Genetic Resources of Cucumber

Rachel P. Naegele and Todd C. Wehner

Abstract The Cucurbitaceae is a monophyletic family without any close relatives. It includes important vegetables such as cucumber, melon, watermelon, squash, pumpkin, and gourd. Within Cucurbitaceae, the genus *Cucumis* includes cultivated species *C. sativus* (cucumber) and *C. melo* (melon), as well as wild species including *C. hystrix*, *C. callosus*, and *C. sativus* L. var. hardwickii. More than 50 species have been identified in *Cucumis* with high levels of phenotypic and genetic diversity found in centers of diversity in Africa, Asia, and India. Primary and secondary centers of diversity can serve as useful sources of variation, and have been widely used to incorporate traits such as disease resistance into cultivated materials. During domestication, cucumber and melon underwent severe bottlenecks, which resulted in low genetic variation despite high phenotypic diversity. Since its domestication, approximately 3000 years ago, cucumber has undergone significant morphological changes from its small-fruited, black spined, seedy progenitor. More than 150 single gene traits have been described in *C. sativus*, including powdery mildew and virus resistance, sex expression, leaf morphology, and parthenocarpy, and molecular markers continue to be rapidly developed.

Keywords Cucumber • *Cucumis sativus* • Gene • Germplasm resources • Plant breeding

Introduction

The Cucurbitaceae or vine crop family is a distinct family without any close relatives (Sikdar et al. 2010). It includes important vegetables such as cucumber, melon, watermelon, squash and pumpkin. Cucumber (*Cucumis sativus* var. *sativus*), grown for fresh and processing markets, is one of the most important cultivated cucurbits with a global production of 70 million tonnes in 2013 (FAOSTAT). Approximately

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Table 1 Top eight producers of cucumbers (fresh and processed) in the world

Production of cucumbers (fresh-market and processing)		
Rank	Country	Production (tons)
1	China	54,315,900
2	Turkey	1,754,613
3	Iran (Islamic Republic of)	1,570,078
4	Russian Federation	1,068,000
5	Ukraine	1,044,300
6	Spain	754,400
7	United States of America	747,610
8	Mexico	637,395
9	Egypt	631,129
10	Uzbekistan	607,397

WorldAtlas.com 2016
http://www.worldatlas.com/articles/the-world-leaders-in-cucumber-production.html

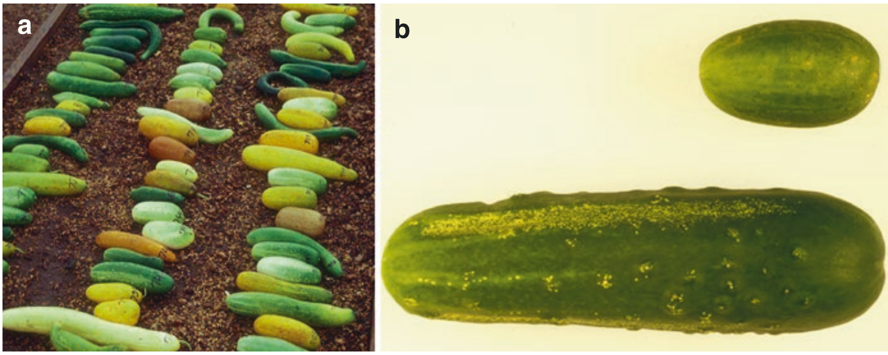

Fig. 1 (**a**) Cultivated cucumber morphological diversity and (**b**) *C.s. var. hardwickii* (*top*) and *C. sativus* (*bottom*)

70 % of the world's production of cucumber is in Asia, with China being the leading producer followed by Turkey, Iran, and Russia (Table 1).

Cucumber probably originated in India, where highly diverse wild as well as cultivated forms are found (Sebastian et al. 2010). Cultivated cucumber and its wild relatives, including *Cucumis sativus* var. *hardwickii*, exhibit large variation in traits such as fruit skin (ridges, colors, speckling), spines (size, density and color), growth habit (vine length and branching), fruit size, sex expression, and flesh bitterness (Fig. 1a). India is the center of diversity for cultivated cucumber. Secondary centers of diversity for cucumber exist in China and the Near East (Meglic et al. 1996; Staub et al. 1999). Accessions of *C. s. var. hardwickii,* which may be more closely related to the original ancestors of cucumber, are found in one of these secondary centers of diversity in the foothills of the Yunnan Province of Southern China (Fig. 1b) (Staub et al. 1999). Other close relatives of cucumber are *Cucumis hystrix* from China and the African *Cucumis* species, such as melon (*Cucumis melo*) and West Indian gherkin (*Cucumis anguria*) (Chen and Kirkbride 2000; Kerje and Grum 2000; Meeuse 1958). Cucumber was domesticated in Asia, and introduced into Europe where the first cultivars were selected in the 1700s (Staub et al. 2008). These early cucumber cultivars were brought to the Americas by Christopher Columbus, and grown by Native Americans from Florida to Canada by the early sixteenth century. Since this time, cucumber has spread across the globe becoming a major vegetable crop.

Cucumber Production

Cucumber is typically eaten fresh, or as a processed product (processing or pickling types) (Staub and Bacher 1997; Staub et al. 2008). The major cucumber market types are the American processing and fresh market types, the Dutch gherkin and greenhouse types, the German Schalgurken type, the Middle Eastern Beit Alpha type, and the Oriental trellis (burpless) type (Shetty and Wehner 2001). Fresh market cucumbers are field or greenhouse grown, and are usually between 15 (U.S. and Mediterranean) to 40 (European) cm in length. In addition to major market types, regionally preferred types also exist, but are less common. These include fresh market like the Persian cucumber (short fruit types grown in high tunnels or greenhouses) mainly marketed in the Middle East, and hermaphroditic 'Lemon' cucumber (shaped similar to a lemon with pale, greenish-yellow skin) (Robinson 2010).

