Classical Genetics and Traditional Breeding

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Abstract

Cucumber is one of the most important vegetable crops grown worldwide, both under open fields and protected conditions. It is originated in India with a secondary centre of diversity in China and the Near East. It is a cross-pollinated crop with no inbreeding depression and is used as a model crop for studying the various genetic and molecular pathways because of its breeding behaviour and smaller genome size. The distribution of the different *Cucumis* species in the primary, secondary and tertiary gene pool is determined based on cross-compatibility, genetic, phylogenetic and molecular evidence. The cultivated cucumbers are generally monoecious in nature, however, a wide diversity in sex forms is recorded in this species. Gynoecious with only female flower is the most important sex form used commercially in hybrid seed production in cucumber. Significant advancement has been made in understanding the genetics of the flowering traits like sex expression and modification. Studies on inheritance and nature of heritability for important vegetative,

fruit and yield-related traits, biotic and abiotic stresses have been reported widely by different research groups. The understanding in the genetics of the important qualitative and quantitative traits facilitated the genomics study in economically important traits. In spite of being highly cross-pollinated in nature, it has very low or negligible inbreeding depression. Different breeding methods are adopted in cucumber based on its genetic architecture and breeding behaviour. Among the popular breeding methods, population improvement, pedigree method and backcross breeding have been adopted widely in the successful development of elite lines with a wide variety of traits. Because of higher yield and better adaptability and resilience, F_1 hybrids are highly popular in cucumber. The development of gynoecious lines is instrumental in developing F_1 hybrids with higher productivity. Protected cultivation in cucumber is largely facilitated by breeding gynoecious parthenocarpic lines. A large diversity is available within the genus *Cucumis* in different parts of Asia and Africa. There is a need to evaluate the entire gene pool for important biotic and abiotic stresses to meet future challenges. Extensive genetic studies need to be conducted for all the traits related to the yield and adaptability of the cucumber genotypes using the available germplasm available with different gene banks and natural diversity.

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12.1 Introduction

The genus *Cucumis* belongs to the gourd family *Cucurbitaceae* and comprises two economically important cucurbit crops, cucumber and melon, grown worldwide. This gourd family consists of around 130 genera and 1,000 species containing several nutritionally important cucurbitaceous vegetables, like *Citrullus lanatus*, *Citrullus amarus, Momordica charantia, Cucurbita pepo, Lagenaria siceraria, Benincasa hispida, Luffa* and *Trichoanthes* species (Renner and Schaefer 2016; Chomicki et al. 2019). With the annexing of Asian and Australian species, so far approximately 66 species have been documented in the genus *Cucumis* (Sebastian et al. 2010; Chomicki et al. 2019; Cheng et al. 2020). Biologically and economically important species, cucumber (*Cucumis sativus*) (20 = 2x = 14) with genome size 367 Mb, is extensively cultivated worldwide including the Indian sub-continent (Zhu et al. 2016). The geographic origin and region of domestication has always been a fundamental question and matter of debate amongst the conflicts regarding the evolution of crop plants. Recent phylogeographic, phylogenetic, molecular and genomic evidences established the Asiatic origin and domestication of cucumber somewhere in the Indo-Gangetic plains with the coexistence of its feral form, *Cucumis sativus* var. *hardwickii* (Sebastian et al. 2010; Qi et al. 2013; Chomicki et al. 2019). These cultivated and feral species of cucumber represent the primary gene pool, while *Cucumis hystrix* (2n = 2x = 24), the wild close relative of cucumber, is considered in the secondary gene pool (Delannay et al. 2010; Li et al. 2011a). Hence, a narrow genetic base is the most important impediment in the genetic improvement programme of *Cucumis*. Cucumber has been regarded as a model for the understanding of various biological processes and organelle genetics as its three genomes exhibit distinct modes of transmission like paternal mitochondrial transmission, maternal and bi-parental transmission for chloroplast and nuclear genes, respectively (Calderon et al. 2012; Weng 2016). It is the first horticultural crop in which the full draft genome was made publically available (Huang et al. 2009). Relatively smaller diploid genome size, short and annual life cycle, less amount of repetitive DNA percentage and enriched diversity of sex forms offer significant opportunities for classical genetic studies and genome research in this crop.

Cucumber is the fourth most important vegetable crop cultivated worldwide with China being the largest producer followed by India. With the acute pentagonal leaf laminae, the cucumber plants are stiffy hairy with bright yellow flowers borne on leaf axils. Monoecious is the predominant sex form in cucumber, and both pistillate and hermaphrodite flowers have inferior ovary (Paris et al. 2011). The economic part of cucumber, tender immature fruits, usually become ready for harvesting at 5–10 days post anthesis and are consumed as salads, cooked vegetables or in processed form (pickles). Since ancient times, cucumber holds a medicinal status in Indian traditional medicine. The abundant quantity of water content, low calories, presence of triterpenoid cucurbitacins (A, B, C, D, E, I), β-carotene and other phytochemicals impart antioxidant, anticancer, antidiabetic, lipid-lowering and ethnomedicinal properties in cucumber (Mukherjee et al. 2013). The fruits are used as cooling agents and seeds for the treatment of skin-related disorders since antiquity. The genetic and genomic resources in cucumber are limited and the development of high yielding varieties with excellent quality has always been the focus of cucumber breeders worldwide. The presence of parthenocarpy and gynoecious traits in cucumber has tremendous potential for the development of suitable hybrids for low-cost greenhouse cultivation (Wu et al. 2016). Traditionally, simple selection-based breeding methods have been proved instrumental for the genetic improvement

of cucumber. Now, the advent of new technologies accompanied by advance genotyping and phenotyping facilities, next-generation sequencing approaches, genomic selection and other molecular tools has facilitated the genetic and genomic research in cucumber, facilitating the conventional breeding approaches like never before.

12.2 Genetic Resources and Gene Pool

Most of the available sources of evidence indicated India as the primary centre of origin of cucumber and the highest amount of diversity in terms of plant growth, branching, fruit shape, size, colour and texture, maturity duration, bitterness and variation flowering is available in this region (Sebastian et al. 2010). A large diversity in feral form *C. s.* var. *hardwickii* with extreme bitterness, smaller fruit size and multiple lateral branching is also recorded in different parts of India. China and the Near East regions are considered as the secondary centres of diversity for cucumber (Meglic et al. 1996; Staub et al. 1997a). Besides the two cultivated species in *C. sativus* (cucumber) and *C. melo* (melon), several other wild species are present within the genus *Cucumis*. Prominent wild species are *C. hystrix*, *C. callosus*, *C. metuliferus*, *C. muriculatus*, *C. agrestis* and *C. s.* var. *hardwickii*. In the different parts of Africa, Asia and India, more than 50 *Cucumis* species have been identified with very wide diversity for different traits by several workers (Lv et al. 2012; Kacar et al. 2012; Weng 2010; Zhang et al. 2012; Qi et al. 2013). The gene pool concept and classification of different species of *Cucumis* into different gene pools was proposed by Bates et al. (1995), den Nijs and Custers (1990), and Raamsdonk et al. (1989). Generally, it is agreed that the species *C. s.* var. *sativus* and var. *hardwickii* belong to the primary gene pool and *C. hystrix* belongs to the secondary gene pool which is partially cross-compatible with cucumber (Chen and Kirkbride

2000; Chen et al. 2004). The tertiary gene pool consists of distantly related species from other genera or sub-genera (e.g., *Cucumis melo* L. and *Cucurbita* L.), with no cross-compatibility with cultivated cucumber (Chung et al. 2006, Staub et al. 1997a, b). The *C. s.* var. *hardwickii* and *C. hystrix* have been used widely for the introgression of economically important traits from these species. The species from the tertiary gene pool were also used in broadening the genetic base of cucumber using technology like in vitro embryo rescue and somatic hybridization.

