

Gone Global: Familiar and Exotic Cucurbits Have Asian Origins

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Cucurbits comprise the highly diverse family known as Cucurbitaceae that includes cultivated, feral, and wild species (Robinson and Decker-Walters, 1997). Many of the cultivated species such as squash (*Cucurbita* spp.), watermelon [*Citrullus lanatus* (Thunb.) Matsum. & Nakai], cucumber (*Cucumis sativus* L.), and melon (*Cucumis melo* L.) are familiar to U.S. and world markets. Others such as bitter melon (*Momordica charantia* L.) are less familiar in the United States. Cucurbits are cultivated more broadly than any other vegetable species after tomato, *Solanum lycopersicum* L. (<<http://faostat.fao.org>>).

Cucurbits exhibit great genetic diversity expressed phenotypically in vegetative, e.g., plant architecture and growth habit, floral, e.g., sex expression, and fruit characters that include size, shape, skin texture, exterior and interior colors, sweetness and flavor, and post-harvest shelf life. They are especially known for their fruit, which may be consumed fresh, cooked or baked, dried, or processed (Robinson and Decker-Walters, 1997). Immature or mature fruit are, depending on the species, consumed as fresh or cooked vegetables. Melon and watermelon are especially well known

for their sweet, flavorful, and colorful fruit that are usually eaten fresh but may be processed in confections or jams (Fig. 1).

Cucurbit seeds are edible fresh (Anon., 2012c) or dried (Fig. 1). They are a source of high-quality vegetable oil (Fig. 1) and the expressed meal is high in edible protein (Jacks et al., 1972). Roots (Gathman and Bemis, 1990) and leaves (Jensen, 2012) of some species may also be used for industrial or culinary purposes.

Asia and cucurbits are intertwined. Origins of the many members of the Cucurbitaceae have been of great interest for 100+ years, some regarded as Old World (Asia and Africa), whereas others are regarded as New World (the Americas) species (for a somewhat dated overview, see Esquinas-Alcazar and Gulick, 1983). Recent analyses indicate, however, an Asian origin of the family Cucurbitaceae and numerous oversea dispersal events (Schaefer et al., 2009).

India and Southeast Asia, including China, comprise the primary and secondary centers of diversity, respectively, of cucumber. India and central and southwest Asia comprise the primary center of diversity for melon with China as a secondary center of diversity (Esquinas-Alcazar and Gulick, 1983). India and Africa are primary centers of watermelon and related species (Esquinas-Alcazar and Gulick, 1983). Melon and cucumber likely moved westward overland through central Asian trade routes, collectively referred to as the Silk Road (Wild, 1992) through central Asia and the Middle East to Europe and Africa and from there onto the New World. In contrast, the center of diversity for watermelon is in Africa (Esquinas-Alcazar and Gulick, 1983); it is thought that cultivated watermelon moved from there to Asia. The center of diversity of bitter melon is the Old World tropics with its highest diversity in India, China, and Southeast Asia (Esquinas-Alcazar and Gulick, 1983). Bitter melon likely

arrived in the United States with Chinese immigrants in the 18th century.

Seedless (tetraploid) watermelon, the product of an early 20th century discovery in Japan, entered the U.S. marketplace at the end of that century, where it quickly gained popularity when bred into a small fruit size background and adapted to U.S. growing conditions. Grafting of watermelon onto disease-resistant rootstocks was developed during the 1920s in Japan and Korea (Davis et al., 2008). This technology holds great promise for melon and watermelon production in the United States as the use of methyl bromide and other soil fumigants become more restricted (Davis et al., 2008).

New resources, i.e., crop germplasm, and technology, e.g., tetraploidy and grafting, contribute to sustainable crop productivity (Day, 1997). We provide an overview of the positive impact of Asian cucurbit germplasm and technology on U.S. melon, cucumber, and watermelon production and the potential for bitter melon, a relatively new commercial crop in the United States with many useful attributes.

MELON

Domestication of melon may have occurred independently in southeast Asia, India, and East Asia (Esquinas-Alcazar and Gulick, 1983; Pitrat, 2012). Today, the primary center of melon diversity is in southwest and central Asia (Turkey, Syria, Iran, Afghanistan, north and central India and Transcaucasia, Turkmenistan, Tajikistan, and Uzbekistan) with secondary centers of diversity in China, Korea, and the Iberian Peninsula (Esquinas-Alcazar and Gulick, 1983).

Genetic diversity of Chinese, Indian, Japanese, and Turkish melon germplasm has been characterized using isozyme and molecular markers (Akashi et al., 2002; Dhillon et al., 2007, 2009; Fergany et al., 2011; Kaçar

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Fig. 1. Examples of processed melon (*C. melo*) and watermelon (*Citrullus lanatus*) fruit. Top, flavoring of cookies in China (*C. melo* ssp. *melo* Reticulatus group). Bottom, from left to right: roasted watermelon seeds in China, watermelon jam in the Republic of South Africa, and melon seed oil in Turkmenistan. All photos courtesy of J.D. McCreight except seed oil (Anon., 2008).

et al., 2012; Luan et al., 2008; McCreight et al., 2004; Nakata et al., 2005; Roy et al., 2012; Tzuri et al., 2005). Studies indicate that Asian melon germplasm was used in the development of the melon genome (Garcia-Mas et al., 2012). The great diversity within melon has been systematically organized numerous times by different investigators in various parts of the world using different and often incomplete samples of the diversity (Pitrat et al., 2000). The most recent reviews of melon genetic diversity and domestication are in agreement on the organization of the botanical groups of the two subspecies of melon, *C. melo* ssp. *agrestis*, with five groups, and *C. melo* ssp. *melo*, with 10 (Pitrat, 2008) or 11 (Burger et al., 2010) groups (Table 1). There are many landraces, farmer selections, and cultivars within these groups. Because they are fully compatible sexually, intermediate types can be found and will likely increase as breeders seek new combinations of traits from two or more of the botanical groups (Dhillon et al., 2012; Pitrat, 2012).

Melons moved from India to central Asia, China, the Middle East, and Europe. The timeline for movement of melons to these areas is unknown, but a recent study of ancient manuscripts, the Hebrew Bible, and images from antiquity document the culture and uses of non-sweet melons in the Chate and Flexuosus groups as early as 1350 B.C. (Janick et al., 2007). Literature from Roman and medieval periods revealed that sweet melons were known in central Asia in the mid-9th century, Khorasan (Turkmenistan, Uzbekistan Afghanistan, Tajikistan, and

northeastern Iran) and Persia by the mid-10th century, and in Andalusia (Spain) by the mid-11th century (Paris et al., 2012). These areas still to this day have a wealth of genetically diverse melon germplasm (Anon., 2008; Escribano et al., 2012; Esquinas-Alcazar, 1981; Mavlyanova et al., 2005a; McCreight et al., 2010).

