.G. Stephenson (2005b), "Multigenerational effects of inbreeding in *Cucurbita pepo* ssp. *texana* (Cucurbitaceae)", *Evolution*, Vol. 59, No. 2, pp. 276-286.

Hemleben, V. et al. (1988), "Organization and length heterogeneity of plant ribosomal RNA genes", in: Kahl, G. (ed.), *Architecture of Eukaryotic Genes*, VCH Verlagsgesellschaft, Weinheim, pp. 371-383.

Hendrix, S.D. (1988), "Herbivory and its impact on plant reproduction", in: Lovett Doust, J. and L. Lovett Doust (eds.), *Plant Reproductive Biology*, Oxford University Press, Oxford, pp. 246-263.

Hodgekinson, I.D. and M.K Hughes (1982), *Insect Herbivory*, Chapman and Hall, New York.

Huang, P.L. et al. (1991), "Two genes encoding 1-aminocyclopropane-1-carboxylate synthase in zucchini (*Cucurbita pepo*) are clustered and similar but differentially regulated", *Proceedings of the National Academy of Sciences USA*, Vol. 88, No. 16, pp. 7 021-7 025.

Hurd, P.D. (1966), "The pollination of pumpkins, gourds and squashes (Genus Cucurbita)", in: Second International Symposium on Pollination, 1964, *Bee World*, Vol. 47 (Supp), pp. 97-98.

Hurd, P.D. and E.G. Linsley (1970), "A classification of the squash and gourd bees *Peponapis* and *Xenoglossa*", *California Publications in Entomology*, Vol. 62, pp. 1-39.

Hurd, P.D. and E.G. Linsley (1967), "South American squash and gourd bees of the genus *Peponapis* (Hymenoptera: Apoidea)", *Annals of the Entomology Society of America*, Vol. 60, No. 3, pp. 647-661, *http://dx.doi.org/10.1093/aesa/60.3.647*.

Hurd, P.D. and E.G. Linsley (1964), "The squash and gourd bees – genera *Peponapis* Robertson and *Xenoglossa* Smith – inhabiting America north of Mexico (Hymenoptera: Apoidea)", *Hilgardia*, Vol. 35, No. 15, pp. 375-477, *http://dx.doi.org/10.3733/hilg.v35n15p375*.

Hurd, P.D., E.G. Linsley and T.W. Whitaker (1971), "Squash and gourd bees (*Peponapis*, *Xenoglossa*) and the origin of the cultivated *Cucurbita*", *Evolution*, Vol. 25, No. 1, pp. 218-234, March, *http://dx.doi.org/10.2307/2406514*.

ISSG, *Global Invasive Species Database*, *www.issg.org* (accessed October 2011).

Jahn, M., H.M. Munger and J.D. McCreight (2002), "Breeding cucurbit crops for powdery mildew resistance", in: Berlanger, R.R. et al (eds.), *The Powdery Mildews, A Comprehensive Treatise*, American Phytopathological Society, St. Paul, Minnesota, pp. 239-248.

Janick, J. and R.E. Paull (2007), *The Encyclopedia of Fruits and Nuts*, CAB International, Oxfordshire, United Kingdom.

Jeffrey, C. (1990), "Systematics of the Cucurbitaceae: An overview", in: Bates, D.M., R.W. Robinson and C. Jeffrey (eds.), *Biology and Utilization of the Cucurbitaceae*, Cornell University Press, Ithaca, New York, pp. 3-9.

Jobst, J., K. King and V. Hemleben (1998), "Molecular evolution of the internal transcribed spacers (ITS1 and ITS2) and phylogenetic relationships among species of the family Cucurbitaceae", *Molecular Phylogenetics and Evolution*, Vol. 9, No. 2, pp. 204-219, April.

Jossey, S. and M. Badadoost (2006), "First report of Tobacco ringspot virus in *Cucurbita pepo* in Illinois", *Plant Disease*, Vol. 90, No. 10, p. 1 361, *http://dx.doi.org/10.1094/PD-90-1361B.*

Julier, H.E. and T.H. Roulston (2009), "Wild bee abundance and pollination service in cultivated pumpkins; farm management, nesting behavior, and landscape effects", *Journal of Economic Entomology*, Vol. 102, No. 2, pp. 563-573, April.

Katzir, N. et al. (2000), "Further ISSR and preliminary SSR analysis of relationships among accessions of *Cucurbita pepo*", *Acta Horticulturae*, Vol. 510, No. 69, pp. 433-439, *http://dx.doi.org/10.17660/ActaHortic.2000.510.69.*

King, F.B. (1985), "Early cultivated cucurbits in Eastern North America", in: Ford, R.I. (ed.), *Prehistoric Food Production in North America*, Anthropological Paper No. 75, Museum of Anthropology, University of Michigan, Ann Arbor, Michigan.

King, K., J. Jobst and V. Hemleben (1995), "Differential homogenization and amplification of two satellite DNAs in the genus *Cucurbita* (Cucurbitaceae)", *Journal of Molecular Evolution*, Vol. 41, No. 6, pp. 996-1 005, December.

King, K. et al. (1993), "Molecular evolution of the intergenic spacer in the nuclear ribosomal RNA genes of Cucurbitaceae", *Journal of Molecular Evolution*, Vol. 36, No. 2, pp. 144-152.

Kirkpatrick, K.J. and H.D. Wilson (1988), "Interspecific gene flow in *Cucurbita: C. texana* vs. *C. pepo*", *Americ. J. of Botany*, Vol. 75, No. 4, pp. 519-527, *www.jstor.org/stable/2444217.*

Kirkpatrick, K.J., D.S. Decker and H.D. Wilson (1985), "Allozyme differentiation in the *Cucurbita pepo* complex: *C. pepo* var. *medullosa* vs. *C. texana*", *Economic Botany*, Vol. 39, No. 3, pp. 289-299, July.

Kreuter, M.H. (2000), "Hormone disbalance and urinary bladder disease", in: *Phyto Novum*, Emil Flachsmann AG, Zurich, Switzerland, pp. 2-24.

Krysan, J.L. and R.F. Smith (1987), "Systematics of the *virgifera* species group of *Diabrotica* (Coleoptera: Chrysomelidae: Galerucinae)", *Entomography*, Vol. 5, pp. 375-484.

Kwon, Y.-S. et al. (2004), "A comparative study of the RAPD and SSR markers in establishing a genetic relationship of the various types of *Cucurbita*", *Korean Journal of Genetics*, Vol. 26, No. 2, pp. 115-122.