Production practices vary widely according to market type (processing vs. fresh), profit margin, geographic region, and cultivar. Pickling cucumber (*C. s.* var. *sativus*) is an immature cucumber used for processing (brining or pasteurizing). Unless mechanized, harvest is labor intensive due to small fruit size, which is generally <15 cm long. India has low labor costs, and has become a major producer of the small size (<8 cm long) for export to Europe, the U.S., and Russia (Ranjan et al. 2008). Nearly 60 processing companies in the states of Karnataka, Tamil Nadu and Maharashtra grow pickling cucumbers on 12,000 ha. Ajax and Sparta (Nunhems) are some of the dominant cultivars, accounting for 2.5 billion seeds in India (P. Arul Murugan, IAP Farm Services Pvt. Ltd., Tamil Nadu, India, personal communication, 2012).

Pickling or processing cucumbers in the U.S. usually grown flat on bare ground, often with overhead or furrow irrigation, with machine harvest to reduce labor and other input costs (Ando and Grumet 2006; Schultheis 2000). This system, while requiring fewer expenses often results in greater disease incidence and more defects (shape/size/color) than slicing cucumbers (Fig. 2). A significant portion of the pickling cucumbers in the southern U.S. is hand-harvested, with 2 or 3 harvests per week for several weeks per season. Harvest begins in early spring in the southernmost states, and then returns in late fall for a second crop.

In the U.S., fresh market cucumbers are grown on raised beds, often with drip irrigation and plastic mulch, to improve fruit quality and reduce disease incidence (Schultheis 2000). Slicing cucumbers are hand-harvested and stored in forced-air cooling until distribution.

Fig. 2 American pickling cucumber graded from right to left based on a diameter scale of 1 (0–25 mm) to 3 (39–51 mm)

Centers of Diversity for Cucumber

The center of origin for cucumber has been a subject of debate for decades. The center of origin and diversity for wild *Cucumis* is likely Africa (Staub et al. 1992). However, the initial domestication of melon and cucumber occurred in the Middle East and Southern Asia, respectively (Dane et al. 1980). Cucumber was previously thought to have originated in Africa (Tapley et al. 1937), China, India, or in the Near East (Vavilov 1926, 1951; Harlan 1975; De Candolle as cited by Hedrick 1919), with domestication occurring later throughout Europe. Recent molecular assessments of *Cucumis* species have suggested that melon and cucumber are, however, of Asian origin and have numerous species-level relatives in Australia and around the Indian Ocean (Renner et al. 2007; Sebastian et al. 2010). Regardless of its origin, cucumber was domesticated about 3000 years ago, and is indigenous to India, which is a primary center of diversity, if not origin (Jeffrey 1980).

Cucumber Taxonomy

Cucumber belongs to the genus *Cucumis* in the subfamily Cucurbitoideae. *Cucumis* includes the cultivated species *C. sativus* (cucumber) and *C. melo* (melon) as well as many wild species, including *C. hystrix*, *C. callosus*, and *C. sativus var. hardwickii*. More than 50 species have been identified within *Cucumis* and there is a large phenotypic and genetic diversity in the populations collected in Africa, Asia, and India (Lv et al. 2012; Kacar et al. 2012; Weng 2010; Zhang et al. 2012a; Qi et al. 2013).

Crosses have been attempted between cultivated cucumber (*C. sativus*) and its relatives (*Cucumis* spp.) but have rarely been successful. The wild *C. hystrix* from

Yunnan Province of Southern China has been crossed with cucumber and progeny with limited fertility were generated (Chen et al. 1995; 1997). From those progeny, fertile amphidiploids were produced to create the synthetic species *C. hytivus* (Chen et al. 1997; Chen and Kirkbride 2000; Sebastian et al. 2010). Furthermore, the development of the fully fertile *C. hytivus*–derived fertile diploids ($2n=2x=14$) from *C. hytivus* and *C. s.* var. *sativus* cross resulted in potentially useful germplasm for plant improvement (Staub and Delannay 2011).

The 1320 *C. s.* var. *sativus* and var. *hardwickii* accessions currently resident in the U.S. National Plant Germplasm System represent the primary cucumber gene pool. These accessions include elite cultivars, breeding lines, heirlooms, collections from the centers of diversity, and exchange accessions from other collections. Within this collection inbreds, hybrids, monoecious, gynoecious, hermaphroditic, parthenocarpic, male sterile, disease resistant, tall, dwarf, determinate, seed dormant, and photoperiodic flowering types are represented.

The secondary gene pool of *C. sativus* includes cross incompatible (e.g. wild African) 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. 1997b, c). Attempts to exploit resources beyond the secondary cucumber gene pool, e.g., *Cucumis metuliferus*, *C. melo,* have been unsuccessful.

In cultivated cucumber and its closely related *C. sativus* var. *hardwickii*, researchers in India, China, Turkey, and the U.S. have shown that genetic diversity is relatively low despite the apparent diversity in morphology (Aydemir 2009; Horejsi and Staub 1999; Innark et al. 2013; Munshi et al. 2007; Lv et al. 2012; Pandey et al. 2013; Staub et al. 1997a, 1999; Zhang et al. 2012a). In local evaluations, high morphological variation was evident in fruit shape, size, color, sex expression, vine growth habit, and seed traits. Lv et al. (2012) evaluated over 3000 accessions representing cultivated, wild and landrace individuals from Asia, Europe and the U.S. using simple sequence repeat (SSR) markers. They reported little genetic diversity among cultivars collected from Europe, West/Central Asia and the U.S. Most of the genetic differentiation was between geographic or market classes. Accessions from China, East Asia, India and the Xishuangbanna province of China had the highest levels of diversity, and were genetically distinct from accessions from the U.S., Europe and West/Central China. These differentiated groups have potential for bringing in novel alleles and haplotypes to broaden the existing genetic pool for specific cucumber market classes. From this study, a core collection representing approximately 80 % of the genetic diversity was developed. This core collection was later re-sequenced using next generation sequencing technologies (Qi et al. 2013).