Current melon cultivars in the United States can be traced to European and Asian (China, India, and Japan) introductions (Tapley et al., 1937; Whitaker and Davis, 1962). Europeans undoubtedly first introduced melons to the Americas. Tapley et al. (1937) stated that melons were reportedly grown by Native Americans as early as 1535 and that "...13 sorts..." of melons were listed in one catalog dated 1806, "...all of which were from the Old World and accounts of which are included in European literature." Nearly 300 popular and obscure muskmelon varieties (*C. melo* ssp. *melo* Reticulatus group) were known in the United States by 1937, and many of them had numerous synonyms, e.g., 51 for 'Rocky Ford' (Tapley et al., 1937). Current descriptions and photographs of many of the varieties described by Tapley et al. (1937) are included in *Melons, for the Passionate Grower* (Goldman and Schrage, 2002).

At the time Tapley et al. (1937) were preparing their list of muskmelon varieties, 'Powdery Mildew Resistant No. 45', or 'PMR 45' (*C. melo* ssp. *melo* Reticulatus group) as it is most widely known, was released (Jagger and Scott, 1937). 'PMR 45' is likely the first melon cultivar intentionally selected for

Table 1. Botanical groups of melon grouped by fruit type and sub-species.^z

Fruit type	Sub-species	
	<i>agrestis</i>	<i>melo</i>
Non-sweet	Acidulus	Chate
	Conomona	Chito'
	Momordica	Flexuosus
Sweet		Tibish
	Makuwa	Adana
	Chinensis	Ameri
		Cantalupensis
		Chandalak
Fragrant		Reticulatus
		Inodorus
		Dudaim

^zBased on Burger et al. (2010) and Pitrat (2008).

^yNot included in Pitrat (2008).

disease resistance in a scientific program of screening exotic germplasm (of Indian origin), crossing of resistant germplasm with susceptible germplasm, and subsequent controlled pollination with one backcross generation and selection for resistance and horticultural type. In this case, the powdery mildew-susceptible, orange flesh 'Hale's Best' muskmelon (*C. melo* ssp. *melo* Reticulatus group; Tapley et al., 1937) was crossed with Calif. 525 (*C. melo* ssp. *agrestis* Momordica group), which was a self-pollinated increase of an Indian melon named 'Big Round' that was brought to the United States by an Indian student of J.T. Rosa (I.C. Jagger, unpublished pedigree note). Their F₁ was resistant to cucurbit powdery mildew (CPM) incited by *Podosphaera xanthii* (Jagger and Scott, 1937; McCreight, 2004) and was self-pollinated to

produce the F₂ progeny. A CPM-resistant F₂ selection was backcrossed to ‘Hale’s Best’ to recombine CPM resistance with the horticultural qualities of ‘Hale’s Best’. Seven generations of inbreeding and selection resulted in ‘PMR 45’ (Jagger and Scott, 1937; Pryor et al., 1946). This cultivar redefined the western U.S. orange flesh shipper-type melon. Calif. 525 was a source of CPM resistance as well

as heat and salt tolerance (Shannon et al., 1984; Whitaker, 1979).

The most common forms of melon in the United States are the muskmelon, commonly referred to in the United States as “cantaloupe,” (*C. melo* ssp. *melo* Reticulatus group) and honeydew (*C. melo* ssp. *melo* Inodorus group). The so-called “mixed melons” that are often present in many mainstream U.S.

markets may include ‘Casaba’, ‘Crenshaw’, ‘Santa Claus’, ‘Juan Canary’ (*C. melo* ssp. *melo* Inodorus group), ‘Charentais’ (*C. melo* ssp. *melo* Cantalupensis group), and ‘Galía’ and more recently ‘Tuscan’ (*C. melo* ssp. *melo* Reticulatus group). Ethnic markets in major metropolitan areas, e.g., Los Angeles and New York City, may also feature the so-called “Russian melons” of central Asia (Uzbekistan and Turkmenistan, primarily; Figs. 2 and 3) or Asian types such as ‘Hami’ (*C. melo* ssp. *melo* Inodorus group) and ‘Sprite’ (*C. melo* ssp. *agrestis* Makuwa group; Fig. 4). These are sweet dessert-type melons. An interesting array of non-sweet, vegetable-type melons may be found in Western niche markets of metropolitan areas. These include the long and slender snake melon (*C. melo* ssp. *melo* Flexuosus group; Fig. 5) that can produce fruit up to 2 m in length (Pitrat, 2008) and various round-to-oval types such as ‘Carosello’ (*C. melo* ssp. *melo* Chate group).

“Wild-like” melons have been found in Central America and the Caribbean Islands, but they were likely either brought from Africa or Asia or resulted from genetic exchange with cultivated melons and are feral, e.g., CR1 (Pitrat, 2012; Staub et al., 2011b). Wild melon populations in North America were classified as *C. melo* Texanus group but are closely related to *C. melo* var. *Conomon* group and *C. melo* *Dudaim* group, e.g., Queen Anne’s pocket melon, based on morphological



Fig. 2. “Gavun kak” is a dried form of melon (*C. melo* ssp. *melo* Inodorus group) for consumption when fresh melons are not readily available in central Asia. Clockwise from top left: Waharman-type melon; strips of the flesh are dried first on a bed of brush and then suspended on strings and finally twisted together for packing and sale. All photos courtesy of J.D. McCreight.



Fig. 4. Melon (*C. melo*) fruits grown in North Carolina. Left bin, ‘Sprite’ (ssp. *agrestis* Makuwa group); right bin, Korean melon (ssp. *agrestis* Makuwa group). Photo courtesy of J.D. McCreight.



Fig. 3. Fruit of Turkmen melons (*C. melo* ssp. *melo*) grown in Imperial Valley, CA, on 6 June 2012, 90 d post-planting. Top, unripe sample of ‘Gyzył Waharman 1’ (Inodorus group), 4.8 kg and 10.1% soluble solids (SS). Bottom, ripe sample of ‘Turkman Zamcha’ (Ameri group), 2.3 kg and 12.9% SS. All photos courtesy of J.D. McCreight.



Fig. 5. Snakemelon fruits (*C. melo* ssp. *melo* Flexuosus group) grown in a greenhouse, Salinas, CA. Photo courtesy of J.D. McCreight.