Lance, D.R. and G.R. Sutter (1990), "Field-cage and laboratory evaluations of semiochemical-based baits for managing western corn rootworm (Coleoptera: Chrysomelidae)", *Journal of Economic Entomology*, Vol. 83, No. 3, pp. 1 985-1 990, *http://dx.doi.org/10.1093/jee/83.3.1085.*

Lebeda, A. and E. Křístová (2000), "Interactions between morphotypes of *Cucurbita pepo* and obligate biotrophs (*Pseudoperonospora cubensis*, *Erysiphe cichoracearum* and *Sphaerotheca fulginea*)", *Acta Hort.* Vol. 510, pp. 210-225, *http://dx.doi.org/10.17660/ActaHortic.2000.510.35.*

Lebeda, A. and E. Křístová (1996), "Genotypic variation in field resistance of *Cucurbita pepo* cultivars to powdery mildew (*Erysiphe cichoracearum*)", *Genetic Resources and Crop Evolution*, Vol. 43, No. 1, pp. 79-84, February.

Lebeda, A. and M.P. Widrlechner (2004), "Response of wild and weedy *Cucurbita* L. to pathotypes of *Pseudoperonospora cubensis* (Berk. & Curt.) Rostov (cucurbit downy mildew)", in: Spencer-Phillips, P.T.N. and M. Jeger (eds.), *Advances in Downy Mildew Research – Volume 2*, Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 203-210.

Lebeda, A., E. Křístková and K. Doležal (1999), "Peroxidase isozyme polymorphism in *Cucurbita pepo* cultivars with various morphotypes and different level of field resistance to powdery mildew", *Sci. Hort.*, Vol. 81, No. 2, pp. 103-112, *http://dx.doi.org/10.1016/S0304-4238(98)00261-1*.

Lebeda, A. et al. (2006), "Cucurbits (Cucurbitaceae; Cucumis spp., Cucurbita spp., Citrullis spp.)", Chapter 8, in: Singh, R.S. (ed.), *Genetic Resources, Chromosome Engineering and Crop Improvement: Vegetable Crops Volume 3*, CRC Press, Boca Raton, Florida, pp. 271-376, *http://dx.doi.org/10.1201/9781420009569.ch8*.

Lecoq, H. and C. Desblez (2009), "Watermelon mosaic virus and zucchini yellow virus", in: Mahy, B.W.J. and M.H.V. Van Regenmortel (eds.), *Desk Encyclopedia of Plant and Fungal Virology*, Academic Press, Oxford.

Lecoq, H., M. Pitrat and M. Clement (1981), "Identification and characterization of a potyvirus that induces muskmelon yellow stunt", *Agronomie*, Vol. 1, pp. 827-834.

Lin, L.S. and J.E. Varner (1991), "Expression of ascorbic acid oxidase in zucchini squash (*Cucurbita pepo* L.)", *Plant Physiology*, Vol. 96, No. 1, pp. 159-165, May.

Lira, R. (1991), *Estudios Taxonómico y Ecogeográfico de las Cucurbitáceas de Latinoamérica, 2^o Reporte Semestral*, International Board for Plant Genetic Resources, Rome.

Lira, R. (1988), *Cucurbitaceae de la Peninsula de Yucatán: Taxonomía y Etnobotánica*, M.S. Thesis, Instituto Nacional de Investigaciones sobre Recursos Bióticos, Xalapa, Veracruz, Mexico.

Lira, R. (1985), "Identidad taxonómica de las calabazas cultivadas (*Cucurbita* spp.) en la Peninsula de Yucatán", *Biótica*, Vol. 10, No. 3, pp. 301-307.

Lira, R., T.C. Andres and M. Nee (1995), "Cucurbita L.", in: Lira, R. (ed.), *Estudios Taxonómicos y Ecogeográficos de las Cucurbitaceae Latinoamericanas de Importancia Económica: Cucurbita*, *Sechium*, *Sicana* y *Cyclanthera*, Systematic and Ecogeographic Studies on Crop Genepools 9, International Plant Genetic Resources Institute, Rome, pp. 1-115.

Lira-Saade, R. and S. Montes-Hernández (1992), "Cucúrbitas (Cucurbita spp.)", in: Hernández-Bermejo, J.E. and J. León (eds.), *Cultivos Marginados: Otra Perspectiva de 1492*, Colección FAO, Producción y Protección Vegetal No. 26, FAO, Rome, pp. 61-75.

Lira-Saade, R., L. Eguiarte Fruns and S. Montes Hernández (2009), *Proyecto Recopilación y Análisis de la Información Existente de las Especies de los Géneros* Cucurbita *y* Sechium *que Crecen y/o se Cultivan en México*, Informe Final, CONABIO, México, D.F, *www.biodiversidad.gob.mx/genes/centrosOrigen/Cucurbita%20y%20Sechium/Informe_Final/Informe%20final%20Cucurbita%20y%20Sechium.pdf*.

Lisa, V. et al. (1981), "Characterization of a potyvirus that causes zucchini yellow mosaic", *Phytopathology*, Vol. 71, No. 7, pp. 667-672, available at: *www.apsnet.org/publications/phytopathology/backissues/Documents/1981Articles/Phyto71n07_667.pdf*.

Lopez, J.F., S. Brune and G.P. Henz (1999), "Metodologia de avaliacao da resistencia de germoplasma de aboboras e morangas a *Phytophthora capsici*", *Horticulura Brasileira*, Vol. 17, Supplement, pp. 30-32 (in Portuguese).

Lovatt, C.J. (1983), "*De novo* purine biosynthesis in intact cells of *Cucurbita pepo*", *Plant Physiology*, Vol. 73, No. 3, pp. 766-772, November.

Loy, J.B. and C.E. Broderick (1990), "Growth, assimilate partitioning, and productivity of bush and vine *Cucurbita maxima*", in: Bates, Robinson and Jeffrey (eds.), *Biology and Utilization of the Cucurbitaceae*, Cornell University, Ithaca, New York and London, pp. 436-447.

Mahzabin, F., S. Parvez and M.F. Alam (2008), "Micropropagation of *Cucurbita maxima* Duch. through shoot tip culture", *Journal Bio-science*, Vol. 16, pp. 59-65.

Maluf, W.R. and E.L.S. Souza (1984), "Resistência ao vírus do mosaico da melancia-1 (WMV-1) em moranga *Cucurbita maxima* Duch", *Horticultura Brasileira*, Vol. 2, pp. 22-25 (in Portuguese).

Mariano, B.N. (2001), "Efectos de la Herbivoría sobre la Adecuación Masculina y Femenina de *Cucurbita argyrosperma* ssp. *Sororia*", PhD Thesis, Instituto de Ecología, Universidad Nacional Autónoma de México, México, D.F.