Singe nucleotide polymorphism (SNP)-based markers confirmed a low genetic diversity within *C. sativus* and homogenous populations across Eurasian, East Asian, and Xishuangbanna regions (Qi et al. 2013). Between the Eurasian and East Asian populations, non-synonymous SNPs in genes associated with resistance to fungi were highly differentiated, particularly in the Eurasian populations. Highest genetic diversity and admixed population structure was found in Indian populations for cucumber, consistent with India serving as a center of diversity for cucumber. In cultivated cucumber, this reduction in genetic diversity is likely due to extreme selection pressure during domestication and small initial population sizes (Qi et al. 2013). As a vining crop, one cucumber plant can cover a large surface area (if not trained on a trellis) and produce many fruit over weeks of harvest. Thus, fewer plants are required to produce enough yield for a community or family compared to grain crops (rice, corn, wheat), or root crops (carrot or beet), which have a lower yield per plant. This comparative increase in yield per plant would allow for smaller populations to be maintained resulting in bottlenecks that may have limited the genetic pool of this self-compatible crop. A smaller genetic pool has made finding agronomically useful traits such as disease and stress resistance in cultivated germplasm more difficult.

Because of low genetic diversity, related species with limited crossability, have been evaluated as sources for new traits of interest. SSR markers developed in *C. sativus* have been transferred, with limited success, and used to characterize genetic diversity in *C. melo, C. hystrix*, *C. s. var. hardwickii*, *C. metuliferus,* and *Lagenaria siceraria* (Bhawna et al. 2015; Weng et al. 2010; Kacar et al. 2012). Genetic diversity varied among these species, but was reported to be low (2–5 alleles per locus). These and other closely related species may serve as additional sources for traits such as disease resistance.

Cucumber Cultivar Improvement

A wide array of breeding and genetic resources for cucumber exist in the cucumber germplasm repositories maintained by the U.S. National Plant Germplasm System, Institute of Vegetables and Flowers at the Chinese Academy of Agricultural Sciences, and the Centre for Genetic Resources in Netherlands. Cucumber was grown in the early 1300s in England, using the earliest greenhouses and was known as “cowcumbers” (Boswell 1949). These early cultivars were planted in Haiti in 1494, and brought to the U.S. soon afterward (Sturtevant 1887). Perhaps the first important American-bred cucumber cultivar of the nineteenth century was ‘Tailby’s Hybrid’, developed by Joseph Tailby of Massachusetts, which was derived from a cross between American and English cultivars and introduced in 1872 (Tapley et al. 1937). The success of ‘Tailby’s Hybrid’ encouraged plant breeders to develop new, early generation cultivars such as ‘Arlington White Spine’, ‘Boston Pickling’, ‘Chicago Pickling’, and ‘Snow’s Pickling’ (Fig. 3).

Some cultivars still available today were introduced to the U.S. more than a century ago. ‘Early Russian’, for example, was described by Naudin in France in 1859 (Naudin 1859) while ‘Early Cluster’ was introduced prior to 1800. Boswell in 1949 concluded that all of the distinct types of cucumber in use at that time were known at least 400 years before (Boswell 1949). Among the market types (American processing and fresh market, Dutch gherkin and greenhouse, German Schalgurken,

Fig. 3 'Snow's Pickling' an early American cultivar (ca. 1905) with poor shape, black spines and light skin color

middle eastern Beit Alpha, and Oriental trellis), there is variation in fruit morphology, growth habit, and disease resistance. Unlike some of their more colorful relatives, cucumbers have few vitamins and minerals in their fruit (Table 2), with the exception of lutein, a carotenoid (Perry et al. 2009; Granado et al. 2003). To date, no studies have examined the variation for lutein content among the cucumber market types. However, work has been done on the inheritance of beta-carotene in cucumber and germplasm released (Cuevas et al. 2010; Staub et al. 2011). In general, cultivated cucumber fruit have few spines, a large mesocarp, bitterfree fruit, and few or no seeds. This is in contrast to its wild relative, *C. s. var. hardwickii* that has small and bitter fruits, a large seed cell, and many seeds citation (Walters et al. 1996). More than 150 single-gene traits have been described in cucumber, and molecular markers are being developed for use in selection (Table 3). For a more comprehensive list of cucumber genes and sources, see the Cucurbit Genetics Cooperative list (http://ars.usda.gov/sotheast-area/charleston-sc/vegetable-research/docs/cgc).

Attempts to incorporate useful genes from secondary cucurbit gene pools (*C. metuliferus* and *C. hystrix*) into cucumber have had limited success (Staub et al. 2008). However, Chen et al. (1995, 1997) successfully made an interspecific cross between cucumber (*C. sativus* var. *sativus* primary gene pool) and *C. hystrix* (H; $2n=2x=24$; secondary gene pool). The F_1 progeny ($2n=2x=19$) derived from this mating were both male and female sterile; chromosome doubling was, therefore,

Table 2 Nutritional composition of cucurbits (amounts per 100 g fresh product)