Table 2. Disease, insect and nematode resistances, and abiotic stress tolerances described in Indian melon germplasm (Dhillon et al., 2012).

Category	Species or common name, or abiotic stress
Fungal	<i>Alternaria cucumerina</i>
	Downy mildew
	Fusarium wilt
	<i>Monosporascus cannonballus</i>
	<i>Golovinomyces cichoracearum</i>
Viral	<i>Podosphaera xanthii</i>
	Cucumber mosaic virus
	Cucumber green mottle mosaic virus
	Cucurbit aphid borne yellow virus
	Cucurbit leaf crumple virus
	Cucurbit yellow stunting disorder virus
	Kyuri green mottle mosaic virus
	Lettuce infectious yellows virus
	Moroccan watermelon mosaic virus
	Papaya ringspot virus
	Squash mosaic virus
	Watermelon chlorotic stunt virus
	Watermelon mosaic virus
Zucchini yellow mosaic virus	
Insect	Cucumber beetle
	<i>Aphis gossypii</i> (and resistance to virus transmission by <i>A. gossypii</i>)
	<i>Aulacophora foveicollis</i>
	<i>Bactrocera (Daucus) cucurbitae</i>
	<i>Bemisia tabaci</i>
	<i>Diaphania hyalinata</i>
	<i>Liriomyza sativae</i>
	<i>Meloidogyne incognita</i>
Nematode	<i>Tetranychus cinnaharinus</i>
	<i>Tetranychus urticae</i>
Abiotic	Salinity
	High temperature
	Drought

characters and random amplified polymorphic DNA and simple sequence repeat markers (Decker-Walters et al., 2002).

Many accessions from India have been found to have genes for resistance to one or more of six fungal pathogens and 13 viruses, seven insect species, and three nematode species and tolerance to salinity, high temperatures, and drought (Dhillon et al., 2012), although not all have been used in breeding melons for the United States (Table 2). In addition, 38 genes and quantitative trait loci for seedling, vegetative, flower and fruit traits, and isozymes have been described in 21 accessions or in offspring from crosses with one or more involving Indian melon accessions (Dhillon et al., 2012).

Twenty-seven Asian, mostly Indian, melon accessions are of special interest to U.S. melon breeding and production (Table 3). Numerous publicly developed selections (to stabilize resistance), breeding lines, and cultivars have been bred from nine of them for the various melon-producing regions of the United States, although genes from many have yet to be transferred to U.S. cultivars. Genes for powdery mildew resistance in Calif. 525, PI 79376, and PI 124112 were transferred to 14 breeding lines and cultivars (Harwood and Markarian, 1968) and are still important in modern releases. The pedigree of breeding line PMR Honeydew includes Calif. 525, PI 79376 (through Resistant Cantaloupe), and

PI 124111 (*C. melo* ssp. *agrestis* Momordica group) (McCreight et al., 1987). ‘Chujuc’ (*C. melo* ssp. *melo* Reticulatus group) and ‘Pacal’ (*C. melo* ssp. *melo* Inodorus group) are recently released cultivars adapted to Texas with these genes (Crosby et al., 2007, 2008). ‘PMR Delicious 51’ (*C. melo* ssp. *melo* Reticulatus group) is a recently released Bender-type melon for the northeast and, possibly, the northwest United States (Henning et al., 2005a; Tapley et al., 1937; Whitaker and Bohn, 1956). Commercial breeders have developed more cultivars, including F₁ hybrids (McCreight, 2007). One additional accession, PI 157083 (*C. melo* ssp. *agrestis* Chinensis or Makuwa group), from China, is of interest as a seedling marker for a unique, single recessive gene that conditions a photosensitive red pigmentation under the epidermis of stems, especially at nodes, and reddish or tan seed color (McCreight and Bohn, 1979). The unidentified pigment is obvious in the stems early each morning but fades quickly through the day, and by the next morning, the pigment intensity has been restored.

Asian melon germplasm continues to be introduced to the United States as specialty melons to meet the demands of specific émigré communities. Hami melons (*C. melo* ssp. *melo* Inodorus group) from the Xinjiang Province in western China include a range of shapes and epidermis and flesh colors (Anon., 2003). ‘Honey Kiss Hami Gold’ grown in Arizona and California is available from May through November (Anon., 2012a). ‘Sprite’ (Fig. 4), which was introduced into the United States from Japan, produces a small, oblong fruit with cream epidermis and firm, white flesh that is very sweet to the taste (up to 18°Brix) and is shipped by North Carolina growers from June through September (Anon., 2012b). ‘Sprite’ has become a popular specialty melon for growers in several southeastern states (Anon., 2012d; Schultheis, 2006).

Korean or Oriental melons (*C. melo* ssp. *agrestis* Makuwa group) are similar to ‘Sprite’ but have bright to light yellow epidermis and prominent although shallow, whitish vein tracts (Fig. 4) (Davis, 1970). The entire fruit, rind, and seeds are edible (Anon., 2012c). Korean melons are commercially grown in California and Mexico for U.S. consumption (Anon., 2010).

Melons from central Asia (*C. melo* ssp. *melo* Ameri and Inodorus groups) have promise for local or regional farmers markets in California and Arizona, which have similar growing conditions and long seasons similar to those found in Uzbekistan and Turkmenistan (Molinar, 2012). Uzbek and Turkmen melon varieties come in a wide range of sizes (0.5 to 17.0 kg) with sugar levels that range up to 25% under ideal conditions and shelf lives from very short (for local markets) to 7 months (Fig. 3) (Anon., 2008; Mavlyanova et al., 2005a, 2005b; McCreight et al., 2010).

CUCUMBER

India and southeast Asia constitute the primary center of diversity for cucumber,

which was domesticated ≈3000 years ago (Dane et al., 1980; Esquinas-Alcázar and Gulick, 1983; Jeffrey, 1980). *Cucumis sativus* houses several cross-compatible botanical varieties including var. *sativus*, the cultivated cucumber (hereafter referred to as *C. s.* var. *sativus*), and the wild, free-living var. *hardwickii* (R.) Alef., hereafter referred to as *C. s.* var. *hardwickii* (Kirkbride, 1993). *Cucumis s.* var. *hardwickii* is considered a feral form of *C. s.* var. *sativus* that grows in the foothills of the Himalayan mountains and is used by native people of northern India as a laxative (Deakin et al., 1971). This botanical variety presents extreme variation from typical cucumber in two Indian accessions, PI 183967 (syn. LJ 90430) from Meghalaya and PI 215589 from Uttar Pradesh (Dijkhuizen et al., 1996) and, thus, has potential for increasing genetic diversity in commercial cucumber (Staub and Kupper, 1985; Staub et al., 1992).