Mariano, N. and R. Dirzo (2002), "*Cucurbita argyrosperma* ssp. *sororia* (L.H. Bailey) Merrick & Bates (Cucurbitaceae), Agüichichi", in: Noguera-Martínez, F. et al. (eds.), *Historia Natural de Chamela*, Instituto de Biología, Universidad Nacional Autónoma de México, pp. 167-170.

Markham, P.G. et al. (1994), "The transmission of geminiviruses by *Bemisia tabaci*", *Pesticide Science*, Vol. 42, No. 2, pp. 123-128, October, *http://dx.doi.org/10.1002/ps.2780420209.*

Martínez-Crovetto, R. (1974), "*Cucurbitaceae*", in: Burkart, A. (ed.), *Flora Ilustrada de Entre Ríos (Argentina)*, Colección Científica del I.N.T.A., Buenos Aires, pp. 63-94.

Martínez-Crovetto, R. (1965), "*Cucurbitaceae*", in: Cabrera, A.L. (ed.), *Flora de la Provincia de Buenos Aires*, Colección Científica del I.N.T.A., Buenos Aires, pp. 390-407.

Martínez-Crovetto, R. (1954), "Synopsis des Cucurbitacées de l'Uruguay", *Notulae Systematicae (Paris)*, Vol. 15, Nos. 1-4, pp. 47-55.

Merrick, L.C. (1995), "Squashes, pumpkins and gourds", in: Smartt, J. and S.W. Simmons (eds.), *Evolution of Crop Plants*, pp. 97-105, Longman Scientific and Technical, London.

Merrick, L.C. (1991), "Systematics, evolution, and ethnobotany of a domesticated squash, its wild relatives and allied species in the genus Cucurbita", PhD Thesis Cornell Univ., Ithaca, NY.

Merrick, L.C. (1990), "Systematics and evolution of a domesticated squash, *Cucurbita argyosperma*, and its wild and weedy relatives", in: Bates, Robinson and Jeffrey (eds.), *Biology and Utilization of the Cucurbitaceae*, Cornell University Press, Ithaca, New York, pp. 77-95.

Merrick, L.C. and D.M. Bates (1989), "Classification and nomenclature of *Cucurbita argyrosperma* Huber", *Baileya*, Vol. 23, pp. 94-102.

Merrick, L.C. and G.P. Nabhan (1985), "Natural hybridization of wild and cultivated *Cucurbita* in Mexico: Implications for crop evolution", *Ecological Society of America Bulletin*, Vol. 66.

Metcalf, R.L. (1986), "Coevolutionary adaptations of rootworm beetles (Coleoptera: Chrysomelidae) to cucurbitacins", *Journal of Chemical Ecology*, Vol. 12, No. 5, pp. 1 109-1 124, May, *http://dx.doi.org/10.1007/BF01638999.*

Metcalf, R.L., R.A. Metcalf and A.M. Rhodes (1980), "Cucurbitacins as kairomones for diabroticite beetles", *Proceedings of the National Academy of Sciences USA*, Vol. 77, No. 7, pp. 3 769-3 772, July.

Metcalf, R.L. et al. (1982), "Cucurbitacin contents and diabroticite (Coleoptera: Chrysomelidae) feeding upon *Cucurbita* spp", *Environmental Entomology*, Vol. 11, No. 4, pp. 931-937, *http://dx.doi.org/10.1093/ee/11.4.931.*

Michener, C.D. (2007), *The Bees of the World*, 2nd edition, Johns Hopkins University Press, Baltimore, Maryland.

Millán, R. (1947), "Los zapallitos de tronco de Sudamérica extratropical", *Darwiniana*, Vol. 7, No. 3, pp. 333-345, January, *www.jstor.org/stable/23211608.*

Millán, R. (1945), "Variaciones del zapallito amargo *Cucurbita andreana* y el origen de *Cucurbita maxima*", *Revista Argentina de Agronomía*, Vol. 12, pp. 86-93.

Mohanty, B.K., S.K. Mohanty and R.S. Mishra (1999), "Genetics of yield and yield components in pumpkin (*Cucurbita moschata*)", *Indian J. of Agric. Sciences*, Vol. 69, No. 11, pp. 781-783.

Montes, H.S. (2002), "Flujo Génico en Calabaza (*Cucurbita* spp.) Dentro del Sistema Milpa en el Occidente de México", PhD Thesis, Facultad de Ciencias, Universidad Nacional Autónoma de México, México, D.F.

Montes-Hernández, S. and L.E. Eguiarte (2002), "Genetic structure and indirect estimates of gene flow in three taxa of *Cucurbita* in western Mexico", *American Journal of Botany*, Vol. 89, No. 7, pp. 1 156-1 163, July, *http://dx.doi.org/10.3732/ajb.89.7.1156*.

Montes-Hernández, S., L.C. Merrick and L.E. Eguiarte (2005), "Maintenance of squash (*Cucurbita* spp.) landrace diversity by farmers' activities in Mexico", *Genetic Resources and Crop Evolution*, Vol. 52 No. 6, pp. 697-707, *http://dx.doi.org/10.1007/s10722-003-6018-4*.

Murkovic, M., A. Hillebrand and J. Winkler (1996), "Variability of fatty acid content in pumpkin seeds (*Cucurbita pepo* L)", *Zeitschrift für Lebensmittel-Untersuchung und -Forschung A*, Vol. 203, No. 3, pp. 216-219, May.

Nabhan, G.P. (1984), "Evidence of gene flow between cultivated *Cucurbita mixta* and a field edge population of wild *Cucurbita* at Onavas, Sonora", *Cucurbit Genetics Cooperative Report*, No. 7.

National Gardening Association (2009), *The Impact of Home and Community Gardening in America*. Harris Interactive, Inc.

Navas-Castillo, J., E. Fiallo-Olive and S. Sanchez-Campos (2011), "Emerging virus diseases transmitted by whiteflies", *Annual Review of Phytopathology*, Vol. 49, pp. 219-248, *http://dx.doi.org/10.1146/annurev-phyto-072910-095235*.

Nee, M. (1990), "The domestication of *Cucurbita* (Cucurbitaceae)", *Economic Botany*, Vol. 44, No. 3, pp. 56-58, July.

Nepi, M. and E. Pacini (1993), "Pollination, pollen viability and pistil receptivity in *Cucurbita pepo*", *Annals of Botany* Vol. 72 No. 6, pp. 527-536, *http://dx.doi.org/10.1006/anbo.1993.1141*.

Nesom, G.L. (2011), "New state records for *Citrullus, Cucumis*, and *Cucurbita* (Cucurbitaceae) outside of cultivation in the USA", *Phytoneuron*, Vol. 1, pp. 1-7, *www.phytoneuron.net/PhytoN-CucurbRecords.pdf*.