12.3 Classical Genetics in Cucumber

During the past 10–15 decades classical genetics has played a central role in enriching our understanding of numerous aspects of biology and expediting crop breeding. The Mendelian principles illuminating heredity were first documented in crop plants and in line with these findings the direct beneficiary was the agriculture sector. The concept of 'gene' was developed in the twentieth century and this acquaintance of gene concept escalated plant breeding for many decades (Vollmann and Buerstmayr 2016). Thereafter, the advent of molecular markers, revamping of molecular genetics and genomics brought significant changes in the theory of gene and consequently accelerated crop breeding. The advancements in genomics have helped in understanding functional, regulatory genetic and epigenetic mechanisms. In addition to genomic selection, the dissection of QTLs controlling complex traits is eye-catching in the Mendelian context as it reveals the loci behaving in Mendelian fashion. Classical genetics have elevated our knowledge of the genetic architecture of plant growth and development in cucumber and stimulated the breeding for qualitative and quantitative traits both in the public and private sectors. Unravelling the genetics of plant architecture traits help breeders to imply appropriate breeding procedures for the genetic improvement

of crop and economically important traits. Cucumber is predominantly monoecious in nature and has become a model for plant growth and physiology, sex expression and organelle genome genetics. The application of Mendelian genetics in cucumber has led to the discovery of a number of genes governing different traits.

12.3.1 Genetics of Flowering and Sex Expression

In the angiosperms, the flowering transition representing a pivotal transition from vegetative to the reproductive stage is probably the most significant transitional development in the life cycle of higher plants. This biological process is governed by both endogenous and exogenous factors (Cho et al. 2017). Determination of sex form in angiosperms is of fundamental biological significance for fertilization, fruit development and seed production. It leads to the formation of unisexual flowers which promotes out-breeding and increase genetic diversity. The majority of the angiosperms are hermaphrodite ($\sim$90%), however, 4–5% of the plant species are monoecious and the rest of the species exhibit dioecy or intermediate sex forms (Charlesworth 2002; Devani et al. 2017). The majority of the species in the *Cucurbitaceae* including cucumber have diverse sex morphotypes (Chen et al. 2016; Pawełkowicz et al. 2019a). A number of intermediate flower types such as gynomonoecious, andromonoecious and trimonoecious have evolved from a common ancestor having hermaphrodite flowers (Pawełkowicz et al. 2019b). Apart from the common monoecious sex form in cucumber, the other types such as gynoecious, androecious, andromonoecious, subgynoecious and trimonoecious have also been reported in naturally distributed genotypes or mutants (Li et al. 2019). Monogenic control is the simplest form of sex type inheritance, while the complex systems are controlled by multiple loci and sex chromosomes. The gene expression studies revealed that in the female flower buds of cucumber the cell division is maintained at a high level in the area containing arrested stamen primordia (ACASP) (Yamasaki et al. 2017). In the petals and stamens of the staminate flower buds, epidermal cell density does not differ significantly, while in the arrested stamens of pistillate flowers buds, epidermal cell density remains quite higher than petals. Thus, despite higher cell division activity, the cell growth is hampered and consequently programmed cell death (PCD) occurs in the cucumber female flower buds (Yamasaki et al. 2017). The genetics of sex expression in cucumber is mainly governed by four loci, *M, F, A, Gy* and their interplays (Robinson et al. 1976; Pan et al. 2018; Li et al. 2019; Pawełkowicz et al. 2019b; Li et al. 2020). Hence, the genetic constitution of different sex types in cucumber is *MMffAA* (monoecious), *MMFFAA* or *MMFFaa* (gynoecious), *MMFfAA* or *MMFfaa* (subgynoecious), *mmffAA* (andromonoecious), *mmFFAA, or mmFFaa* (bisexual or hermaphrodite) and *MMffaa or mmffaa* (androecious). Numerous environmental, epigenetic, other genes or QTLs and hormonal factors affecting sex transition have also been well studied (Li et al. 2019; Pawełkowicz et al. 2019b; Li et al. 2020). The various genes and their encoded proteins with function determining sex expression in cucumber have been comprehensively reviewed by Pawełkowicz et al. (2019b). The molecular characterization of *F* locus determined that an additional copy of ACC (1-aminocyclopropane-1-carboxylic acid) synthase gene '$CsACS_1G$' exists in the gynoecious cucumber lines (Mibus and Tatlioglu 2004; Pawełkowicz et al. 2019b). Likewise, the *M* locus represents *CsACS2* gene (Li et al. 2009). The recessive '*gy*' allelic form is responsible for more stable female sex expression and '*h*' allele (*andromonoecious*-2) controls the bisexual flower development (Pawełkowicz et al. 2019b). '*In-F*' and '*Tr*' are liable for escalating the action of '*F*' gene and trimonoecious sex form, respectively. Ethylene, the gaseous plant hormone, has been credited to control the flower sex in cucumber throughout many decades and has the practical

utility in female flower production in cucurbits (Wang et al. 2010; Pan et al. 2018; Xin et al. 2019). The ethylene biosynthesis involves the conversion of methionine to SAM (S-adenosylmethionine), SAM into *ACC* (1-aminocyclopropane-1-carboxylate) by *ACC* synthase, and eventually, ACC oxidase causes the oxidation of ACC to ethylene (Chen et al. 2016; Pan et al. 2018; Xin et al. 2019). The subgynoecious trait in cucumber which exclusively leads to the formation of female flower sex at later stages is controlled by one pair of recessive '*mod-F2*' gene and one pair of incompletely dominant '*Mod-F1*' gene (Chen et al. 2011). Pati et al. (2015) revealed monogenic dominant control of gynoecious sex expression in the cucumber gynoecious line GBS-1, while a dominant gene was reported to control the parthenocarpy in the cucumber inbred lines PPC-2 and GPC-1 (Jat et al. 2019).

12.3.2 Genetics of Important Vegetative, Fruit and Yield-Related Traits

Improvement of cucumber for economically important traits requires information about genetics and the nature of inheritance of these traits. Understanding the genetic makeup for various vegetative traits enables the plant breeder to develop desirable plant types with optimum growth parameters to maintain the balance of source-sink relationship. The knowledge of the genetics of various fruit quality-related traits such as skin colour, fruit length, fruit diameter, fruit weight, shape index, bitterness, glossiness, warty fruits, green flesh colour, orange/yellow fruit flesh colour and peduncle length is indispensable for improvement programme in cucumber (Yuan et al. 2008; Song et al. 2016a). The traits like fruit weight, fruit length and the number of fruits per plant have a direct correlation with fruit yield in cucumber and the traits like the number of days to anthesis. The first flower node is related to precocity.