The wild, free-living *C. hystrix* is sparingly cross-fertile with cucumber and is found in the Yunnan Province of southern China (Chen et al., 1995, 1997), but fertile amphidiploids synthesized from a *C. hystrix* × *C. s.* var. *sativus* cross resulted in a synthetic species called *C. hytivus* (Chen and Kirkbride, 2000; Chen et al., 1997; Sebastian et al., 2010). Furthermore, the development of the fully fertile *C. hytivus*-derived fertile diploids ($2n = 2x = 14$; SS) from *C. hytivus* × *C. s.* var. *sativus* crosses resulted in potentially useful germplasm for plant improvement (Staub and Delannay, 2011). The incorporation of genes from the secondary gene pool of cucumber such as *C. hystrix* is potentially useful to cucumber breeding given that *C. hystrix* possesses novel genes for disease resistance, e.g., gummy stem blight (*Didymella bryoniae*), that are not present in cultivated cucumber (Chen et al., 2003). Backcrossing with concurrent initial molecular-based genotyping and selection for genetic diversity in *C. sativus* × *C. hystrix*-derived populations increased genetic diversity (phenotypic and genotypic) in cucumber (Delannay et al., 2010) and resulted in the development of 94 inbred backcross lines (IBLs) from the second backcross to cucumber [S_3BC_2 (*C. sativus* × *C. hytivus*) *C. sativus*] for use in cucumber improvement (Staub and Delannay, 2011). The genetic distance (GD) between parental lines (*C. sativus* and *C. hytivus*) was 0.85, and the GD between the 94 IBLs ranged between 0.16 and 0.75. These IBLs differ in days to flower, sex expression, lateral branch number, number of fruits per plant, and fruit length and diameter ratio. Although the performance of these IBLs are predicted to differ depending on growing environment, strategic crossing of these IBLs with elite lines may allow for the development of broad- and narrow-based populations using phenotypic and/or marker-assisted selection (Fan et al., 2006).

The 1400+ *C. s.* var. *sativus* and var. *hardwickii* accessions currently resident in the U.S. National Plant Germplasm System (USDA, ARS, North Central Regional Plant

Introduction Station, Ames, IA) represent the primary cucumber gene pool. The secondary gene pool of *C. sativus* includes cross-incompatible, e.g., wild African species, or sparingly cross-compatible, e.g., *C. hystrix*, species (Chen et al., 1997; Chung et al., 2006). The tertiary gene pool of cucumber consists of distantly related species from other genera or sub-genera, e.g., *Cucumis melo* L. and *Cucurbita* L., which do not hybridize with cucumber (Chung et al., 2006; Staub et al., 1987). Attempts to exploit resources beyond the primary cucumber gene pool, e.g., *Cucumis metuliferus*, *C. melo*, have either been unsuccessful or unrepeatable.

Assessments of genetic diversity in *C. s. var. sativus* and *var. hardwickii* using isozymes, restriction fragment length polymorphisms, and random amplified polymorphic DNA indicate that diversity in *C. s. var. sativus* is relatively low (3% to 8%) when compared with other cross-fertilized species of *Cucumis* (10% to 25%) (Dijkhuizen et al., 1996; Esquinas-Alcazar, 1977; Horejsi and Staub, 1999). Polymorphism level in *C. s. var. hardwickii* (17% to 25%) is predictably higher than *C. s. var. sativus* (Dijkhuizen et al., 1996; Horejsi and Staub, 1999). Furthermore, genetic diversity analysis indicates that Indian and Chinese cucumbers differ substantially (Staub et al., 1999) and that *C. s. var. Xishuangbannanensis* (possesses an orange endocarp high in carotenoids) accessions from the Yunnan Province, China, are unique based on their pedigree, nutritional attributes, and restricted production range (Simon and Navazio, 1997). Genetic variation in Chinese accessions high in carotenoid pigment variation (orange color) has been incorporated into U.S. processing cucumber germplasm to improve human health (Staub et al., 2011a).

Cucumber is typically eaten fresh, i.e., fresh or slicing market types, or as a processed product (processing or pickling types) (Staub and Bacher, 1997; Staub et al., 2008). The major fruit types are the American processing and fresh market types, the Dutch gherkin and greenhouse types, the German Schalgurken type, the Mid-East Beit Alpha type, and the Oriental trellis (burpleless) type. Fresh market types are grown in fields or greenhouses and are 15 (U.S. and Mediterranean) to 40 (European) cm in length. Sfran (compact fruit types marketed in the Persian Gulf) and “lemon” cucumber (shape similar to a lemon with pale, greenish yellow skin; hermaphroditic) are less common fresh market types.

Gherkin cucumber (*C. s. var. sativus*) is a tiny immature cucumber used for pickling. Harvest of gherkins is labor-intensive as a result of their small size, which is generally less than 7.5 cm long. India has, as a result of the low labor costs, become a major producer of gherkins for export to Europe, the United States, Russia, and other Commonwealth of Independent States. Nearly 60 processing companies in the states of Karnataka, Tamil Nadu, and Maharashtra grow gherkins on \approx 12,000 ha. Ajax and Sparta (Nunhems) are currently the dominant cultivars and account for 2.5 billion seeds in India alone (P. Arul

Murugan, IAP Farm Services Pvt. Ltd., Tamil Nadu, India, personal communication, 2012).

Cucumis sativus var. *hardwickii*, principally PI 183967 and PI 215589, was used in breeding to increase yield in commercial cucumber through new plant architecture, fruiting habit and leaf size (Horst and Lower, 1978; Sece and Staub, 1999; Staub and Kupper, 1985; Staub et al., 1992). Its fruit quality characteristics (bitter, small seedy fruit) and lack of disease resistance have been, however, an impediment to ultimate use in commercial pickling cucumber cultivars (Horst and Lower, 1978; Staub et al., 2008). Nevertheless, potentially useful *C. s. var. hardwickii*-derived germplasm (PI 183967 and PI 215589) has been released. For example, the gynoeocious, multiple disease-resistant, white spine cucumber population WI 6383 and its derived highest yielding lines (WI 5098 and WI 5551) were developed from a *C. s. var. sativus* \times *var. hardwickii* mating (Staub et al., 1992), but their poor internal characteristics and brining quality have precluded their widespread use in cucumber breeding.