Newsom, L.A., S.D. Webb and J.S. Dunbar (1993), "History and geographic distribution of *Cucurbita pepo* gourds in Florida", *Journal of Ethnobiology*, Vol. 13, No. 1, pp. 75-97, Summer, *https://ethnobiology.org/sites/default/files/pdfs/JoE/13-1/Newsom.pdf*.

Nishida, R., M. Yokoyama and H. Fukami (1992), "Sequestration of cucubitacin analogs by New and Old World chrysomelid leaf beetles in the tribe Luperini", *Chemoecology*, Vol. 3, No. 1, pp. 19-24, April.

Oliver, L., S. Harrison and M. McClelland (1983), "Germination of Texas gourd (*Cucurbita texana*) and its control in soybeans (*Glycine max*)", *Weed Science*, Vol. 31, No. 5, pp. 700-706, September, *www.jstor.org/stable/4043694*.

OMAFRA, (2011), "Pumpkin and squash production", Ontario Ministry of Agriculture, Food and Rural Affairs, Ontario, *www.omafra.gov.on.ca* (accessed October 2011).

Paris, H.S. (2011), "Characterization of the *Cucurbita pepo* collection at the Newe Ya'ar Research Center, Israel", *PGR Newsletter*, Vol. 126, pp. 41-45.

Paris, H.S. (2003), "Genetic control of irregular striping, a new phenotype in *Cucurbita pepo*", *Euphytica*, Vol. 129, No. 1, pp. 119-126, January.

Paris, H.S. (2002), “Multiple allelism at a major locus affecting fruit coloration in *Cucurbita pepo*”, *Euphytica*, Vol. 125, No. 2, pp. 149-153, May.

Paris, H.S. (2001), “History of the cultivar-groups of *Cucurbita pepo*”, *Horticultural Reviews*, Vol. 25, pp. 71-170, *http://dx.doi.org/10.1002/9780470650783.ch2.*

Paris, H.S. (2000), “Gene for broad, contiguous dark stripes in cocozelle squash (*Cucurbita pepo*)”, *Euphytica*, Vol. 115, No. 3, pp. 191-196, October.

Paris, H.S. (1997), “Genes for developmental fruit coloration of acorn squash”, *Journal of Heredity*, Vol. 88, No. 1, pp. 52-56.

Paris, H.S. (1989), “Historical records, origins and development of the edible cultivar groups of *Cucurbita pepo* (Cucurbitaceae)”, *Economic Botany*, Vol. 43, No. 4, pp. 423-443, October-December, *www.jstor.org/stable/4255187.*

Paris, H.S. (1986), “A proposed subclassification for *Cucurbita pepo*”, *Phytologia*, Vol. 61, pp. 133-138.

Paris, H.S. and S. Cohen (2000), “Oligogenic inheritance for resistance to zucchini yellow mosaic virus in *Cucurbita pepo*”, *Annals of Applied Biology*, Vol. 136, No. 3, pp. 209-214, June, *http://dx.doi.org/10.1111/j.1744-7348.2000.tb00027.x.*

Paris, H.S. et al. (2003), “Assessment of genetic relationships in *Cucurbita pepo* (Cucurbitaceae) using DNA markers”, *Theoretical Applied Genetics*, Vol. 106, No. 6, pp. 971-978, April, *http://dx.doi.org/10.1007/s00122-002-1157-0.*

Parodi, L.R. (1935), “Relaciones de la agricultura prehispánica con la agricultura argentina actual”, *Anales de la Academia Nacional de Agronomía y Veterinaria*, Buenos Aires, Vol. 1, pp. 115-167.

Piperno, D.R., T.C. Andres and K.E. Stothert (2000), “Phytolits in *Cucurbita* and other neotropical Cucurbitaceae and their occurrence in early archaeological sites from the lowland American tropics”, *Journal of Archaeological Science*, Vol. 27, No. 3, pp. 193-208, March, *http://dx.doi.org/10.1006/jasc.1999.0443.*

Provvidenti, R. (1990), “Viral diseases and genetic sources of resistance in Cucurbita species”, in: Bates, D.M., R.W. Robinson and C. Jeffrey (eds.), *Biology and Utilization of the Cucurbitaceae*, Cornell University Press, Ithaca, New York, pp. 427-435.

Provvidenti, R. and D.M. Tricoli (2002), “Inheritance of resistance to squash mosaic virus in a squash transformed with the coat protein gene of pathotype 1”, *HortScience*, Vol. 37, No. 2, pp. 575-577, *http://hortsci.ashspublications.org/content/37/3/575.full.pdf.*

Provvidenti, R., D. Gonsalves and H.S. Humaydan (1984), “Occurrence of zucchini yellow mosaic virus in cucurbits from Connecticut, New York, Florida, and California”, *Plant Disease*, Vol. 68, pp. 443-446, *www.apsnet.org/publications/plantdisease/backissues/Documents/1984Articles/PlantDisease68n05_443.PDF.*

Puchalski, J.T. and R.W. Robinson (1990), “Electrophoretic analysis of isozymes in *Cucurbita* and *Cucumis* and its application for phylogenetic studies”, in: Bates, D.M., R.W. Robinson and C. Jeffrey (eds), *Biology and Utilization of the Cucurbitaceae*, Cornell University Press, Ithaca, New York, pp. 60-76.

Purcifull, D.E. et al. (1984), “Serological relationships and partial characterization of zucchini yellow mosaic virus isolated from squash in Florida”, *Plant Disease*, Vol. 68, No. 3, pp. 230-233, *http://dx.doi.org/10.1094/PD-69-230.*

Qasem, J.R. and N. Issa (2005), “Allelopathic effects of squash (*Cucurbita pepo* L cv Scarlette) on certain common weed species in Jordan”, in: Harper, J.D. et al. (eds.), *Proceedings of the 4th World Congress on Allelopathy: “Establishing the Scientific Base”*, Wagga Wagga, New South Wales, Australia, 21-26 August 2005, pp. 258-262.

Quesada, M., J.A. Winsor and A.G. Stephenson (1996), "Effects of pollen competition on the reproductive performance in cucurbit hybrids (Cucurbitaceae): F1 and backcross generations", *Canadian J. of Botany*, Vol. 74, No. 7, pp. 1 113-1 118, *http://dx.doi.org/10.1139/b96-136*.

Quesada, M., J.A. Winsor and A.G. Stephenson (1993), "Effects of pollen competition on progeny performance in a heterozygous cucurbit", *American Naturalist*, Vol. 142, No. 4, pp. 694-706, October, *http://dx.doi.org/10.1086/285564*.

Quesada, M. et al. (1991), "Effects of genotype on pollen performance in *Cucurbita pepo*", *Sexual Plant Reproduction*, Vol. 4, No. 3, pp. 208-214, July.