12.3.2.1 Vegetative Traits

Multiple lateral branching is one of the most important vegetative traits directly associated with higher yield in cucumber. Increased yield due to multiple lateral branching is mainly because of the increased number of fruits per plant. Number of lateral branches was found to be positively correlated (r = 0.58 to 0.42) with the number of fruit per plant in a processing cucumber population in two locations over two years (Fazio 2001). Similarly, very high and significant positive correlation between MLB and fruit yield was reported by several workers in a diverse population of cucumber (Cramer and Wehner 1998a, b; Cramer and Wehner 1999). Inheritance study of multiple lateral branching concluded that this trait is quantitatively inherited (at least four genes; Wehner 1989) with additive genetic variance and a narrow sense heritability (h^2) of 0.00 to 0.61 in different population. The hair-like structures called trichomes are widely present on different plant organs including vegetative parts such as stems, leaves and tendrils. The occurrence of trichomes acts as the first line of defence in plants against different insect pests, pathogens, transpiration, UV irradiation and adverse temperature (Cui et al. 2016). Numerous spontaneous cucumber glabrous mutants have been reported and well-characterized (Table 12.1). The first such mutant in cucumber was *cucumber glabrous-1* or *mict* (*microtrichome*) (Li et al. 2015). Similarly, several types of compact plant mutants have been illustrated in cucumber providing compact plant architecture. The specific helical coiling organs called tendrils are also an important vegetative trait in vine plants like cucurbits. The knowledge of genetics, cloning and expression pattern of gene network crucial for tendril development is essential to elucidate tendril organogenesis and utilization in cucumber breeding (Chen et al. 2017). In this regard, various tendril-less mutants have been identified in cucumber. The leaf colour mutants mainly resulted from the inactivation of chloroplast genes. Further, leaf variegation is a frequently observed genetic phenomenon in

Table 12.1 Genetics of quantitative and qualitative traits in cucumber

Trait	Inheritance	Remarks	Reference(s)
Fruit traits			
Tuberculate fruit	Single dominant	Confers warty fruits	Walters et al. (2001), Wang et al. (2020)
Fruit epidermal feature, tubercule size	Single recessive	Control the size of fruit tubercules formation	Yang et al. (2019)
Soft spines	Single recessive	Receptor kinase gene regulating multicellular trichomes	Guo et al. (2018)
Number of spines	Single recessive	Recessive to Ns, confers numerous spines	Zhang et al. (2016)
Fruit spine density	Single recessive	Confers high density of fruit spines	Zhang et al. (2016)
Colour of spines	Single dominant	Confers black colour spines	Li et al. (2013)
Immature fruit colour	Single recessive	White skin colour in immature fruits	Liu et al. (2015)
Yellow-green peel mutant	Single recessive	Confers yellow-green immature fruit colour. It is recessive to dark green and epistatic to light green colour	Hao et al. (2018)
Light green peel	Single recessive	Light green skin colour	Zhou et al. (2015)
Fruit size	Quantitative	Round fruit shape	Pan et al. (2017)
Mango fruit mutation	Single recessive	Exhibits extensive morphological differences in leaves, flowers, fruit, and seeds. Multiple effects on flower growth, female and male sterility	Niu et al. (2018)
Carpel number variation	Simply inherited recessive	Three carpels are incompletely dominant to five	Li et al. (2016)
Fruit length	Quantitative	Determines mature fruit length in cucumber	Wei et al. (2016)
Ovary length	Quantitative	*ovl3.1 and ovl3.2* are major effect QTLs; determines ovary length in cucumber	Wei et al. (2016)
Fruit peduncle length	Quantitative, one major additive gene and additive-dominant polygenes	Provided basis for breeding of long fruit peduncle trait	Song et al. (2016)
Vegetative traits			
Trichome	Single recessive	Trichomes on the hypocotyl	Li et al. (2015)
Trichome	Single recessive	Glabrous stem, petioles and leaves whereas the surface of the fruits, sepals, fruit peduncles and sparse and fine hairs on flower pedicels	Yang et al. (2011)
Trichome	Single recessive	Glabrous phenotype on all aerial organs	Pan et al. (2015)
Trichome less mutant	Single recessive	Absence of trichomes on all aerial organs	Zhao et al. (2015)

Table 12.1 (continued)

Trait	Inheritance	Remarks	Reference(s)
Plant architecture	Single recessive	Dwarf plant habit, reduced internode length	Li et al. (2011b), Wang et al. (2017)
Plant architecture	Single recessive	Interact with *bushy* gene to provide dwarf plant habit	Li et al. (2011b)
Tendril less mutant	Single recessive	Absence of tendrils, less trichomes, reduced vine length	Chen et al. (2017)
Tendril less mutant	Single recessive	Spontaneous tendrilless mutant formed branches instead of tendrils	Chen et al. (2017)
Variegated leaf	Single recessive	Confers yellow, white or green sectors in the young leaf throughout the life cycle, contains defective chloroplast	Cao et al. (2018)
Virescent leaf	Single recessive	Displays light yellow cotyledon and true leaf	Miao et al. (2016)
Virescent leaf	Single recessive	Light-sensitive virescent-yellow leaf mutant turns green under low light conditions	Song et al. (2018a)
Curly leaf mutant	Single semi-dominant and single dominant	Upward rolled leaf phenotype, curly petals	Rong et al. (2019)
Round leaf	Single recessive	Determine round leaf shape with smooth margin	Zhang et al. (2018)
Fruit quality and flesh color			
Bitterness	Single recessive	Non-bitter foliage and fruits	Andeweg and DeBruyn (1959), Zhang et al. (2013)
Bitterness	Single dominant	Extremely bitter fruits	Zhang et al. (2013)
Fragrance	Single recessive	Pandan-like fragrance in cucumber	Yundaeng et al. (2015)
β-carotene	Single recessive	Orange colour endocarp	Bo et al. (2012)
Flesh thickness	Quantitative	Control the flesh thickness in cucumber	Xu et al. (2015)
Green flesh colour	Quantitative	Major effect QTL for flesh colour and flesh extract colour	Bo et al. (2019)

tropical and subtropical plants mainly. In cucumber, the EMS-induced variegated leaf mutant reflecting green-yellow-white variegation phenotype has been reported (Cao et al. 2018). Leaf virescent is another mutant that causes light yellow cotyledons or true leaf. In cucumber also different virescent leaf colour mutants are reported, which are mainly under the genetic control of recessive nuclear genes (Table 12.1).

12.3.2.2   Fruit-Related Traits

As compared to other members of *Cucurbitaceae,* the cucumber fruits are recognized by a distinguished 'wart' character having economic importance (Xu et al. 2015). Both warty and non-warty types of peel are present in cucumber, where the warty type is predominant in Chinese cultivated types and the majority of American and European types are having non-warty-type

traits. The warty type of fruit peel trait is dominant to the non-warty type (Table 12.1) (Walters et al. 2001; Wang et al. 2007). The cucumber fruits are characterized by the presence of tubercles, thick cuticles and trichomes (large trichomes are called spines) (Yang et al. 2019). Trichomes are significant and specific traits that emerged from the epidermal cells of almost all the land plants. The soft spine trait in cucumber, governed by '*ts*' gene, could regulate the breeding of cucumber fruits with tender spines (Guo et al. 2018). The inheritance of genes governing different epidermal features and other fruit quality traits in cucumber is presented in Table 12.1. The number of fruit spines is also an important fruit quality trait in cucumber and has been reported to be governed by different genes such as *s, s-2, s-3, ss* and *ns* (Zhang et al. 2016). The black colour spines on the cucumber fruit surface are specialized trichomes and this trait is dominant to white spines (Li et al. 2013; Liu et al. 2019). The *B* locus determining black spine colour has been characterized as an *R2R3-MYB* transcription factor, *CsMYB60,* which regulates the flavonols and proanthocyanidins pigment in black spines (Liu et al. 2019). Likewise, the immature cucumber fruit skin colour is a pivotal agronomic trait influencing consumer choice apart from dull or glossy and mottled or uniform skin. Different skin colours in cucumber like yellow-green, dark green, white and light green are under genetic control (Table 12.1) (Liu et al. 2015). The MutMap and genotyping analysis determined the *CsMYB36* transcription factor conferring yellow-green peel mutant in cucumber (Hao et al. 2018). Cucumber fruit size is a quantitative trait measured by fruit length (L) and diameter (D) or length/diameter (L/D) ratio (Pan et al. 2017). The fruit size variation in cucumber is controlled by several QTLs such as *FS3.2, FS3.3* and *FS2.1, FS2.2* that are involved in fruit elongation and radial growth, respectively (Wang et al. 2014; Pan et al. 2017). To some extent, the ovary shape is also a decisive factor in determining fruit shape (Wei et al. 2016). Fruit shape is a highly heritable character and is largely influenced by cell division and environmental factors. In this context, Zhang et al. (2019)