Cucurbit	Water (%)	Protein (g)	Fat (g)	Carbohydrate (g)	Fiber (g)	P (mg)	Na (mg)	K (mg)	Vitamin A (IU)	Thiamin (mg)	Riboflavin (mg)	Niacin (mg)	Vitamin B_6 (mg)
Cucumber	96	0.5	0.1	2.9	0.6	17	2	149	45	0.03	0.02	0.30	0.05
Melon, casaba	92	0.9	0.1	6.2	0.5	7	12	210	30	0.06	0.02	0.40	–
Melon, honeydew	90	0.5	0.1	9.2	0.6	10	10	271	40	0.08	0.02	0.60	0.06
Pumpkin	92	1.0	0.1	6.5	1.1	44	1	340	1600	0.05	0.11	0.60	–
Squash, acorn	88	0.8	0.1	10.4	1.5	36	3	347	340	0.14	0.01	0.70	0.15
Squash, summer	94	1.2	0.2	4.4	0.6	35	2	195	196	0.06	0.04	0.55	0.11
Squash, winter	89	1.5	0.2	8.8	1.4	32	4	350	4060	0.10	0.03	0.80	0.08
Squash, zucchini	96	1.2	0.1	2.9	0.5	32	3	248	340	0.07	0.03	0.40	0.09
Watermelon	93	05	0.2	6.4	–	10	1	100	590	0.03	0.03	0.20	–

http://www.nal.usda.gov/

Table 3 A selection of cucumber markers associated with phenotypic traits

Tissue	Trait	Gene	Chromosome	Source	Reference
Fruit	Tuberculate	*Tu*	5	S52, S94, S110	Zhang et al. (2010)
	Fruit shape				
	Uniform immature fruit color	*u*	5	9930	Maio et al. (2011), Yang et al. (2014)
	Glossy fruit skin	*d*	5	9110Gt, S06, S23, S76	Maio et al. (2011), Yang et al. (2014)
	Netted fruit	*H*	5	9110Gt	Maio et al. (2011)
	Fruit ribbing	*Fr*	5	9930	Maio et al. (2011)
	Yellow flesh color	*yf*	7	PI 120815	Lu et al. (2015)
	Orange flesh color	*R*	4		Bo et al. (2012)
	Orange skin color	*B*	4	WI7200	Li et al. (2010)
	Black spines	*B*	4	WI7200	Li et al. (2010), Cavagnaro et al. (2010), Yang et al. (2012, 2013)
	Bitterness	*bi-1*	5	9930	Zhang et al. (2012a, b)
	White skin	*w*	3		Dong et al. (2012)
	Weight	*fw*	1,2,3,4,6		Cavagnaro et al. (2010), Yang et al. (2012, 2013)
	Flesh thickness	*fft*	2	D8	Xu et al. (2015, 2014)
	Neck length	*fnl*	3,4,5,6		Xu et al. (2014)
	Spine density	*Fsc*	4,5,6		Cavagnaro et al. (2010), Yang et al. (2012, 2013)
	Diameter	*fd*	1,3,4,5,6		Cavagnaro et al. (2010), Yang et al. (2012, 2013)
Leaf					
	Little leaf	*ll*		H-19	Cavagnaro et al. (2010), Yang et al. (2012, 2013)
	Virescent	*v-1, vl*	6	9930	Maio et al. (2011), Yang et al. (2012, 2013), Cavagnaro et al. (2010)
	Bitterness	*BI, Bt-1*	6	9930	Maio et al. (2011), Zhang et al. (2012a, b)
	Glabrous –2, Glabrous –3	*gl-2, gl-3*	2		Cavagnaro et al. (2010), Yang et al. (2011, 2013), Pan et al. 2015)

(continued)

Table 3 (continued)

Tissue	Trait	Gene	Chromosome	Source	Reference
Growth habit					
	Determinate	*de*	6	H-19	Weng (2014)
	No lateral branch	*nlb*	1		Jiang et al. (2008)
	Compact	*cp*	4	PI 308915	Li et al. (2011)
	Cotyledon length/width	*cl/cw*	1,3		Miao et al. (2012)
Flower	Gynoecious	*F*	6	9110Gt	Maio et al. (2011), Win et al. (2015)
	Time to flower	*FT*	1	Muromskij	Lu et al. (2014)
	Sex ratio	*sex*	5,6	H-19	Fazio et al. (2003)
Disease	Angular leaf spot	*psl*		H 603	Olczak-Woltman et al. (2009)
	Powdery mildew	*pm*	1,3,5	CS-PMR1, Santou	Fukino et al. (2013), He et al. (2013)
	Zucchini yellow mosaic virus	*Zym*	6	A192-18	Amano et al. (2013)
	Downy mildew	*dm*	1,3,4,5,6,7	*C. hystrix*, K8	Bai et al. (2008); Ding et al. (2007); Zhang et al. (2013)
	Fusarium wilt	*Foc2.1*	2	*9110Gt*	Zhang et al. (2014)

performed to produce a fertile amphidiploid (HHCC, $2n=4x=38$) using embryo culture (Chen et al. 1998). This amphidiploid was subsequently self-pollinated for several generations resulting in fertile germplasm that was designated a new species, *C. hytivus* (Chen and Kirkbride 2000). The incorporation of genes from the secondary gene pool of cucumber such as *C. hystrix* is potentially useful to cucumber breeding, especially given that *C. hystrix* has novel genes for disease resistance, such as gummy stem blight caused by *Didymella bryoniae*, that are not present in cultivated cucumber (Chen et al. 2003).

Plant Architecture

Manipulation of plant architecture, stem length, and sex expression, with adjustments in plant population density have resulted in higher yield (Lower and Edwards 1986; Staub et al. 2008). For example, cultivars used in once-over mechanical harvest perform better if they have concentrated fruit set. Predominantly gynoecious and completely gynoecious types are preferred over monoecious for that reason. Determinate plant types also have a concentrated fruit set compared with indeterminate types, requiring fewer harvests (George 1970; Kauffman and Lower 1976). With stressful (low fertility, low water) production conditions, however, indeterminate plant type is better yielding than determinate.