Gynoeocious sex expression provides great potential for increased yield. Genes for gynoeocy in PI 220860 (Republic of Korea) resulted in the development of MSU 713-5, GY 3, and ‘Spartan Dawn’ pickling cucumbers (Peterson, 1975).

Resistances to numerous diseases have been transferred from Asian germplasm into U.S. commercial cucumber cultivars: leaf spot from PI 197088 (India), anthracnose from PI 175111 (India), bacterial wilt from PI 200818 (Burma), target leafspot from PI 109484 (Turkey), and powdery and downy mildews from PI 197087 (Assam, India), PI 197085 (Assam, India), and PI 212233 (Japan). Recent acquisitions from China, Japan, Pakistan, Philippines, and Taiwan have complemented the breeding efforts with the older accessions for the incorporation of disease resistance (Block and Reitsma, 2005; Staub et al., 2002).

WATERMELON

Watermelon was for many years thought to have originated in southern Africa because it was found growing wild throughout the area and reached maximum diversity there. The citron (*Citrullus lanatus* var. *citroides*) grows wild throughout southern Africa and may be related to the wild ancestor of watermelon. The secondary center of diversity for watermelon is China. Colocynth (*Citrullus colocynthis*), a related species, grows wild in India. Areas of the Middle East as well as countries near the Mediterranean Sea may also be good places to collect old landraces and wild accessions of *Citrullus*. For a review of watermelon, see Wehner (2008).

The colocynth may also be a wild ancestor of watermelon and is now found native in North and West Africa. Fruit of colocynth are small with a maximum diameter of 75 mm. The flesh is bitter and the seeds are small and brown. Crosses of *C. lanatus* with *C. colocynthis* produced F₁ hybrids with nearly regular

meiosis. The pollen was 30% to 40% fertile, and 35% of the seeds were fertile. The original wild watermelons probably had hard, non-sweet, sometimes bitter, white flesh, similar to the citron and colocynth.

Watermelon has been cultivated in Africa for over 4000 years and was probably brought to the Middle East by humans who domesticated the crop plant for their use as food as well as cattle feed. Watermelon was probably brought to China by way of the Silk Road from the Middle East. Cultivation of watermelon began in ancient Egypt and India and is thought to have spread from those countries through the Mediterranean area, the Near East, and Asia. Central Asia is, as a result, a tertiary center of diversity for watermelon.

Priorities for collection of *Citrullus* germplasm include India (especially the Indo-Gangetic plains and areas in the northwest parts of the country), south and southwest Africa (Kalahari Region), the southern areas of the former Soviet Union (Kazakhstan, Uzbekistan, Turkmenistan), Iran, and tropical Africa. Recent work in germplasm collection and exchange has provided the U.S. Dept. of Agriculture (USDA) germplasm system with a total of 51 *Citrullus* accessions that were collected during a scientist exchange visit with the People’s Republic of China in 1994. Later, in 1996, a team of four researchers collected germplasm of *Citrullus* in the Republic of South Africa. Twenty-two melon landraces were collected in Turkmenistan in 2008 (McCreight et al., 2010).

Several germplasm collections, along with current cultivars marketed by seed companies, represent the major sources of germplasm for watermelon breeders. The USDA collection is stored at the Regional Plant Introduction Station, Griffin, GA, with the backup collection at the National Center for Genetic Resources Preservation (formerly the National Seed Storage Laboratory), Fort Collins, CO. There are 3837 (1538 currently available) accessions in the collection. The collection includes representatives of all *Citrullus* species and botanical varieties. In addition, \approx 300 heirloom cultivars are kept at the National Center for Genetic Resources Preservation.

China is the major producer of watermelon in the world. Consumers there have a preference for red flesh color first but with a large interest in canary yellow as well. Flesh color can be scarlet red, coral red, orange, canary yellow, salmon yellow (golden), or white. Scarlet red ($Y^{Scr}Y^{Scr}$) is dominant to coral red ($Y^{Cr}Y^{Cr}$), which is dominant to orange (y^Oy^O), which is dominant to salmon yellow (yy). Canary yellow (CC) is dominant to non-canary yellow (cc) and epistatic to (overcomes) the y locus for red–orange–salmon yellow. Coral red is recessive to the white flesh color, which is found in citron. Canary yellow flesh color was introduced to the United States from Chinese cultivars and may be higher in citruline and arginine than red-fleshed cultivars.

Watermelon cultivars are categorized by fruit size, shape, and rind pattern (Wehner et al., 2001). Fruit sizes are termed mini (less than 4.0 kg), icebox (4.0 to 5.5 kg), small (5.5

Table 3. Asian melons reported resistant to one or more of diseases and insect pests and tolerant to abiotic stresses of importance in the United States and derived breeding lines and cultivars.

Accession	Origin	Resistance or stress tolerance	Derived germplasm	References
Ames 31282	China	Powdery mildew	PMR 50, 'PMR 45', PMR Honeydew	Liu et al., 2010; USDA-ARS, 2012
Calif. 525	India	Powdery mildew		Jagger and Scott, 1937; McCreight et al., 1987; Pryor et al., 1946
PI 79376	India	Salinity and high temperature Powdery mildew	Resistant Cantaloupe, 'PMR 5', 'PMR 6', 'PMR 7', 'Homegarden', 'Howell Spartan', 'Wescan', 'Perlita', 'Dulce', PMR Honeydew 'Golden Perfection'	Whitaker, 1979 Harwood and Markarian, 1968; McCreight et al., 1987
PI 123517	India	Alternaria leaf spot	MR-1	Brasher, 1965
PI 124101	India	<i>Tetranychus urticae</i>	PI 124111F, MR-1, 'Mainstream'	East et al., 1992
PI 124111	India	<i>Alternaria cucumerina</i> Downy mildew		Thomas et al., 1990
PI 124112	India	Powdery mildew	'Georgia 47', 'Edisto', 'Campo', 'Jacumba', PMR Honeydew	Nugent et al., 1979; Thomas, 1986; Thomas et al., 1988
PI 124431	India	Downy mildew		Harwood and Markarian, 1968; McCreight et al., 1987
PI 124440	India	Powdery mildew		Epimat and Pitrat, 1989
PI 157076	China	<i>Cucurbit aphid borne yellowing virus</i>	'Georgia 47', 'Edisto', 'Seminole', 'Delta Gold', 'PMR Delicious 51'	Harwood and Markarian, 1968; Henning et al., 2005a
PI 157082	China	<i>Papaya ringspot virus</i> <i>Tetranychus urticae</i>		Dogimont et al., 1997
PI 161375	Korea	Resistance to virus transmission		McCreight and Fashing-Burdette, 1996
PI 164320	India	<i>Aphis gossypii</i>		East et al., 1992
PI 164343	India	<i>Aphis gossypii</i>	'Mainstream'	Dogimont et al., 1997
PI 164723	India	Cucumber beetle <i>Tetranychus urticae</i>		Wolukau et al., 2007
PI 179901	India	<i>Aphis gossypii</i>		Zumiga et al., 1999
PI 180280	India	<i>Bemisia tabaci</i> Powdery mildew Downy mildew		Pitrat and Lecocq, 1980
PI 180283	India	<i>Papaya ringspot virus</i>		Boissot et al., 2008
PI 182938	India	<i>Papaya ringspot virus</i>		Boissot et al., 2008
PI 223637	Iran	<i>Watermelon mosaic virus</i>		Nugent et al., 1979, 1984
PI 282448	India	Powdery mildew		East et al., 1992
PI 313970	India	<i>Liriomyza sativae</i> <i>Aphis gossypii</i>		Boissot et al., 2008
(syn. 90625)		<i>Bemisia tabaci</i> Powdery mildew <i>Lettuce infectious yellows virus</i>		Boissot et al., 2003
PI 323498	China	<i>Cucurbit aphid borne yellowing virus</i>		McCreight, 2003; McCreight and Coffey, 2011
PI 378062	Japan	<i>Cucurbit yellow stunting disorder virus</i> <i>Cucurbit leaf crumple virus</i> <i>Didymella bryoniae</i>		McCreight, 2000
PI 4124723	India	Virus complex that induces interveinal mottling and yellowing <i>Fusarium</i> wilt		Dogimont et al., 1997