reported five interacting QTLs (*FS1.1, FS1.2, FS2.1, FS3.1* and *FS6.1*) related to fruit shape in cucumber. Here *FS3.1* is accountable for elongated fruit shape and *FS6.1* for enhancing fruit diameter. Carpel number is another important fruit quality trait in cucumber influencing internal quality, fruit shape and size (Li et al. 2016). The commercially available different cucumber types in markets have generally three carpel numbers; however, the deviation from three numbers is also present which can vary from 2 to 7. The fine genetic mapping revealed that *CsCLV3* is the candidate gene for '*cn*' controlling the carpel number variation in cucumber (Li et al. 2016). The fruit length in cucumber is reported to be controlled by QTLs and is affected by agronomic and environmental conditions (Wei et al. 2016). In a recent study, Wei et al. (2016) reported 8 QTLs for immature and mature cucumber fruit length (Table 12.1). Flesh thickness is also an important trait in cucumber having a central role in yield trait. The flesh thickness in cucumber is a polygenic trait (Xu et al. 2015).

12.3.2.3 Quality, Flesh Colour and Miscellaneous Traits

Cucurbitacins are the important components of cucumber fruit and foliage as they release toxins as defensive agents against insect pests and herbivores (Zhang et al. 2013). Breeders mostly look for fruits with low bitterness which is also caused by cucurbitacins. Numerous genes have been identified and well-characterized for controlling this trait (Table 12.1). Thus bitterness in cucurbits has complex genetics and is also affected by environmental factors. In cucumber, a non-bitter line was identified in an American cultivar Long Green where the non-bitterness is governed by a monogenic recessive gene (Table 12.1) (Andeweg and DeBruyn 1959). Similarly, other genes governing bitterness or non-bitterness in cucumber were identified like *bi-2, bi-3, Bt-1, Bt-2* and their inheritance is in a single-locus fashion. The *bi-1* is epistatically recessive to the *bi-3* allele and cause non-bitter foliage and fruits as well.

β-carotene is one of the most important carotenoids having antioxidant and anticancer

properties. Cucumber itself has less quantity of β-carotene 22–48 lg/100 g FW (Kandlakunta et al. 2008). However, a botanical variety of cucumber, Xishuangbanna gourd (XIS; *Cucumis sativus* L. var *xishuangbannanesis* Qi et Yuan), found in the Xishuangbanna area of China is a good source of β-carotene (Bo et al. 2012). The mature fruits of this gourd have orange colour endocarp/mesocarp with β-carotene content of about 700 µg/100 g FW. It is cross-compatible with cultivated cucumber and could be used for the breeding of cucumber with high β-carotene content. The orange flesh colour is under the genetic control of recessive genes as demonstrated by several broad-based crosses of XIS gourd x commercial hybrids (Navazio and Simon 2001). Cuevas et al. (2010) reported that the quantity of mesocarp β-carotene content is governed by two recessive genes while in the endocarp it is controlled by a single recessive gene.

12.4 Genetics of Biotic and Abiotic Stress Resistance

Cucumber is the most important cucurbit vegetable cultivated worldwide and suffers from several biotic and abiotic stresses. The production and productivity of this crop are reduced significantly because of numerous biotic and abiotic stresses (Table 12.2). Different bacterial, fungal and viral diseases cause huge yield loss in cucumber. Breeding strategies have been focused on host plant resistance against different types of viral, fungal and bacterial pathogens in cucumber. The resistance to diseases is mainly accompanied by *R* genes (Harris et al. 2013). A series of defence signalling cascades are activated by *R* gene-mediated recognition of invasive pathogen effectors, which results in systematic acquired resistance (SAR) in crop plants. The major fungal pathogens affecting cucumber are powdery mildew, downy mildew, *Alternaria* leaf spot, anthracnose, scab, gummy stem blight, damping off and fusarium wilt. The bacterial pathogens affecting cucumber fruit yield and quality includes bacterial wilt, angular leaf spot

and bacterial fruit blotch. Likewise, the viral diseases also cause huge loss in cucumber and include cucumber mosaic virus, squash mosaic virus, Zucchini yellow mosaic virus, cucumber green mottle mosaic virus, cucurbit aphid-borne yellows virus, tomato leaf curl New Delhi begomovirus and tomato yellow leaf curl virus. For disease resistance breeding, the understanding of the genetics of resistance is one of the basic requirements. The unravelling of classical and molecular genetics of disease resistance is the most challenging and practically relevant job in crop plants (Keller et al. 2000; Dong et al. 2019; Chen et al. 2020). Varying results of inheritance of disease resistance for different fungal, bacterial and viral pathogens have been reported in varying sources of cucumber (Table 12.2). Inconsistent reports are available regarding resistance to biotic stresses in cucumber such as dominant, recessive, epistatic and quantitative. Different types of inheritance could be due to the use of different approaches to measure the resistance, source of resistance and environmental conditions. Powdery mildew (PM) and downy mildew (DM) are two major devastating fungal diseases in *Cucumis* species. The linkage analysis has revealed that downy mildew [*Pseudoperonospora cubensis* (Berk. and Curt.) Rostov] and powdery mildew (*Sphaerotheca fuliginea* Poll.) genes are either tightly linked loci or have the same chromosome location in cucumber (Olczak-Woltman et al. 2011). The identification of linked molecular markers has facilitated markers-assisted breeding for resistance to various diseases in cucumber. The resistance to downy mildew is mainly governed by recessive genes; however, in the breeding line GY14A of cucumber, polygenic resistance to downy mildew was reported (Olczak-Woltman et al. 2011). Likewise, recently many reports have reported quantitative resistance to downy mildew in cucumber (Zhang et al. 2013; Wang et al. 2016; Li et al. 2018; Wang et al. 2018b). Similarly, inheritance of resistance to powdery mildew in cucumber has been investigated with inconsistent results. The genetics of resistance to powdery mildew in cucumber is quite complex involving multiple