Seedling Traits

Early evaluation of populations at the seed or seedling stage is extremely useful for reducing population size and minimizing undesirable individuals. This evaluation can occur by testing for the presence of molecular markers associated with traits of interest, or by using phenotypic markers. In cucumber, phenotypic markers have been identified for fifteen traits including non-lethal and lethal color mutants, growth habit and bitterfree leaves. The five non-lethal color mutants include virescent (*v*) (Poole 1944; Tkachenko 1935), variegated virescence (*vvi*) (Abul-Hayja and Williams 1976), yellow cotyledons-1 (*yc-1*) (Aalders 1959), yellow cotyledons-2 (*yc-2*) (Whelan and Chubey 1973; Whelan et al. 1975), and yellow plant (*yp*) (Abul-Hayja and Williams 1976). Four of the color mutants cause seedling lethality: chlorophyll deficient (*cd*) (Burnham et al. 1966), golden cotyledon (*gc*) (Whelan 1971), light sensitive (*ls*) (Whelan 1972), and pale lethal (*pl*) (Whelan 1973). Other seedling phenotypic traits include bitterfree foliage (*bi*), with no cucurbitacins in the leaves (Andeweg and DeBruyn 1959), and blind (*bl*) (Carlsson 1961), with no growing point on the seedlings. Delayed growth (*dl*) (Miller and George 1979), long hypocotyl (*lh*) (Robinson and Shail 1981), revolute cotyledons (*rc*) (Whelan et al. 1975), stunted cotyledons (*sc*) (Shanmugasundarum and Williams 1971;

Shanmugasundarum et al. 1972), and nuclear (*Ch*) (Kozik and Wehner 2006, 2008) and chloroplast (Chung et al. 2007; Gordon and Staub 2011) derived chilling resistance are other seedling traits.

Stem and Leaf Traits

Most cucumber cultivars have indeterminate plant habit, where the stem elongates continuously, and 1–2 primary lateral branches originating from the main stem (Lower and Edwards 1986; Staub et al. 2008). Some cultivars also produce secondary lateral branches (originating from primary lateral branches) under some growing conditions, which is under polygenic control (Fazio et al. 2003). More branching occurs when plants are grown at low density. Cucumber plants can be indeterminate, determinate (*de*), or compact (*cp*) (Lower and Edwards 1986). Determinate cultivars have the stem terminating in flowers, and are dwarf as well. Determinate plants are not as short as compact plants. Leaf size is also controlled by a major gene designated *ll*. Plants with *Ll Ll* have large leaves (80–100 cm^2) and plants with *ll ll* have little leaves (25–40 cm^2) (Pierce and Wehner 1990; Fazio et al. 2003). Intermediate leaf types have been also identified in progeny from crosses between normal and little leaf types.

The *C. s.* var. *sativus* line H-19, a mutant type referred to as “Arkansas Little Leaf” (originally AR 79–75), and *C. s.* var. *hardwickii* differ from typical *C. s.* var. *sativus* commercial types in their multiple fruiting, i.e., the sequential setting of fruit without inhibition) and multilateral branching habit (Fazio et al. 2003). Although line H-19 bears processing type fruit (12–15 cm in length) that are similar to normal-leafed *C. s. sativus* types on an indeterminate multilateral branching habit, fruit of *C. s.* var. *hardwickii* are relatively small (3–5 cm in length). Yield and quality of H-19 was optimum when grown at 300,000 plants/ha and harvested at 10 % oversized fruit (Schultheis et al. 1998).

Cucumber stem or vine length can be modified by seven genes: bush (*bu*) (Pyzenkov and Kosareva 1981), compact (*cp*) (Kauffman and Lower 1976), determinate (*de*) (Denna 1971; George 1970; Hutchins 1940), dwarf (*dw*) (Robinson and Mishanec 1965), tall height (*T*) (Hutchins 1940), and *In-de* that behaves as an intensifier for *de* (George 1970). These genes can also have pleiotropic effects on leaf size, shape, or fruit production. Rosette (*ro*), which can affect height, is characterized by muskmelon-like leaves (de Ruiter et al. 1980).

Leaf and foliage characteristics (shape, color, glabrousness, size) can also be affected by genes not affecting stem length. Eight in particular are responsible for leaf shape: blunt leaf apex (*bla*) (Robinson 1987a), cordate leaves-1 (*cor-1)* (Gornitskaya 1967), cordate leaves-2 (*cor-2*) (Robinson 1987b), crinkled leaf (*cr*) (Nazavari et al. 1963; Odland and Groff 1963), divided leaf (*dvl*) (den Nijs and Mackiewicz 1980), ginko leaf (*gi*) (John and Wilson 1952), littleleaf (*ll*), (Goode et al. 1980; Wehner et al. 1987) and umbrella leaf (*ul*) (den Nijs and de Ponti 1983).

Fig. 4 Locule number variation from 2 (*left*) to 5 (*right*)

Leaf arrangement (opposite vs. alternate), color (golden vs. green) and glabrousness (trichomes vs. no trichomes) exhibit variation, and have been linked to single genes. Golden leaves (g), not to be confused with golden cotyledons, results in a golden color on the lower leaves of the plant (Tkachenko 1935). Opposite leaf arrangement (*opp*) is inherited as a single recessive gene that is linked to *m* (andromonoecious flowers) and *l* (locule number) (Fig. 4). Unfortunately, incomplete penetrance makes the opposite leaf arrangement difficult to distinguish from normal plants with alternate leaf arrangement (Robinson 1987c). Glabrous leaves (the absence of trichomes) is controlled by two independently inherited genes, glabrate (glb) and glabrous (Inggamer and de Ponti 1980; Robinson and Mishanec 1964; Whelan 1973). Genes for short petiole (*sp.*) (den Nijs and Boukema 1985) and tendrilless (*td*) (Rowe and Bowers 1965) have also been identified.