(Continued on next page)

Table 3. (Continued) Asian melons reported resistant to one or more of diseases and insect pests and tolerant to abiotic stresses of importance in the United States and derived breeding lines and cultivars.

Accession	Origin	Resistance or stress tolerance	Derived germplasm	References
		Resistance to stress tolerance	AR 5, AR Topmark, AR Hale's Best Jumbo	Kishaba et al., 1992; McCreight et al., 1984
		<i>Aphis gossypii</i> and resistance to virus transmission by <i>A. gossypii</i>		Boissot et al., 2003
		<i>Bemisia tabaci</i>		Kishaba et al., 1998
		Cucumber beetle		
		<i>Liriomyza sativae</i>		Kennedy et al., 1978
		Downy mildew		Epinat and Pitrat, 1989
		<i>Cucurbit aphid borne yellowing virus</i>		Dogimont et al., 1997
		<i>Watermelon mosaic virus, Papaya ringspot virus, Zucchini yellow mosaic virus</i>	'Hannah's Choice'	Gilbert et al., 1994; Henning et al., 2005b
PI 420145	Japan	<i>Didymella bryoniae</i>		Wolukau et al., 2007
"Wild melon"	India	<i>Monosporascus cannonballus</i>		Dhillon et al., 2012

to 8.0 kg), medium (8.0 to 11 kg), large (11 to 14.5 kg), and giant (greater than 14.5 kg).

Mini watermelon cultivars were developed for home garden use in the northern United States. New Hampshire Midget was a popular mini cultivar that was developed in 1951 by the University of New Hampshire using several cultivars that included Favorite Honey. Mini watermelons became popular for commercial growers with the introduction of the mini seedless type. That type is especially popular for off-season (winter) production as well as for sales to those with small families.

Cultivars used for breeding mini seedless cultivars included cultivars from China and Japan. Asian cultivars have high fruit quality and small fruit size and were important for development of the inbred parents for the production of mini seedless hybrids. The advantage of the Asian cultivars was their higher quality compared with cultivars such as 'New Hampshire Midget', particularly rind toughness and flesh sweetness.

Hybrid watermelon seed production has been improved using male-sterile mutants, some of which were obtained from China (Guner and Wehner, 2004a). Male sterility is used to keep seed costs low by reducing labor inputs. Hybrid production with the Chinese male-sterile genes can be done using alternating rows of the male-sterile (female) parent and the male-fertile (male) parent with honeybees or other insect pollinators to move the pollen from the male parent rows to the female parent rows.

The gynoecious mutant, *gy*, is an important new trait discovered in China (Jiang and Lin, 2007). The gynoecious mutant offers the same advantage of male sterility of not having to remove the staminate flowers daily from the plants in the seed parent rows to avoid self- and sib-pollination. Also, it may be more useful than genic male sterility because the plants can be self-pollinated late in the season to get 100% gynoecious plants for seeding in the isolation block for hybrid production.

Papaya ringspot virus-watermelon strain (PRSV-W, formerly *Watermelon mosaic virus-1*), *Watermelon mosaic virus*, and *Zucchini yellow mosaic virus* are the most important viruses of watermelon in the United States (Adlerz and Crall, 1967; Provvidenti, 1993). The major control strategies involve insecticides to eliminate the insect vectors, herbicides to remove alternate hosts, or genetic resistance (Provvidenti, 1993). Accessions with highest resistance to PRSV were PI 244017, PI 244019, PI 482342, PI 482318, and PI 485583 (Guner et al., 2002; Strange et al., 2002). All of the resistant accessions PRSV are from Africa.

Zucchini yellow mosaic is a relatively new disease of watermelon, caused by the potyvirus, *Zucchini yellow mosaic virus* (Guner and Wehner, 2004b). Resistant accessions have been identified in the watermelon germplasm collection maintained by the USDA. Resistant accessions include PI 386015, PI 386016, PI 386018, and PI 386019 from Iran

as well as PI 537277 from Pakistan. These five Asian accessions are from the related species *C. colocynthis*, which is interfertile with watermelon (*C. lanatus*).

Watermelon is one of the most resistant cucurbit species to powdery mildew (*Podosphaera xanthii*, formerly *Sphaerotheca fuliginea*). However, there are a few regions of the world where powdery mildew is a problem on watermelon. For example, watermelons grown in southern India are affected with the disease, but not in northern India. In southern India, 'Arka Manik' is resistant to powdery mildew. The *pm* gene causes susceptibility to the disease, but most cultivars have the resistance allele, *Pm* (Guner and Wehner, 2004a). Powdery mildew is becoming more of a problem in the United States, especially in the western states, and has been reported in the southeastern states. Accessions with resistance have been identified in the watermelon germplasm collection maintained by the USDA. Two *C. colocynthis* accessions from Iran are highly resistant: PI 386015 and PI 386024 (Davis et al., 2007; Tetteh et al., 2010).