Table 12.2 Genetics of biotic and abiotic stress resistance in cucumber

Biotic stress	Genetics	Source	Reference (s)
Fusarium Wilt (*Fusarium oxysporum* f. sp. *cucumerinum*) race 1	Single dominant	SMR18	Vakalounakis (1993)
Scab (*Cladosporium cucumerinum*)	Single dominant	SMR18	Vakalounakis (1993)
Fusarium Wilt (*Fusarium oxysporum* f. sp. *cucumerinum*)	Polygenic	Rijiecheng	Dong et al. (2019)
Downy mildew (*Pseudoperonospora cubensis*)	Three recessive genes	Aojihai	Shimizu et al. (1963), Olczak-Woltman et al. (2011)
Downy mildew (*Pseudoperonospora cubensis*)	Single recessive	Poinsett	Fanourakis and Simon (1987), Olczak-Woltman et al. (2011)
Downy mildew (*Pseudoperonospora cubensis*)	Quantitative	K8	Zhang et al. (2013)
Downy mildew (*Pseudoperonospora cubensis*)	Quantitative	PI 197088	Li et al. (2018)
Downy mildew (*Pseudoperonospora cubensis*)	Quantitative	W17120	Wang et al. (2016)
Powdery mildew (*Erysiphe cichoracearum* and *Sphaerotheca fuliginea*)	Two recessive genes	Natsufushinari	De Ruiter et al. (2008), Chen et al. (2020)
Powdery mildew	Single recessive	PI 200815, PI 200818	De Ruiter et al. (2008), Chen et al. (2020)
Powdery mildew	Single recessive	Wisconsin SMR 18	De Ruiter (2008), Chen et al. (2020)
Powdery mildew	Quantitative	PI 197088	Wang et al. (2018b)
Powdery mildew	Quantitative recessive	WI 2757	He et al. (2013)
Powdery mildew	Quantitative recessive	NCG122	Liu et al. (2017b)
Gummy stem blight (*Didymella bryoniae*)	Quantitative and mainly governed by three pairs of additive epistatic major genes	PI 183967	Zhang et al. (2017)
Cucumber vein yellowing virus	Monogenic, incompletely dominant	CE0749	Pujol et al. (2019)
Scab (*Cladosporium cucumerinum*)	Single dominant	9110Gt	Zhang et al. (2010)
Target leaf spot (*Corynespora cassiicola*)	Single recessive	D31	Wen et al. (2015)
Cucumber mosaic virus	Quantitative	02245	Shi et al. (2018)

(continued)

Table 12.2 (continued)

Biotic stress	Genetics	Source	Reference (s)
Angular leaf spot (*Pseudomonas syringae* pv. *lachrymans*)	Polygenic recessive	Gy14	Slomnicka et al. (2018)
Low temperature totlrance	Quantitative	CG104 tolerance inbred line	Dong et al. (2019)
Waterlogging tolerance	Quantitative	PW0832	Yeboah et al. (2008)
Salt tolerance	Quantitative	CG104	Liu et al. (2021)
High temperature tolerance	Quantitative	02245	Dong et al (2020)
Low temperature germination ability	Quantitative	Coolgreen	Yagcioglu et al. (2019)
Low temperature tolerance	Quantitative	65G	Song et al. (2018b)

genes and metabolic pathways (Chen et al. 2020). The classical genetics revealed multiple recessive genes for powdery mildew resistance in Puerto Rico 37, while 1–2 major and 1–2 minor genes in PI 197,087 (Barnes and Epps 1956; Chen et al. 2020). In the line PI 2,008,151 the resistance to PM was controlled by one recessive gene, while in Natsufushinari two recessive genes were reported. Then, a major recessive gene (*s*), one major dominant gene (*R*) and a dominant suppressor gene (*I*) were reported to control the resistance to PM in two varieties P1212233 and P123514 (Shanmugasundaram et al. 1971, 1972). Further, numerous genetic loci carrying resistance to powdery mildew were identified in cucumber (Table 12.2). Scab (*Cladosporium cucumerinum*) is another most prevalent disease of cucumber throughout the world. The monogenic dominant resistance to scab has been reported in cucumber (Zhang et al. 2010). Target leaf spot (TLS) (*Corynespora cassiicola*) caused by a phytopathogenic fungus having a wide host range of > 530 plant species severely affects cucumber (Wen et al. 2015). The nature of genetics of resistance to TLS in cucumber is complex and quantitative, dominant, recessive inheritance has been reported. In a study, the single dominant gene 'Cca' was reported to control the resistance in Royal Sluis 72502 cucumber (Abul-Hayja et al. 1978). Gummy stem blight (GSB) (*Didymella bryoniae*)

is another major disease of cucurbits causing significant yield loss of up to 80% (Zhang et al. 2017). The genetics of resistance to GSB is complex and is polygenic in nature. The bacterial pathogen (*Pseudomonas syringae* pv. *lachrymans*) causes angular leaf spot (ALS) in cucumber and the polygenic inheritance of resistance has been reported in cucumber (Olczak-Woltman et al. 2009). Recently, Slomnicka et al. (2018) reported recessive *psl* locus governing resistance to ALS including QTLs.

An ipomovirus, cucumber vein yellowing virus (CVYV) transmitted by whitefly was first reported in the Mediterranean basin (Pujol et al. 2019). Its effective control relies on breeding disease resistance cucumber cultivars, for which the knowledge of genetics and availability of molecular markers is crucial. Recently, the monogenic and incompletely dominant mode of inheritance of resistance to CVYV was reported in cucumber (Pujol et al. 2019). CMV (cucumber mosaic virus) having a wide host range was first reported in cucumber in 1934 (Shi et al. 2018). The varying reports of the genetics of resistance to CMV such as dominant, recessive, polygenic and monogenic are available (Shi et al. 2018). Wasuwat and Walkers (1961) reported monogenic dominant resistance to CMV in Wisconsin SMR 12, while in another study the resistance was under the control of three independent dominant genes (Kooistra 1969). Resistance to

cucumber mosaic virus (CMV) in *C. sativus* var. *hardwickii* is reported by Munshi et al. (2008) and they have reported single recessive gene controlling resistance.

Environmental stresses like drought, heat and salinity are major abiotic stresses affecting crop yield and quality of most horticultural crops. The promising results for combating abiotic stresses based on conventional breeding approaches have not been met due to their complex quantitative nature. The understanding of complex quantitative genetics and identification of genes/QTLs are prerequisites to curb the adverse effects of abiotic constraints on crop plants. Among the various stresses, salinity stress has several adverse effects on horticultural crops including cucurbits (Sharma et al. 2016; Elsheery et al. 2020). The production of cucumber is significantly reduced by salinity. In a study, the role of epistatic and additive gene effects was demonstrated for salinity tolerance in cucumber salt-tolerant line 11411S (Kere et al. 2013). Drought is another major abiotic stress affecting cucumber, and tolerance to drought is a complex quantitative trait regulated by different mechanisms (Wang et al. 2018a). In the heavy rainfall area, cucumber production is constrained by waterlogging. The genetics of waterlogging tolerance is dependent on various morphological and physiological traits which are quantitative in nature (Yeboah et al. 2008; Xu et al. 2017). The waterlogging tolerance in cucumber line PW0832 is having a moderately high narrow-sense heritability, enabling the use of PW0832 for breeding tolerant cultivars in cucumber (Yeboah et al. 2008).

Heat stress, another major abiotic stress in cucumber, leads to drastic yield loss by disrupting the expression of proteins mainly associated with photosynthesis (Xu et al. 2018). Hence, the heat-tolerant genotypes have high photosynthetic activity relative to heat-sensitive genotypes when exposed to high-temperature stress. The cucumber is a thermophilic cucurbit with an optimum temperature of 25–30 °C for growth and development and temperature above 35 °C leads to heat stress in cucumber with wilting of stem and leaves in a short time span at 50 °C (Yu et al. 2018). Calmodulin has been reported to play a role in heat stress in crop plants. In this context, Yu et al. (2018) reported that overexpression of *CsCaM3,* isolated from inbred line '02–8', resulted in high-temperature stress tolerance in cucumber. Recently, Wang et al. (2019) reported that heat stress resistance in cucumber inbred line 'L-9' is under the genetic control of a single recessive gene. Different stress-responsive gene families such as heat shock proteins and tonoplast sugar transporters (TST) playing a role in plant growth and development have been identified. The identification and characterization of genes, QTLs, involved in resistance to different abiotic stresses could promulgate the development of abiotic stress-tolerant cultivars in cucumber.