Radovich, T. (2011), "Farm and forestry production and marketing profile for pumpkin and squash", Specialty crops for Pacific Island agroforestry at: *www.ctahr.hawaii.edu*.

Rehm, S. et al. (1957), "Bitter principles of the Cucurbitaceae. VII. The distribution of bitter principles in this plant family", *Journal of the Science of Food and Agriculture*, Vol. 8, No. 12, pp. 679-686, December, *http://dx.doi.org/10.1002/jsfa.2740081203*.

Rieseberg, L.H. and A.V. Harter (2006), "Molecular evidence and the evolutionary history of the domesticated sunflower", in: Motley, T. (ed), *Darwin's Harvest: New Approaches to the Origins, Evolution, and Conservation of Crops*, Columbia Univ. Press, New York, pp. 31-48.

Robinson, R.W. and D.S. Decker-Walters (1997), *Cucurbits. Crop Production Science in Horticulture*, No. 6, CAB International, Cambridge, United Kingdom.

Rochelle, L.A. (1974), "Descriçao taxonômica de cultivares de *Cucurbita maxima* Duch. e *C. pepo* L", *Anais de Escuela Superior de Agricultura* "*Luiz de Queiroz*, Vol. 31, pp. 667-700, *http://dx.doi.org/10.1590/S0071-12761974000100051*.

Rodríguez, I. and R. Lira (1992), "Diversidad, biología reproductiva y relaciones de Cucurbita fraterna L.H. Bailey, con especies cultivadas del género", in: *Resúmenes Simposio Etnobotánica 92*, Jardines Botánicos de Córdoba, Spain.

Rudich, J. (1990), "Biochemical aspects of hormonal regulation of sex expression in cucurbits", in: Bates, D.M., R.W. Robinson and C. Jeffrey (eds.), *Biology and Utilization of the Cucurbitaceae*, Cornell University Press, Ithaca, New York, pp. 127-134.

Rzedowski, G.C. and J. Rzedowski (2001), *Flora Fanerogámica del Valle de México*, 2nd edition, Instituto de Ecología y Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Pátzcuaro, Michoacán, Mexico.

Sanjur, O.I. et al. (2002), "Phylogenetic relationships among domesticated and wild species of *Cucurbita* (Cucurbitaceae) inferred from a mitochondrial gene: Implications for crop plant evolution and areas of origin", *Proceedings of the National Academy of Sciences USA*, Vol. 99, No. 1, pp. 535-540, January.

Sasu, M.A. et al. (2010), "Floral transmission of *Erwinia tracheiphila* by cucumber beetles in a wild *Cucurbita pepo*", *Environmental Entymology*, Vol. 39, No. 1, pp. 140-148, February, *http://dx.doi.org/10.1603/EN09190*.

Sauer, J.D. (1993), *Historical Geography of Crop Plants*, CRC Press, Boca Raton, Florida.

Schabort, J.C. (1978), "Cucurbitacin 19-hydroxylase in *Cucurbita maxima*", *Phytochemistry*, Vol. 17, No. 6, pp. 1 062-1 064, *http://dx.doi.org/10.1016/S0031-9422(00)94283-3*.

Scheerens, J.C. et al. (1987), "Floral development, flowering patterns, and growth rate of monoecious and gynoecious buffalo gourd", *Journal of the American Society for Horticultural Science*, Vol. 112, No. 3, pp. 574-578, May.

Schuster, D.J., J.B. Kring and J.F. Price (1991), "Association of the Sweetpotato whitefly with a silver leaf disorder of squash", *HortScience*, Vol. 26, No. 2, pp. 155- 156, available at: *http://hortsci.ashspublications.org/content/26/2/155.full.pdf*.

See, E.F., W.A. Wan Nadiah and A.A. Noor Aziah (2007), "Physico-chemical and sensory evaluation of breads supplemented with pumpkin flour", *ASEAN Food Journal*, Vol. 14, No. 2, pp. 123-130.

Singh, A.K. (1990), "Cytogenetics and evolution in the Cucurbitaceae", in: Bates, D.M., R.W. Robinson and C. Jeffrey (eds.), *Biology and Utilization of the Cucurbitaceae*, Cornell University Press, Ithaca, New York, pp. 10-28.

Sisko, M., A. Ivancic and B. Bohanec (2003), "Genome size analysis in the genus *Cucurbita* and its use for determination of interspecific hybrids obtained using the embryo-rescue technique", *Plant Science*, Vol. 165, No. 3, pp. 663-669, *http://dx.doi.org/10.1016/S0168-9452(03)00256-5*.

Smith, B.D. (2006), "Eastern North America as an independent center of plant domestication", *Proceedings of the National Academy of Sciences USA*, Vol. 103, No. 33, pp. 12 225-12 226, *http://dx.doi.org/10.1073/pnas.0604335103*.

Smith, B.D. (2001), "Documenting plant domestication: The consilience of biological and archaeological approaches", *Proceedings of the National Academy of Sciences USA*, Vol. 98, No. 4, pp. 1 324-1 326, *http://dx.doi.org/10.1073/pnas.98.4.1324*.

Smith, B.D. (1992), *Rivers of Change: Essays on Early Agriculture in Eastern North America*, Smithsonian Institution Press, Washington, DC.

Smith, C.E. (1986), "Preceramic plant remains from Guila Naquitz", in: Flannery, K.V. (ed.), *Guila Naquitz, Archaic Foraging and Early Agriculture in Oaxaca, Mexico*, Academic Press, New York, pp. 265-274.

Smith, B.D., C.W. Cowan and M.P. Hoffman (1992), "Is it an indigene or a foreigner?", in: Smith, B.D. (ed.), *Rivers of Change: Essays on the Origin of Agriculture in Eastern North America*, Smithsonian Institution Press, Washington, DC, pp. 67-100.

Sowls, L.K. (1997), *Javelinas and Other Peccaries: Their Biology, Management, and Use*, Texas A&M University Press, College Station, Texas.

Spencer, L.J. and A.A. Snow (2001), "Fecundity of transgenic wild-crop hybrids of *Cucurbita pepo* (Cucurbitaceae): Implications for crop-to-wild gene flow", *Heredity*, Vol. 86, Pt. 6, pp. 694-702, June.

Stephenson, A.G., B. Devlin and J.B. Horton (1988), "The effects of seed number and prior fruit dominance on the pattern of fruit production in *Cucurbita pepo* (zucchini squash)", *Annals of Botany*, Vol. 62, No. 6, pp. 653-661.

Strider, D.L. and T.R. Konsler (1965), "An evaluation of the *Cucurbita* for scab resistance", *Plant Disease Reporter*, Vol. 49, pp. 388-391.

Sun, J. et al. (2005), "Cucurbitacin Q: A selective STAT3 activation inhibitor with potent antitumor activity", *Oncogene*, Vol. 24, No. 20, pp. 3 236-3 245, May.