Watermelon is one of the most susceptible of the cucurbit species to gummy stem blight caused by *Didymella bryoniae* (Gusmini et al., 2005). The disease occurs throughout the southern United States, particularly the Southeast. Field and greenhouse tests for resistance have been developed, but it can be difficult to get reproducible results. The USDA collection of PI accessions has been screened for gummy stem blight resistance by several teams of researchers. Some accessions have resistance to the disease, including PI 211915 from Iran, an accession of *C. lanatus*.

BITTER GOURD

Bitter gourd is an important vegetable domesticated in eastern India and southern China (Walters and Decker-Walters, 1988). It is cultivated commercially in Asia on ≈340,000 ha annually (Arvind Kapur, Rasi Seeds, personal communication). It is also cultivated in smaller volumes in the southern United States and Australia (Northern Territory, Queensland, New South Wales, Victoria) using Asian cultivars. Asian varieties are also grown in Ghana for fresh fruit export to European countries for their Asian communities. Its cultivation is gaining ground in Zambia, Congo, and Madagascar for local consumption and export. Nearly 60% of the bitter gourd production area is devoted to open-pollinated varieties (Ajay Dayal, Rasi Seeds, personal communication). Seed companies release numerous hybrid varieties each year in Asia that are more consistent for quality and yield than open-pollinated cultivars. Four hundred thirty-four bitter gourd accessions that originated from more than 15 countries are housed in the genebank of AVRDC-The World Vegetable Center, Taiwan.

Consumers prefer bitter gourd fruit at a physiologically immature or unripe stage and

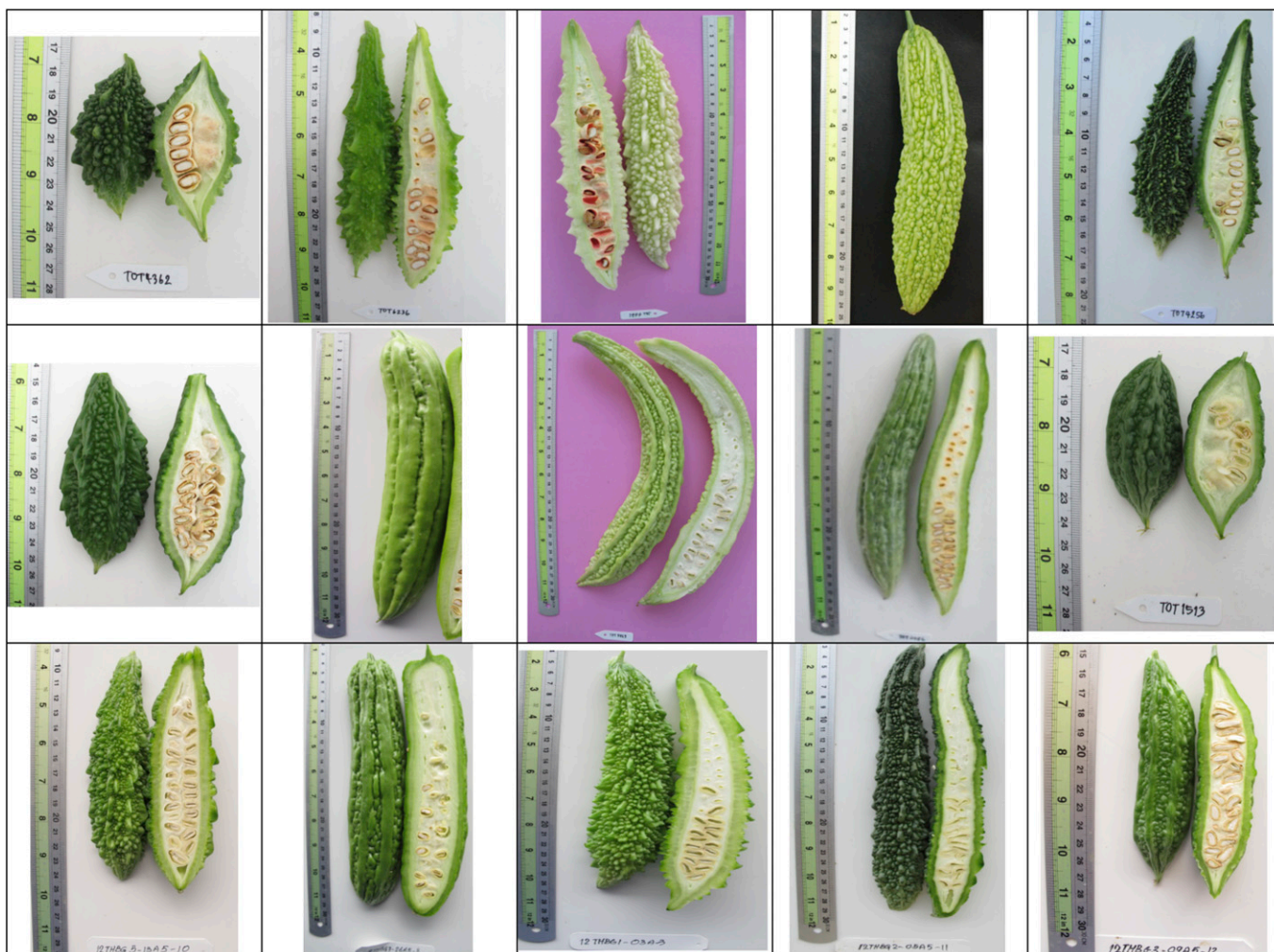


Fig. 6. Bitter gourd fruit type variation. Photos courtesy of Ms. Supunsa Phethin.

it is correlated with fresh bright appearance of fruits and immature creamy white seed-coat. Consumers display a wide range of preference for fruit color, shape, skin pattern and size, which varies between and within countries. Fruit color ranges from white or cream to light green to dark green and the various shapes include cylindrical, elliptical, spindle, and conical. Fruits of different varieties may have regular or irregular longitudinal ridges and warty skin. On the basis of these fruit types, nearly 20 market types of bitter gourd exist in Asia (Fig. 6) and half of these are grown in south Asia alone (India, China, Nepal, Bangladesh, Sri Lanka).

Asian consumers cook bitter gourd fruits with other vegetables, stuffed or stir-fried, or add them to soups to produce a slightly bitter flavor. Fruits are blanched, parboiled, or soaked in saltwater before cooking to reduce the bitter taste. Flowers and young shoots are also used in various Asian dishes to add flavor. Bitter gourd tea prepared from dried fruit is a popular health drink in Japan and some other Asian countries. In many African countries, the fruit is used as a purgative and vermifuge, and leaves are boiled in water and taken to treat diarrhea and dysentery (Ross, 2003).