Flower Femaleness and Parthenocarpy

Most cucumber cultivars are monoecious (staminate and pistillate flowers) or gynoecious (pistillate flowers only). However, androecious (staminate flowers), hermaphroditic (perfect flowers), andromonoecious (staminate and perfect flowers), and trimonoecious (staminate, perfect, and pistillate flowers) types also exist (Lower and Edwards 1986). Monoecious hybrid cultivars have been available since 1945, when Oved Shifriss developed ‘Burpee Hybrid’, but the high cost of hybrid seed limited their commercial use. Plants having all pistillate or all perfect flowers are commonly used in hybrid production (Kubicki 1969). Typically, flowering cucumber plants begin producing staminate flowers, transitioning to perfect or pistillate flower production as the plant matures. Sex expression varies within the cucumber germplasm and has been successfully incorporated by plant breeders into cultivars with improved fruit yield and quality (Staub et al. 2008). Development of gynoecious cultivars reduced the cost of producing hybrid seed and improved earliness and adaptation to mechanical harvesting. Germplasm with the gynoecious gene was brought from Korea to the U.S. by E. Meader and distributed by the U.S.D.A. Plant Introduction system as PI 220860. Peterson (1960) backcrossed the gynoecious gene into ‘Wisconsin SMR 18’ to develop MSU 713–5, the female parent of the first

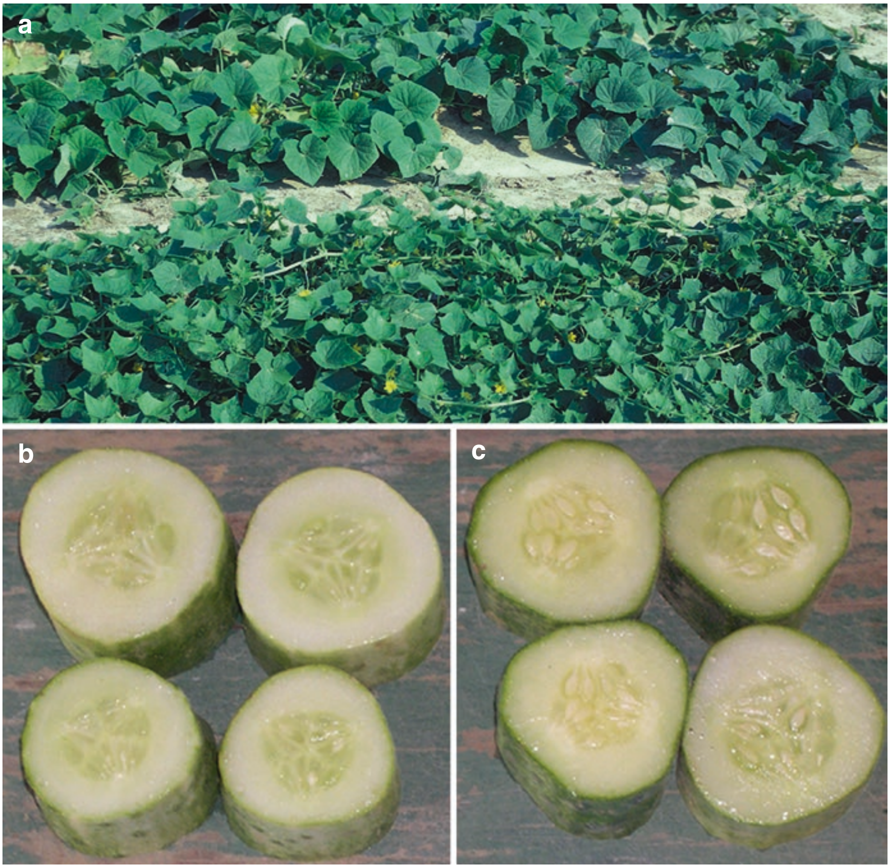

Fig. 5 Regular cucumber leaves (**a**, *top*) compared to little-leaf (**a**, *bottom*) and seed cell of (**b**) parthenocarpic and (**c**) seeded cucumbers

gynoecious hybrid cultivar, 'Spartan Dawn'. Gynoecy has replaced the need for male sterility in hybrid production. However, at least five genes for male sterility have been described (Robinson and Mishanec 1967; Shanmugasundarum and Williams 1971; Whelan 1972).

One of the more important traits to be incorporated into recent cultivars is parthenocarpy, or fruit set without pollination. Gynoecious cucumbers require the addition of a pollenizer to provide pollen for fruit set. Often, 15 % pollenizer (a monoecious hybrid cultivar) seeds are mixed with 85 % gynoecious hybrid for sale to the grower as a blend. Parthenocarpic cucumbers do not need a pollenizer to be grown in the production field or greenhouse, do not need bees or other pollinators, and may also have a concentrated fruit set (Fig. 5) (Staub et al. 2008). Parthenocarpy, first discovered in the early 1900s, is controlled by a single incompletely dominant gene *Pc* (Pike and Peterson 1969). Other genes are involved in controlling the trait, producing a range of parthenocarpic fruit set, with narrow-sense heritability of

0.33–0.62, and 5–13 effective factors (Sun et al. 2006a). Parthenocarpy was first available in greenhouse slicers, then in greenhouse Beit Alpha type for production in high tunnels, and in pickling type for field production. The parthenocarpic trait can be transferred to new types with a few backcrosses from a donor line (Sun et al. 2006b). Slicing cucumbers for open field production are now becoming available. Parthenocarpy results in high yield, seedless fruit, which provide for easier slicing. Although there have been problems with the fruit skin (exocarp) becoming tough in the large sizes at harvest.