Systax Database at the University of Ulm, *www.biologie.uni-ulm.de/systax* (accessed October 2011).

Tallamy, D.W. et al. (2005), "Western corn rootworm, curcubits and cucurbitacins",in: Vidal, S. et al. (eds.), *Western Corn Rootworm: Ecology and Management*, pp. 67-93, CAB International, Oxfordshire, United Kingdom, *http://web.missouri.edu/~hibbardb/CV_files/Tallamy%20et%20al%20chap04%20proof.pdf*.

Tallamy, D.W. et al. (1998a), "Cucurbitacins as feeding and oviposition deterrents to insects", *Environmental Entomology*, Vol. 26, No. 3, pp. 678-683, *http://dx.doi.org/10.1093/ee26.3.678*.

Tallamy, D.W. et al. (1998b), "Sequestered cucurbitacins and pathogenicity of *Metarhizium anisopliae* (Moniliales: Moniliaceae) on spotted cucumber beetle eggs and larvae (Coleoptera: Chrysomelidae)", *Environmental Entomology*, Vol. 27, No. 2, pp. 366-372, *http://dx.doi.org/10.1093/ee/27.2.366*.

Tapley, W.T., W.D. Enzie and G.P. Van Eseltine (1937), *The Vegetables of New York, Vol. 1, Part 4: The Cucurbits*, New York Agricultural Experiment Station, Geneva, New York.

Tepedino, V.J. (1981), “The pollination efficiency of the squash bee (*Peponapis pruinosa*) and the honey bee (*Apis mellifera*) on summer squash (*Cucurbita pepo*)”, *Journal of the Kansas Entomological Society*, Vol. 54, No. 2, pp. 359-377, April, *www.jstor.org/stable/25084168.*

Teppner, H. (2000), “*Cucurbita pepo* (Cucurbitaceae): History, seed coat types, thin-coated seeds and their genetics”, *Phyton – Annales Rei Botanicae*, Vol. 40, Fasc. 1, pp. 1-42, *www.landesmuseum.at/pdf_frei_remote/PHY_40_1_0001-0042.pdf.*

Theis, N., K. Kesler and L.S. Adler (2009), “Leaf herbivory increases floral fragrance in male but not female *Cucurbita pepo* subsp. *texana* (Cucurbitaceae) flowers”, *American Journal of Botany*, Vol. 96, No. 5, pp. 897-903, May, *http://dx.doi.org/10.3732/ajb.0800300.*

Thomas, A. (1971), “The incidence and economic importance of watermelon mosaic virus”, *New Zealand Journal Agricultural Research*, Vol. 14, No. 1, pp. 242-247, *http://dx.doi.org/10.1080/00288233.1971.10421320.*

Torres-Ruiz, R.A. and V. Hemleben (1994), “Pattern and degree of methylation in ribosomal RNA genes of *Cucurbita pepo* L”, *Plant Molecular Biology*, Vol. 26, No. 4, pp. 1 167-1 179.

USDA (2011a), *PLANTS Database*, United States Department of Agriculture, *http://plants.usda.gov* (accessed September 2011).

USDA (2011b), *Federal Noxious Weed List*, United States Department of Agriculture, *http://plants.usda.gov/java/noxious* (accessed September 2011).

USDA (1994), “Availability of determination of nonregulated status for virus resistant squash”, *Federal Register*, Vol. 59, Issue 238, 13 December, pp. 64 187-64 189.

US Environmental Protection Agency (1999), “Notice of Filing a Pesticide Petition to Establish a Tolerance for Certain Pesticide Chemicals in or on Food”, *Federal Register*, Vol. 64, 1 September, pp. 47 788.

van de Ven, W.T.G. et al. (2000), “Local and systemic changes in squash gene expression in response to silverleaf whitefly feeding”, *The Plant Cell*, Vol. 12, No. 8, pp. 1 409-1 423.

Vidal, M. et al. (2010), “Pollination and fruit set in pumpkin (*Cucurbita pepo*) by honey bees”, *Revista Brasileira de Botanica*, Vol. 33, No. 1, pp. 106-113, January/March, *http://dx.doi.org/10.1590/S0100-84042010000100010.*

Weeden, N.F. (1984), “Isozyme studies indicate that the genus *Cucurbita* is an ancient tetraploid”, *Cucurbit Genetics Cooperative Report*, Vol. 7, pp. 84-85, Article 37, available at: *http://cuke.hort.ncsu.edu/cgc/cgc07/cgc7-37.html.*

Weeden, N.F. and R.W. Robinson (1990), “Isozyme studies in Cucurbita”, in: Bates, D.M., R.W. Robinson and C. Jeffrey (eds.), *Biology and Utilization of the Cucurbitaceae*, Cornell University Press, Ithaca, New York, pp. 51-59.

Weiling, F. (1959), “Genomanalytische Untersuchungen bei Kürbis (*Cucurbita* L.)”, *Zuchter*, Vol. 29, No. 4, pp. 161-179, January.

Wessel-Beaver, L. (2000a), “*Cucurbita aryrosperma* sets fruit in fields where *C. moschata* is only pollen source”, *Cucurbit Genetics Cooperative Report*, Vol. 23, pp. 62-63, Article 20, *http://cuke.hort.ncsu.edu/cgc/cgc23/cgc23-20.html.*

Wessel-Beaver, L. (2000b), “Evidence for the center of diversity of *Cucurbita moschata* in Columbia”, *Cucurbit Genetics Cooperative Report*, Vol. 23, pp. 54-55, Article 16, *http://cuke.hort.ncsu.edu/cgc/cgc23/cgc23-16.html.*

Whitaker, T.W. (1974), “Cucurbita”, in: King, R.C. (ed.), *Handbook of Genetics*, Plenum Press, New York, pp. 135-144.

Whitaker, T.W. (1968), "Ecological aspects of the cultivated *Cucurbita*", *HortScience*, Vol. 3, No. 1, pp. 9-11.

Whitaker, T.W. (1951), "A species cross in *Cucurbita*", *J. of Heredity*, Vol. 42, No. 2, pp. 65-69.

Whitaker, T.W. (1947), "American origin of the cultivated cucurbits", *Annals of the Missouri Botanical Garden*, Vol. 34, No. 2, pp. 102-111, May, *www.jstor.org/stable/2394459*.

Whitaker, T.W. and W.P. Bemis (1965), "Evolution in the genus *Cucurbita*", *Evolution*, Vol. 18, No. 4, pp. 553-559, December, *http://dx.doi.org/10.2307/2406209*.