12.5   Traditional Breeding

Crop domestication and human civilization are co-evolutionary processes connected with plant breeding. The crop breeding approaches have tremendous potential and have been used successfully in agriculture for the past five to ten decades to enhance the yield and genetic gain of crop plants. Plant breeding can be demonstrated as a consequent accumulation of favourable alleles in the elite genotypes and resulting new phenotypes. The rediscovery of Mendel's laws urged the use of genetic principles in plant breeding. As most of the commercial traits are under the genetic control of polygenic loci, quantitative genetics became an integral part of plant breeding. Plant breeding involves the creation, selection and fixation of superior phenotypes for the generation of superior crop genotypes. The selection of desirable types among the different variants is the core of plant breeding. In the crop plants including cucurbits, the course of domestication led to the deliberate selection of high yield-related traits, robust plant architecture and ease of harvesting. The domestication of cucumber from its feral form *Cucumis sativus* var. *hardwickii* was accomplished about 3000 years ago (Qi et al. 2013). There are six major groups of cucumber based upon fruit

character variation and geographic origin. The small size fruits having numerous small spines are French cornichons and are mainly used for pickling. The European greenhouse types are having long and smooth fruits suitable for salad purpose. Other types having short fruits, protruding warts and large spines are American pickling cucumbers. While fruits having medium to long sizes with thick skin, protruding warts bearing large spines are American slicing cucumbers. The other types are medium-short Middle Eastern cucumbers having tiny spines and are wartless, thus used for pickling and slicing as well. In contrast, the Far Eastern cucumbers are quite long in size bearing protruding warts and spines. Generally, the short-fruited types are used for pickling purpose, while long-fruited types are consumed as fresh and cooking, or in Orient. In addition, another two groups have been reported, one from South-western China and another from Nepal and high elevations of the Indian region. The genetic improvement of cucumber is a complex process that entails the crossing of elite germplasms followed by refinement of populations and isolation of desirable inbred lines for commercial hybrid development.

12.5.1   Breeding Behaviour, Objectives and Breeding Methods

12.5.1.1   Breeding Behaviour

It is imperative to understand the typical breeding behaviour of the cucumber before undertaking any breeding programme as this crop is different from most of the typical cross-pollinated crops. Cucumber is entomophilous in nature and the bee-like *Apis florea*, *Apis dorsata* and *Apis mellifera*, *Nomioides* sp., *Helictine* sp. are the major pollinating agents. Few beetles like *Conpophilus* sp. and moths like *Planidia* sp. *Pygargonia* sp. are reported to be acting as a pollinator in certain areas. However, the different species of honeybees are the main agents to effect pollination in most of the cucumber-growing areas. The cucurbits group of vegetables is significantly different from other classical cross-pollinated vegetable crops like cabbage, onion, carrot etc. in terms of their breeding behaviour and system. Although it is out-crossing in nature, however, the extent of the inbreeding depression is significantly low. Therefore, it is possible to practice single plant selection even from F_2 population to derive superior genotypes. In heterozygous crops like cucumber with low or insignificant inbreeding, depression is explained by a homozygous balance in the crops. This is mainly because of higher planting distance and growing of small population over time. All the genes showing deleterious effects under homozygous condition are eliminated in the process of evolution. Therefore, selfing in these crops is not affected through inbreeding depression. Therefore, different modified breeding methods of both self-pollinated and cross-pollinated crops are practised in cucumber based on the breeding objectives.

12.5.1.2   Breeding Objectives

The development of high-yielding cultivars with good fruit quality is the primary objective of cucumber breeders. Breeding cultivars with earliness character and high female to male flower ratio is another important aim of cucumber breeders. The uniform maturity, long-lasting ability, desirable fruit shape as influenced by market and consumers are also a major focus of the cucumber breeding programme. The major breeding objectives practised worldwide may be summarized as follows:

   i. Lowest node number at which first pistillate flower appear which gives an indication of early maturity.

  ii. High female to male flower ratio.

 iii. Attractive light green/green fruits with smooth fruit surface without prominent spines and prickles, crispy with tender flesh.

 iv. Uniformly long cylindrical fruits without a neck.

  v. Fruits free from carpel separation showing hollow spots.

 vi. Non-bitter fruits.

vii. Minimum number of seeds at marketable maturity.

viii. Resistance to important diseases and pests like downy mildew, powdery mildew, leaf spot, Fusarium wilt, leaf curl and mosaic viruses, fruit fly, aphid and mites.

ix. Capacity for high mineral utilization by the plants to produce higher yields.

x. Bunching fruit habit producing multiple pistillate flowers on individual nodes for harvesting finger size fruits to suit whole fruit canning for export especially in the case of gherkin.

xi. Gynoecious, parthenocarpic with multiple pistillate behaviours for protected condition.

The genetic improvement for different quantitative and qualitative traits ranging from plant architecture, fruit quality, flesh colour, prolonged shelf life, β-carotene and processing quality to biotic stress resistance is another important focus of cucumber breeders. The use of biotic stress-resistant hybrids/varieties is the most cost-effective, simple and eco-friendly means of combating various crop plant diseases. Hence, in the early genetic improvement programmes of cucumber, disease resistance breeding has been the major objective of breeders. Determining sex expression and development of stable gynoecious/parthenocarpic lines in cucumber for greenhouse cultivation is important for higher yield potential. Nowadays, in the era of climate change, abiotic stress resistance is also one of the components of cucumber genetic improvement programmes. Despite being cross-pollinated crop, self-compatibility is predominant in cucumber due to more homozygote balance and thus, it does not reflect significant inbreeding depression.

12.5.1.3 Breeding Methods

Owing to insignificant inbreeding depression in cucumber, the individual plant selection is successfully practised. The major breeding approaches in cucumber include mainly the introduction, pureline selection, mass selection, recurrent selection, pedigree method followed by hybridization, single seed descent method,

backcrossing and heterosis breeding (Sitterly 1972; Wehner 1988; Zijlstra et al. 1995; Delannay et al. 2010; Jat et al. 2019). Breeding methods are determined by the objective for improvement and traits under consideration. Breeding objectives are mainly driven by the market demand and the methods are dependent on the targeted product to be developed. Most of the breeding methods have a few sequential steps like population development and improvement, development of desirable lines, identification of parental combination for hybrid development, identification for parents for stress tolerance and evaluation under multiple locations to realize the actual potential of a developed genotype. Different methods for improvement are generally adopted in parallel to achieve the breeding objectives. Population improvement is practised to develop the base population with desirable traits like earliness, higher yield, fruit quality as one component. At the same time, the pedigree method followed by hybridization is also adopted if we want to combine some of the desirable traits for two different parents into a single genotype. Another component of the same breeding programme could be back-crossing for introgression of a particular trait like disease resistance to any other major gene for its introgression in widely cultivated variety/parent of hybrid deficient for that trait (Staub and Grumet 1993). With the advent of molecular markers and next-generation sequencing technology, the functional genomics has become an integrated component to accelerate the efficiency of the classical improvement programme. The major breeding methods adopted for the improvement of different traits of cucumber are as follows.

i. Recurrent selection: This is the most popular breeding method for the improvement of quantitative traits in different cross-pollinated crops. Because of the large plant size and nature of our crossing, this method is not used frequently in cucumber improvement. Under the condition of the limited number of researchers involved and resources, this method may not be the most suitable as it requires handling a large number of population over a period of time. However, this is the most effective method to

improve complex traits like fruit yield. This method requires initial genetic resources with large diversity for traits like fruit size, fresh colour, biotic stress resistance for substantial gain through this method (Wehner and Cramer 1996). The typical selection cycle for recurrent selection (mass, full and half-sibs) in cucumber is 2–3 years because of its plant size and generation cycle (Wehner 1989).