Yield

Cucumis sativus var. *hardwickii*, including accessions LJ 90430, PI 183967 and PI 215589, has been used to increase genetic diversity for yield in commercial cucumber (Staub and Kupper 1985). Its fruit quality characteristics (small, bitter, seedy fruit) and lack of disease resistance have limited its use however (Horst and Lower 1978; Staub et al. 2008). Germplasm based on *C. s.* var. *hardwickii* has been released, but their poor internal characteristics and brining quality have precluded their widespread use so far (Staub et al. 1992).

Marker-assisted selection for fruit yield and quality has been an effective tool in cucumber improvement (Behera et al. 2011; Fan et al. 2006; Fazio et al. 2003; Robbins and Staub 2009). Yield heritability is believed to be relatively low ($R^2 = 0.17–0.56$; number of green fruit) depending on the study, and recurrent selection for yield has resulted in small gains (Robbins and Staub 2009; Wehner and Cramer 1996; Wehner 1989). Despite the small, but significant gains, yield comparisons of cultivars developed from 1969 to 1987 have demonstrated a consistent increase in production across locations and years (Wehner 1989). Backcrossing with molecular-based genotyping, along with selection for genetic diversity in *C. sativus* populations has increased diversity (phenotypic and genotypic) in cucumber (Delannay and Staub 2010), and resulted in the release of 94 inbred backcross lines (IBL) for use in cucumber improvement (Staub and Delannay 2011). Unlike crops such as maize, heterosis has been shown to have only a small effect in cucumber (Cramer and Wehner 1999).

Disease Resistance

Pre- and post-harvest diseases are a limitation for cucumber production. It has been estimated that diseases result in economic losses of 30–100 % each year (St. Amand and Wehner, 1991). In the U.S. alone, it has been estimated that $20 million is spent annually to control just *Pseudoperonospora cubensis*. Economically important diseases worldwide include bacterial wilt (*Erwinia tracheiphila*; principally home garden), anthracnose (*Colletotrichum lagenarium*), angular leaf spot (*Pseudomonas* *lachrymans*), downy mildew (*Pseudoperonospora cubensis*), Fusarium wilt (*Fusarium oxysporum* f. sp. *cucumerinum*), gummy stem blight (*Didymella bryoniae*), powdery mildew (*Podosphaera xanthii*), scab (*Cladosporium cucumerinum*), and target leaf spot (*Corynespora cassiicola*). There are also several important viruses (CMV, PRSV, WMV, ZYMV) and fruit rots (*Pythium* spp., *Phytophthora capsici*, *Rhizoctonia solani*) that can be controlled using genes for resistance.

Development of cucumber cultivars with improved disease resistance in the U.S. began in the late 1920s, when R.H. Porter brought cucumber mosaic virus resistant germplasm back from China (Porter 1929). He bred the cultivar Shamrock in 1943, which was derived from the cross 'Chinese Long' × 'Davis Slicer' (Anonymous 1957). Disease resistance has been moved into commercial cucumber cultivars from PI accessions as follows: leaf spot (PI 1970888, India), anthracnose (PI 175111, India), bacterial wilt (PI 200818, Burma), target leafspot (PI 109484, Turkey), and powdery and downy mildew (PI 197087, India; PI 197085, India; and PI 212233, India). Recent acquisitions from China, Japan, Pakistan, the Philippines, and Taiwan have added new resources disease resistance (Block and Reitsma 2005; Staub et al. 2002).

Cucumber Downy Mildew

Cucumber downy mildew, caused by *Pseudoperonospora cubensis*, is a foliar disease of cucumber. Prior to 2004, the disease was controlled through a single recessive gene, *dm-1,* identified in a cucumber PI accession collected in India (PI 197087) (van Vliet and Meysing 1974). The *dm-1* gene was incorporated in the 1960s into two cultivars: Pixie and Poinsett. After 2004, the *dm*-1 gene was less effective in maintaining resistance to the pathogen. Additional sources of resistance have been identified in cucumber accessions PI 197088 and 197085, and cultivars Chinese Long and Yuanfeng. Each of these sources of resistance have undesirable fruit quality traits for slicing, pickling and European greenhouse markets (Criswell et al. 2010; Call et al. 2012). Quantitative trait loci (QTL) mapping has identified five or more genes contributing to resistance from Chinese long, and Yanfeng (Pang et al. 2013). Three QTL for resistance were identified in PI 197085, but no genetic mapping has been done on PI 197088 to date (Szczechura et al. 2015). Sources of resistance have also been identified in *C. melo* (PI 124111), but attempts to move those into *C. sativus* have failed (Lebeda et al. 1996). In *C. hystrix*, resistance QTL co-localized with those detected in 'Chinese Long', suggesting that these may be allelic variants of existing resistance genes and not new loci. The main QTL in these studies appear to be located on chromosome 5, with a smaller-effect QTL located on chromosomes 6.

Powdery Mildew

Powdery mildew, caused by the pathogen *Podosphaera fusca*, is a foliar pathogen of cucurbits causing reduction in yield and fruit quality. Three genes have been described for powdery mildew resistance (*pm-1*, *pm-2*, and *pm-3*), with a possible fourth (*pm-h*) contributing to seedling hypocotyl resistance (Fukino et al. 2013; He et al. 2013; Sakata et al. 2006). Accession PI 197088, in addition to downy mildew resistance, has genes for resistance to powdery mildew. A QTL study identified four QTL, including one with major effects. However, the QTL were not linked to a specific chromosome, nor was the possible connection between powdery and downy mildew resistance evaluated. A study in *C. melo* reported linkage between downy and powdery mildew resistance using the resistant accession PI 124112 (McCreight et al. 2013; Olczak-Wotman et al. 2011; Perchepied et al. 2005). This linkage was also observed in cucumber by van Vliet and Meysing (1977) in the downy and powdery resistant accession PI 197087. In WI 2757, a line with moderate levels of downy mildew resistance, six QTL for powdery mildew resistance were identified (Call et al. 2012; He et al. 2013). These QTL were located on chromosomes 1, 3, 4, and 5. In addition to downy and powdery mildew resistance, PI accessions 197085, 197087, and 197088 also have moderate resistance to angular leaf spot and anthracnose, making them useful parents during plant breeding.