Whitaker, T.W. and G.W. Bohn (1950), "The taxonomy, genetics, production and uses of the cultivated species of *Cucurbita*", *Economic Botany*, Vol. 4, No. 1, pp. 54-81, January-March, *www.jstor.org/stable/4251961*.

Whitaker, T.W. and G.N. Davis (1962), *Cucurbits: Botany, Cultivation, and Utilization*, Interscience Publishers, New York.

Whitaker, T.W. and R.W. Robinson (1986), "Squash breeding", in: Bassett, M.J. (ed.), *Breeding Vegetable Crops*, AVI Publishing, Westport, Connecticut, pp. 209-242.

Wilson, H.D. (1998), "Free-living *Cucurbita pepo* in the United States: Viral resistance, gene flow and risk assessment", *http://botany.csdl.tamu.edu/FLORA/flcp/flcp1.htm*.

Wilson, H.D. (1990), "Gene flow in squash species: Domesticated *Cucurbita* species may not represent closed genetic systems", *BioScience*, Vol. 40, No. 6, pp. 449-455, June, *http://dx.doi.org/10.2307/1311392*.

Wilson, H.D. (1989), "Discordant patterns of allozyme and morphological variation in Mexican *Cucurbita*", *Systematic Botany*, Vol. 14, No. 4, pp. 612-623, October-December, *http://dx.doi.org/10.2307/2419006*.

Wilson, H.D., J. Doebley and M. Duvall (1992), "Chloroplast DNA diversity among wild and cultivated members of *Cucurbita* (Cucurbitaceae)", *Theoretical and Applied Genetics*, Vol. 84, No. 7, pp. 859-865, September.

Wilson, H.D., R. Lira and I. Rodríguez (1994), "Crop/weed gene flow: *Cucurbita argyrosperma* Huber and *C. fraterna* L.H. Bailey (Cucurbitaceae)", *Economic Botany*, Vol. 48, No. 3, pp. 293-300, July-September, *www.jstor.org/stable/4255643*.

Wu, J. et al. (2011), "Molecular diversity of Chinese *Cucurbita moschata* germplasm collections detected by AFLP markers", *Scientia Horticulturae*, Vol. 128, No. 1, pp. 7-13, February, *http://dx.doi.org/10.1016/j.scienta.2010.12.006*.

Xia, T. and Q. Wang (2006), "D-*chiro*-inositol found in *Cucurbita ficifolia* (Cucurbitaceae) fruit extracts plays the hypoglycemic role in streptozocin-diabetic rats", *Journal of Pharmacy and Pharmacology*, Vol. 58, No. 11, pp. 1 527-1 532, November.

Xu, Y. et al. (2004), "Inheritance of resistance to zucchini yellow mosaic virus and watermelon mosaic virus in watermelon", *Journal of Heredity*, Vol. 95, No. 6, pp. 498-502, December.

Zhang, M. et al. (2010), "Inhibition of pancreatic cancer cell growth by cucurbitacin B through the modulation of signal transducer and activator of transcription 3 signaling", *Pancreas*, Vol. 39, No. 6, pp. 923-929, August, *http://dx.doi.org/10.1097/MPA.0b013e3181ce719e*.

Zitter, T.A., D.L. Hopkins and C.E. Thomas (1996), *Compendium of Cucurbit Diseases*, APS (American Phytopathological Society) Press, St. Paul, Minnesota.

Zomlefer, W.B. (1994), *Guide to Flowering Plant Families*, University of North Carolina Press, Chapel Hill and London.

Zraidi, A. et al. (2007), "A consensus map for *Cucurbita pepo*", *Molecular Breeding*, Vol. 20, No. 4, pp. 375-388, November, *http://dx.doi.org/10.1007/s11032-007-9098-6*.

Annex 2.A1
List of taxonomic names of various *Cucurbita*

The primary source of the information in Table 2.A1.1 is "The Plant List" at: *www.theplantlist.org*.

The Plant List is the result of collaboration between the Royal Botanic Gardens, Kew and Missouri Botanical Garden. The collaboration between these groups enabled the creation of the list by combining multiple checklist data sets held by these institutions and other collaborators. Based on information from these sources, The Plant List provides the name agreed by the collaborators to be an "accepted" name, as well as synonyms by which that species has been known. It also contains "unresolved" names for which the contributing data sources did not contain sufficient information to decide whether they were "accepted" names or synonyms.

Other sources are also available, and information from these sources has also been incorporated: e.g. USDA-ARS Germplasm Resources Information Network at: *www.ars-grin.gov*.

The rightmost column of Table 2.A1.1 enumerates the names of cultivars offered as examples in the chapter in relation to the cultivated *Cucurbita* species.

The reader should be aware that botanists over time have applied some 400 names at various taxonomic ranks to the huge range of diversity observed in the *Cucurbita* (Nee, 1990).

Table 2.A1.1. **List of taxonomic names of various *Cucurbita***

Names used preferentially in text	Synonyms	Associated names found in literature	Varietal names in text
C. argyrosperma Huber *C. argyrosperma* ssp. *argyrosperma*	*C. argyrosperma* var. *callicarpa* *C. argyrosperma* var. *palmeri* *C. argyrosperma* ssp. *sororia* *C. argyrosperma* var. *stenosperma*	*C. palmeri* *C. sororia* *C. kellyana*	Green striped cushaw White cushaw Magdalena striped Papago Japanese pie Silver seed gourd
C. digitata	None recorded	*C. cordata* *C. palmata* *C. californica* *C. cylindrata*	
C. ecuardorensis	None recorded		
C. ficifolia Bouche	*C. ficifolia* f. *leucosperma* *C. ficifolia* f. *melanosperma* *C. ficifolia* var. *mexicana*	*C. melanosperma*	
C. foetidissima Kunth	*C. foetidissima* var. *foetidissima* *C. foetidissima* var. *scabridifolia*	*C. scabridifolia*	
C. galeottii			
C. lundelliana			
C. maxima Duchesne	*C. maxima* ssp. *maxima* *C. maxima* var. *triloba* *C. maxima* var. *turgida* *C. maxima* var. *zapallito* *C. maxima* var. *zipinka*	*C. andreana*	Delicious Hubbard Buttercup Mammoth whale French turban

Table 2.A1.1. **List of taxonomic names of various *Cucurbita*** (*cont.*)