Bitter gourd abounds in nutrients such as beta-carotene, vitamin C, folic acid, magnesium, phosphorus, and potassium (Yuwei et al., 1991). Recently the species has been considered as one of five crops, along with scuba rice, mung beans, disease-resistant bananas, and drought-hardy maize that have the potential to save the world (Rose, 2012). Saponins, momordicosides K and L, and momordicines I and II cause bitter taste of fruit (Harinantenaina et al., 2006; Yasuda et al., 1984). Bitter gourd has medicinal properties in addition to its use as a vegetable and is often used in folk medicine to treat Type 2 diabetes, a rapidly spreading non-communicative disease that afflicts 346 million people worldwide with 80% of these people living in low-income and middle-income countries (WHO, 2013). Bitter gourd fruit contain compounds (saponins, lipids) linked to anti-diabetic effects (Kloman et al., 2010). Mass evaluation of leading commercial hybrids and genebank accessions of bitter gourd for these bioactive compounds and other micronutrients is being pursued at the AVRDC–The World Vegetable Center, which may help to identify bitter gourd germplasm with increased phytochemistry/phytonutrient content. In addition, bitter

gourd plants contain a range of bioactive compounds with potential to control many other diseases. For example, momordin I is reported to be tumor-protective, momordicines I and II act as anti-microbials, and acylglucosylsterols as having anti-mutagenic, chitinase bacteriostatic effects (Nerukar et al., 2008; Njoroge and van Luijk, 2004; Yuwei et al., 1991). Preliminary studies (in vitro as well as in vivo) using bitter gourd fruit extract and its various purified fractions including MAP 30 have proven anticancer activity (Basch et al., 2003; Battelli et al., 1996; Ganguly et al., 2000; Licastro et al., 1980; Ng et al., 1994; Sun et al., 2001).

ROOTSTOCKS AND GRAFTING

Cucurbit grafting originated in Asia (Japan, Korea) in the 1920s as an effective tool to manage soilborne fusarium wilt (*Fusarium* spp.) on watermelon (Davis et al., 2008) and is now common in Japan, Korea, and China for watermelon, cucumber, melon, and bitter gourd (Table 4). This horticultural practice was introduced to Western countries in the early 1990s and is now rapidly expanding worldwide. Japan and Korea are the major exporters of grafted cucurbit seedlings (Lee

Table 4. Use of grafted cucurbits in Asia (Lee et al., 2010).

Country	Watermelon			Cucumber			Melon			Bitter gourd		
	Area (ha)	Grafted (%)	Rootstock ^z	Area (ha)	Grafted (%)	Rootstock ^z	Area (ha)	Grafted (%)	Rootstock ^z	Area (ha)	Grafted (%)	Rootstock ^z
Japan	13,000	92	Ls Cl	12,800	75	Cmm Cf	10,500	30	Cmm Cm	—	—	—
Korea	20,756	95	Ls Cmm	5,630	75	Cmm Cf	6,607	90	Cmm	—	—	—
China	2,162,456	20	Ls Cl	1,702,77	30	Cm Sa Cf	570,874	5	Cm Cmm Cl	200,000	2	Lc
Taiwan	13,431	35	Cmm Ls	2,666	11	—	6,441	0.1	—	1,802	30	La Cm

^zCf = *Cucurbita ficifolia*; Cm = *Cucurbita moschata*; Cmm = *Cucurbita maxima* × *C. moschata*; Cl = *Citrullus lanatus*; La = *Luffa aegyptica*; Lc = *Luffa cylindrica*; Ls = *Lagenaria siceraria*; Sa = *Sicyos angulatus*.

et al., 2010). In addition to control of soilborne diseases, use of rootstocks has resulted in improved plant vigor through efficient use of nutrients and water, cold tolerance, heat tolerance, and tolerance to salinity and wet soil conditions (Lee et al., 2010).

The main rootstocks for watermelon for control of fusarium wilt are bottle gourd (*Lagenaria siceraria* Mol. standl.), interspecific hybrids *C. maxima* × *C. moschata*, and wild watermelon (*C. lanatus* var. *citroides*) (Davis et al., 2008). Interspecific *Cucurbita* hybrid rootstocks also provide heat and drought tolerance but often result in the loss of watermelon flesh quality, which has been attributed to changes in flesh maturation (King et al., 2010). Interspecific *Cucurbita* hybrid rootstocks are powdery mildew-susceptible.

Bottle gourd is the main rootstock for watermelon grafting in Japan (Oda, 2002). Multiple disease-resistant accessions of bottle gourd of Asian origin will be helpful in breeding multiple disease-resistant rootstocks. Bottle gourd accession PI 271353, which was collected in India, was reported to be resistant to powdery mildew and *Zucchini yellow mosaic virus* (Kousik et al., 2008).

The common rootstock for melon grafting, a *C. moschata* × *C. maxima* hybrid, provides partial protection to soilborne disease and abiotic stresses but reduces fruit quality.

Fusarium wilt-resistant melon rootstocks give complete protection to susceptible melon scions without adversely affecting fruit quality or yield. Melon rootstocks resistant to root knot nematodes (*Meloidogyne* spp.) are not available commercially, but a couple of accessions of Indian snampmelon (*Momordica* group) and “wild melon” have been reported resistant to nematodes (Dhillon et al., 2007; Roy et al., 2012). Indian melon landraces (*Momordica* and *Acidulus* groups, and “wild”) should be evaluated for vigorous root growth, resistance to soilborne pathogens (*Fusarium* spp., *Monosporascus* spp.) and nematodes (*Meloidogyne* spp.), and suitability for potential use as rootstocks as well as for breeding resistant melon cultivars.

Cucumber grafting is practiced to increase cold tolerance and resistance to fusarium wilt. Specific genotypes of *C. moschata* that cause bloomless (wax-free) cucumber fruit are used as cucumber rootstocks in Japan. These bloomless fruits have a distinct appearance and enhanced shelf life (Sakata et al., 2008).

Cucurbit rootstock breeding research work is primarily undertaken in China, Japan, and Korea, mostly by private industry. The focus is to improve disease resistance and vigor, and there is a continuous need to develop/select suitable rootstock/scion combinations with high fruit quality traits such as improved fruit appearance and texture and enhanced concentration of health-promoting compounds.

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