Fruit Rots and Seedling Diseases

Bacterial, fungal and oomycete pathogens can cause fruit rot and seedling disease on cucumber. *Phytophthora* fruit rot caused by the oomycete pathogen *Phytophthora capsici*, is a serious disease in field-grown cucumbers. Small, dark, water soaked lesions develop on infected fruit, eventually encompassing the whole fruit with white sporangia resembling powdered sugar (Hausbeck and Lamour 2004). The disease reduces yield in the field, and, if infected cucumbers are not detected early, can also spoil shipments after harvest (Hausbeck and Lamour 2004). An age-related resistance was detected during the course of screening a cucumber core collection for resistance (Gevens et al. 2006). More recently, screening of the full U.S. cucumber PI collection led to identification of three possible sources of young fruit resistance, PIs 109483, 178884, and 214049 (Colle et al. 2014). Resistance to other *Phytophthora* species also has been identified. In a greenhouse evaluation for seedling damping off using *Phytophthora dreschsleri*, a single resistant cultivar, PS 547, was identified (Nazavari et al. 2016). Another oomycete pathogen, *Pythium aphanidermatum*, can cause fruit rot (cottony leak), as well as seedling damping off. Similar to *P. capsici*, *P. aphanidermatum* starts as small water soaked lesions on the fruit, eventually turning into large fluffy-white lesions (Favrin et al. 1988). Cottony leak is primarily managed by fungicide applications, since no sources of resistance have been reported.

Belly rot, caused by the soilborne pathogen *Rhizoctonia solani*, is a minor disease of cucumber. In optimal conditions, the disease results in small water-soaked lesions on the lower surface of the fruit that reduce yield and quality (Uchneat and Wehner 1998). Sources of resistance have been identified in pickling and slicing cucumber backgrounds to belly rot (Uchneat and Wehner 1998; Wehner et al. 2004). In one study, four sources of resistance were identified from PI accessions 163216, 197088, 357852, and 280096 in field and lab-based evaluations (Wehner et al.

2004). However, no studies to date have determined the genetic inheritance of resistance to this disease. Infection by *R. solani* can also result in seedling damping off, though no sources of resistance have been identified for this disease. Likewise, *Fusarium spp.* also cause fruit rot, damping off, and wilt in cucumber (Zitter 1998). Sources of resistance have been identified for specific *Fusarium sp.* (Rose and Punja 2004). Using the resistant inbred line "9110Gt", a single QTL (*Foc2.1*) was found associated with resistance (Zhang et al. 2014).

Viruses

Several viruses of cucumber cause serious yield loss, leaf damage, or fruit defects. *Cmv* is a single dominant gene controlling resistance to cucumber mosaic virus found in the cucumber cultivar Chinese Long. Multiple potyviruses, including zucchini yellow mosaic virus (ZYMV), watermelon mosaic virus (WMV), the watermelon strain of papaya ringspot virus (PRSV-W) and Moroccan watermelon mosaic virus (MWMV) all infect cucumber. Several sources of resistance have been identified to these viruses, often within the same genetic material (Wang et al. 1984; Provvidenti 1987). ZYMV resistance in TMG-1 is controlled by a single recessive gene (Provvidenti 1987). Watermelon mosaic virus resistance was controlled by two genes, *wmv-1-1* ('Surinam') and *wmv* ('Kyoto 3 Feet') (Cohen et al. 1971). Further studies have suggested that this may be a quantitative trait, with *wmv-2*, *wmv-3*, and *wmv-4* being identified in TMG-1 (Wang et al. 1984). Additional QTL reported in melon accession PI 161375 provide further support that WMV resistance is polygenic (Guin-Aragones et al. 2014). Analyses of relationships among resistances to the different potyviruses and allelism among different sources of resistance, suggest that multiple resistances may be conferred by either a single gene or tightly linked loci (Wai et al. 1997; Grumet et al. 2000). *Zucchini yellow mosaic virus* (ZYMV) resistance is controlled by a single recessive gene $zym^{A192-18}$ located on chromosome 6 (Amano et al, 2013). *Papaya ringspot virus* (PRSV) resistance was mapped in a segregating F_2 population and a single recessive gene $prsv^{02245}$ was also identified on chromosome 6 (Tian et al. 2015).

Future Research Needed

Much progress has been made in describing phenotypic traits of cucumber, and determining their heritability (quantitative traits) and the genes involved in their control (qualitative traits) since the initial cultivars were developed in the 1700s. A genome sequence is now available for cucumber, as well as genetic information on population structure and diversity, and molecular markers for fruit quality and disease resistance traits. As molecular and sequencing technologies continue to improve, and molecular markers become increasingly economical to use, we can look forward to faster or more efficient selection of traits for use in cultivar development.

In order to continue this trend, genetic resources need to be continually developed, maintained and utilized. Germplasm from primary, secondary and tertiary centers of origin have been collected, stored, and evaluated in the national and international germplasm centers. That includes the heirloom and elite cultivars, as well as some of the gene mutant type-lines. It is imperative that more type-lines are included in the germplasm collections, as traits are identified. This may also encourage researchers to find or generate novel or alternate gene mutants. Useful genes, such as those for fruit quality and disease resistance, have been incorporated from wild or unadapted backgrounds into elite inbreds such as Marketmore, Poinsett, and WI 2757. This germplasm enhancement work makes use of these genes easier for cultivar development, and we hope that prebreeders will continue to do so. In addition, there is a need for continued collection and exchange of cucumber germplasm all over the world. Expanded collections will help feed a growing population, and counter new pest, disease and weed problems.

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