A population with a broad genetic base can be developed by inter-crossing 2–4 elite and distantly related hybrids. Manual inter-crossing among at least 20 elites, diverse genotypes with 2–3 generations followed by pollination with insects for 2 or more generations allying selection pressure thereafter is very effective in creating wide-based population. Simple recurrent selection is recommended for a set of highly heritable traits. Reciprocal recurrent selection (RRS) can be practised to develop two populations with less heritable traits like yield-associated components (Cramer and Wehner 1998a, Cramer and Wehner 1999). RRS is effective in developing two different populations for their use in hybrid development although this method is cost and labour-extensive. Identification of a method for large-scale evaluation is the prerequisite for population improvement (Wehner 1989). In the typical cross-pollinated-based breeding models, recurrent selection methods with at least 200 individuals (or progenies of individuals) per population are evaluated and the selected 20 are inter-crossed to create the next cycle of selection. Once a unique population is developed, the elite population can then be released as commercial cultivars or lines are developed for their use in hybrid evaluation and production (Wehner 1998a, 1998b).

ii. Line development:

a. *Pedigree selection:* This is more common and widely used in the development of improved lines for commercial cultivation as a variety, or development of parents for hybrid development in cucumber. Two widely adopted genotypes which are complementary to each other in terms of traits were used for crossing in developing F_1 and F_2 progenies. One parent may have traits yield, early maturity and good fruit quality while other parents could have acceptable yield, earliness, disease resistance and devoid of fruit quality. F_2 progenies are developed by selfing or sibbing of the F_1 plant(s) and selected F_2 plants are used in developing F_2 progenies. From the F_3 families, in general, the best plant is selected for further progeny advancement. Family row selection is practiced for quantitative traits in F_4 and the number of plants per family is selected for developing the next generation. The F_6 families are generally uniform and behave like inbred without much segregation within the family. The selection typically involves the use of eight-plant plots for traits such as early flowering, number of pistillate flowers, and fruit number and quality. In terms of number of plant families selected are 54 F_2 plants, 36 F_3 plants, 24 F_4 families and 18 F_5 lines. Improvement of traits of low heritability in cucumber (e.g., yield and quality components) that are associated with QTLs having complicated negative associations and epistatic effects may benefit from the application of phenotypic and marker-assisted selection strategies (Behera et al. 2010).

b. *Single-seed descent*: This is a modified form of the pedigree method used in the rapid development of inbreds taking the advantage of greenhouse and off-season nursery without selection till the advanced generation (F_6 onwards). This method is more effective for the improvement of quantitative traits like yield, earliness and may not be the best method for the improvement of traits like disease resistance. However, the selection for several quantitative traits can be performed through the removal of plants/families with undesirable traits. This method can be practised only when there is a facility for rapid generation advancement.

c. *Backcrossing*: This method is used for the transfer of one or more traits controlled by major genes with qualitative inheritance (resistance to downy mildew, determinate growth habit, nematode resistance) into an inbred which is superior for yield and quality

but lacks one or more major trait. Generally, six generations of backcrossing are needed for the introgression of a major gene with a nuclear genome of the recurrent parent. However, the approach differs based on whether the trait is controlled dominant or recessive gene.

For the transfer of a trait controlled by a recessive gene, the recurrent parent is crossed with the donor parent, and the F_1 is backcrossed to the recurrent parent. In one scheme, the F_1 is self-pollinated to produce the F_2, which segregates for the trait of interest. Individuals from the F_2 that possess the trait are backcrossed to the recurrent parent to produce the BC_1. The BC_1 generation is then self-pollinated to produce the BC_1F_1, which is evaluated for the trait. Individuals possessing the trait of interest are selected and backcrossed to the recurrent parent. This process is repeated until the BC_6 generation where the best individuals are self-pollinated and selected for the trait to produce the improved inbred. For the transfer of a trait controlled by a dominant gene, the recurrent parent is crossed with the donor parent, and the F1 is subsequently backcrossed to the recurrent parent. The BC_1 generation is then evaluated, and individuals possessing the trait are backcrossed to the recurrent parent. This process is repeated until the BC6 generation where the best individuals are self-pollinated and selected for homozygous expression of the trait using progeny testing.

Backcross breeding has played a significant role in cucumber genetic improvement. During 1995, the inter-specific cross between primary gene pool and secondary gene pool species, *Cucumis sativus* and *Cucumis hystrix,* respectively was attempted (Chen et al. 1997). The progeny of this cross was male and female sterile, thus subsequent chromosome doubling resulted in fertile amphidiploids species. The self-pollination for subsequent generations led to the development of new species *Cucumis hystivus* ($2n = 4x = 38$). It has practical implications in the incorporation of gummy stem blight resistance in commercial cultivars as *Cucumis hystrix* is a carrier of resistant genes to this

particular disease. The marker-assisted backcross breeding and selection in inter-specific derived population may be useful for enhancing the cucumber genetic diversity. In this context, Behera et al. (2011) reported introgression backcrossing employing *C. hystivus* for increasing genetic variability in cucumber. Breeding for major diseases and the development of resistant cultivars has been successfully achieved in cucumber. Numerous wild species of *Cucumis* such as *Cucumis africanus*, *Cucumis anguria*, *Cucumis ficifolius* and *Cucumis myriocarpus* can be used in backcross breeding programmes as they are the carrier of disease-resistant genes.

The first breeding effort for downy mildew resistance in cucumber started in the USA during the twentieth century in 1939, when Chinese Long and Puerto Rico No. 37, the moderately resistant cultivars were crossed with the commercial cultivars (Barnes 1961; Holdsworth et al. 2014). Subsequently, many resistant cultivars were released by the public sector such as 'Marketmore', Marketmore 97, Platinum, 'Salt and Pepper' and 'Poinsett' series in the pedigrees of numerous fresh market cultivars. The monogenic or oligogenic resistance derived from 'Chinese Long' or PI 197087 was contained in most of the released cultivars. Recently, Holdsworth et al. (2014) by employing the pedigree method of selection followed by hybridization developed the downy mildew resistant line 'DMR-NY264'. 'Kaohsuing No 3', a heat and moisture tolerant cucumber cultivar, was developed in Taiwan by adopting the Pedigree method of selection following the bulk population method and then subsequently five generations of selfing (Liu et al. 2017a). The saturated and high-density genetic linkage map has been developed in cucumber (Behera et al. 2011; Zhu et al. 2016). The selection efficiency during population improvement can be enhanced through marker-assisted selection (MAS). Japanese Long Green, Straight 8 and Poinsett are important introductions of cucumber in India.

iii. Heterosis breeding: When a good number of improved lines are available with a breeder, heterosis breeding by making all possible combinations is the next logical step to exploit

heterosis for yield and other related traits. If the number of lines is very large, it may not be possible to make evaluate all possible combinations as the number of combinations even for 30 parents will be [30 x (30–1)]/2 = 435 without including the reciprocals. Therefore, it may not be possible to make all possible combinations and we have to select the parents based on their traits and they should be complementary to each other. In cucumber, a large number of publicly developed inbreds/open-pollinated lines have been recommended for commercial cultivation and they are improved with several desirable traits. However, the F_1 hybrids provide an avenue for proprietary protection of commercial inbred lines, and private sector stakeholders are mainly involved in the development of hybrids mainly because of the scope for propriety protection.