Names used preferentially in text	Synonyms	Associated names found in literature	Varietal names in text
C. moschata Duchesne	*C. moschata* var. *argyrosperma* *C. moschata* var. *columbiana* *C. moschata* var. *meloniformis* *C. moschata* f. *yokohamana*		Butternut squash Golden cushaw
C. okeechobeensis (Small) L.H. Bailey *C. okeechobeensis* ssp. *martinezii* (L.H. Bailey) T.C. Andres & G.P. Nabhan	*C. okeechobeensis* ssp. *martinezii*	*C. martinezii*	
C. pedatifolia L.H. Bailey	*C. moorei*	*C. moorei*	
C. pepo L. *C. pepo* ssp. *ovifera* (L.) D.S. Decker *C. pepo* ssp. *pepo* *C. pepo* ssp. *ovifera* var. *texana* (Scheele) D.S. Decker *C. pepo* ssp. *ovifera* var. *ozarkana* D.S. Decker	*C. pepo* var. *akoda* *C. pepo* var. *americana* *C. pepo* var. *condensa* *C. pepo* var. *fibropulposa* *C. pepo* var. *flogra* *C. pepo* ssp. *fraterna* *C. pepo* var. *georgica* *C. pepo* ssp. *gumala* *C. pepo* var. *kintogwa* *C. pepo* var. *maxima* *C. pepo* var. *medullosa* *C. pepo* var. *melopepo* *C. pepo* var. *moschata* *C. pepo* var. *ovifera* *C. pepo* var. *ozarkana* *C. pepo* var. *texana* *C. pepo* var. *sororia* *C. pepo* ssp. *texana* *C. pepo* var. *toonas* *C. pepo* var. *torticollis*	*C. fraterna* *C. texana* *C. pepo* L. var. *cylindrica* *C. pepo* L. var. *clypeata* *C. pepo* L. var. *fastigata* *C. pepo* L. var. *longa* *C. pepo* L. var. *recticollis* *C. pepo* L. var. *turbinata*	Black zucchini Fordhook bush Connecticutt field Table queen Cherokee roaster Orange ball Miniature ball Striped pear
C. radicans		*C. gracilior*	

Source: Adapted from "The Plant List" (2011).

References

Nee, M. (1990), "The domestication of *Cucurbita* (Cucurbitaceae)", *Economic Botany*, Vol. 44, No. 3, pp. 56-58, July.

The Plant List (2011), A working list of all known plant species created through a collaboration between the Royal Botanic Gardens, Kew and Missouri Botanic Gardens, *www.theplantlist.org* (accessed October 2011).

USDA-ARS (n.d.), Germplasm Resources Information Network (GRIN), United States Department of Agriculture, Agricultural Research Service, *www.ars-grin.gov* (accessed October 2011).

Annex 2.A2
Horticultural types in *Cucurbita* species

Table 2.A2.1. **Horticultural types in *Cucurbita* species**

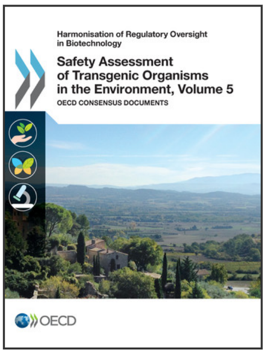
Species	Type	Description	Typical cultivars
C. argyrosperma	Cushaw	Striped, green or white hard rind. Pear shaped or with a straight or curved neck.	Green striped cushaw; Japanese pie; Tennessee sweet potato
C. maxima	Banana	Elongated fruit pointed at the ends. Orange or pink moderately hard rind.	Banana; Pink banana
	Delicious	Top shaped. Orange or green hard rind.	Delicious; Golden delicious
	Hubbard	Round at the middle tapering at each end. Blue, orange or green, hard warty rind.	Hubbard; Blue hubbard; Golden hubbard
	Marrow	Lemon-shaped with orange hard rind.	Boston marrow
	Show	Very large globular, sutured, light orange fruit. Moderately hard rind.	Atlantic giant; Big Max
	Turban	Turban shaped with a large button. Hard rind.	Turks turban; Warren; Turks cap
C. moschata	Tropical pumpkin	Round, oblate or irregular shape. Green, buff, yellow or piebald hard rind.	La Primera; Seminole; Solar
	Cheese	Variable shape, smooth, hard, buff-coloured hard rind.	Dickinson; Kentucky field
	Crookneck	Long, curved or straight neck. Smooth, hard rind, usually buff.	Golden crookneck; Walthan butternut; Zenith
	Bell	Bell-shaped. Orange flesh. Tan hard rind.	Seminole; Upper ground sweet potato
C. pepo	Acorn	Acorn-shaped grooved fruit. Dark green, orange or white hard rind.	Heart of gold; Table ace; Tay belle
	Cocozelle	Long, cylindrical, bulbous blossom end. Striped or variegated green soft rind.	Cocozelle; Long cocozelle
	Crookneck	Elongated with narrow, curved neck. Yellow soft rind.	Dixie; Yellow summer crookneck; Supersett
	Ornamental gourd	Variously shaped and coloured. Smooth or warty hard rind.	Orange ball; Crown of thorns
	Pumpkin	Large, round, oval oblate shape. Mostly orange, sometimes white relatively soft rind.	Connecticutt field; Howden Jack-be-little; Small sugar
	Scallop	Flattened with scalloped margins. White, yellow, green or bicoloured soft rind.	Peter pan; Sunburst; White bush scallop
	Straightneck	Long, cylindrical, yellow soft rind.	Enterprise; Goldbar; Multipic
	Vegetable marrow	Short, tapered, cylindrical. Light green.	Clarita; Goya; Zahra
	Zucchini	Uniformly cylindrical. Green or yellow to gray soft rind.	Dividend; Revenue; Spineless beauty

Some of the types listed in Table 2.A2.1 are not grown in production agriculture. For example, “Show” pumpkins are grown for competition in the heaviest fruit contests held in various parts of the United States. The 2000 winner weighed in at 517 kilograms. Other types that are regionally important and of historical interest are certain cushaw and vegetable marrow squash. These cultivars can be bought commercially at concerns dedicated to the preservation of heirloom varieties (e.g. *www.sandhillpreservation.com*).

Also, it should be noted that this annex offers examples only as a means of illustrating the types and varieties that can be associated with the various *Cucurbita* species. Paris (1989), for example, notes that for *C. pepo* alone, hundreds or perhaps thousands of named cultivars exist.

Reference

Paris, H.S. (1989), "Historical records, origins and development of the edible cultivar groups of *Cucurbita pepo* (Cucurbitaceae)", *Economic Botany*, Vol. 43, No. 4, pp. 423-443, October-December, *www.jstor.org/stable/4255187*.



From:

Safety Assessment of Transgenic Organisms in the Environment, Volume 5

OECD Consensus Documents

Access the complete publication at:

https://doi.org/10.1787/9789264253018-en

Please cite this chapter as:

OECD (2016), “Squashes, pumkins, zucchinis and gourds (Cucurbita species)”, in *Safety Assessment of Transgenic Organisms in the Environment, Volume 5: OECD Consensus Documents*, OECD Publishing, Paris.

DOI: https://doi.org/10.1787/9789264253018-5-en