The phenomenal success in heterosis breeding in cucumber is mainly due to manipulation of sex expression to the desired direction. Most of the F_1 hybrids are gynoecious x gynoecious or gynoecious x monoecious, though monoecious x monoecious hybrids are also available in some particular segments. The genetic control of sex mechanism in cucumber, especially of the gynoecious sex form, has made it possible to exploit heterosis in cucumber. Gynoecy condition where all the flowering nodes in the main, secondary and tertiary branches bear pistillate flowers in the leaf axils is important for sex form, which has made phenomenal exploitation of hybrid vigour possible in cucumber. Hybrids in cucumber are important not only for yield and earliness but also for external attributes of uniformity of size and shape, especially in slicing cucumber. Most of the F_1 hybrids have attractive colour, flesh texture and other quality traits and multiple resistances to diseases due to the fact that dominant genes control resistance to some important diseases. Different methods can be adopted for the production of hybrid seed of a cucumber. Since flowers of cucumber are very small and a large amount of seed can be obtained from a single cross bagging of female flowers of monoecious line, hand pollination can be effectively practised for seed production.

The commercial production of gynoecious cucumber seed was made possible only when it was discovered that gynoecious inbreds could self-reproduce if a growth regulator is applied to induce male flower formation (Robinson 1999). Peterson and Anhder (1960) for the first time discovered the effect of gibberellic acid (1500–2000 ppm) on the promotion of male flower formation in cucumber. However, due to erratic male flower induction by the use of gibberellic acid, application of silver compound such as silver nitrate (250–400 ppm) is done to induce male flowers. Silver ions inhibit ethylene action and thus promote male flower formation in gynoecious cucumber plants. However, due to phytotoxic effects such as burning of plants, silver thiosulphate (400 ppm) is now widely used by seed producers for the maintenance of gynoecious cucumber lines. It induces male flowering of cucumber plants over a longer period and is less phytotoxic compared to silver nitrate. When the temperature exceeds beyond 30 °C the stability of gynoecious sex expression is affected. Unfortunately, the temperate gynoecious lines are unstable for gynoecy under high temperature and long photoperiodic conditions because of their thermospecific response for gynoecious stability. That is why the gynoecy in cucumber did not receive much attention in tropical countries.

Efforts have been directed during the recent past towards developing gynoecious sex forms under our tropical and indigenously adapted background and two lines, DC-102 and DC-103 with stable gynoecious sex even at temperatures around 40 °C have been developed at IARI. These are being tested further to exploit in heterosis breeding programme at Division of Vegetable Science, ICAR-Indian Agricultural Research Institute, New Delhi. Hybrids of cucumber are produced mainly by crossing gynoecious lines with monoecious lines. Though other systems of producing gynoecious hybrid seeds such as gynoecious x gynoecious have been proposed, gynoecious x monoecious hybrids are still the most widely grown (Robinson 1999). Most of the commercial hybrids based on gynoecious cucumber lines are a blend of

gynoecious hybrid and monoecious seed. In addition, homozygous gynoecious hybrid seed has been produced by crossing two gynoecious lines after one has been treated with a growth regulator to induce male flowers (Robinson 1999). The gynoecious cultivars or hybrids should be protected from pollination, because due to fertilization, their fruits may become misshapen. Exogenous application growth regulators, viz., MH (100–200 ppm) or Ethrel (150–200 ppm) for temporary suppression of male flower in the female line of monoecious plants has also been commercially adopted for producing F_1 hybrids. The North Indian conditions permit a very short growing period for cucumbers and maximum yield realization could not be obtained under open fields. So protected cultivation technology with proper training, pruning and nutritional support can be exploited for off-season breeding of cucumber. Greenhouse production technology has shown a four-fold realization of yield in commercial hybrid Pusa Sanyog during the off-season as compared with cultivation under open conditions.

In India, the first report of heterosis breeding in cucumber was demonstrated during 1970s with the release of the first gynoecious x monoecious hybrid 'Pusa Sanyog' by IARI, Regional Station, Katrain, Kullu Valley, Himachal Pradesh. Then a monoecious x monoecious hybrid, Pant Sankar Kheera 1 was released by GBPUAT, Pantnagar. Recently, one gynoecious x monoecious F1 hybrid, Pusa Cucumber Hybrid-18 has been developed by the Division of Vegetable Science, ICAR-Indian Agricultural Research Institute, New Delhi. Sex expression has played a significant role in heterosis breeding in cucumber. The development of gynoecious hybrid cultivars in cucumber is achieved by crossing gynoecious and monoecious parents. The growing of gynoecious and parthenocarpic hybrids under protected cultivation has enhanced the productivity manyfold. Generally, the blending of gynoecious and monoecious types (10%) is maintained in many commercial seedlots of cucumber for making sufficient pollen available in the pollination of complete gynoecious x gynoecious hybrids.

12.5.2 Breeding for Protected Cultivation

Cucumber is one of the leading vegetable crops grown under protected cultivation worldwide. Development and availability of a particular plant type are required for its successful cultivation under protected condition. Generally, indeterminate plant type with the constant internode length throughout the length of the vine is suitable under such condition. The growth habit is important in breeding programmes as it increases yield and availability period to a greater extent. Ideotype breeding along with the incorporation of useful genes for the parthenocarpic character can be utilized on a large scale in poly-houses. Parthenocarpic, gynoecious cucumber genotypes are suitable for protected cultivation as these varieties develop fruits automatically without any pollination. Breeding effort should be concentrated on important fruit characteristics such as shape, colour, spine type (coarse or fine), spine colour (white or black), skin thickness and surface warts, high TSS, crispness, enhanced shelf life, resistance to biotic and abiotic stress, highly responsive to fertilizer, photo and thermo insensitiveness. The emphasis, however, is to develop parthenocarpic, gynoecious F_1 hybrids with wider adaptability. The development of suitable ideotype, novel genes for biotic and abiotic stress resistance is the need of the hour for breeding cucumber varieties/F_1 hybrids suitable for protected cultivation. The increased farm income under protected cultivation has made the cultivation of cucumber more popular worldwide. Further, plant breeding efforts have permitted to solve specific problems of varieties suitable for protected cultivation as well as general problems which also benefit the open field cultivation. Ideotype breeding along with the incorporation of useful genes in crops like parthenocarpic can be utilized on a large scale in poly-houses. Gene 'pc' responsible for parthenocarpy, 'F' responsible for short inter-nodal length can be utilized through pure line and backcross breeding methods to establish them in plant population in parthenocarpic cucumber.

Breeding parthenocarpic cucumber hybrids for field production is more difficult than for greenhouse production. For the greenhouse hybrids, fruit set at the first five lower nodes is not important since fruit that is set at the lower nodes are removed. For outdoor production, it is essential that fruit set starts as early as possible at the lower nodes. Thus, for the development of outdoor parthenocarpic cucumber hybrids, it is necessary to utilize the parental lines with a high percentage of parthenocarpy and less dependent on the environment.

Keeping in view the above facts, the concept of poly-house vegetable breeding programme was developed at Pantnagar during 2002 in cucumber and tomato. Some of the good genotypes were isolated and pure line and hybrid breeding programmes were adopted for improvement of these genotypes. After three years of multi-location testing at tarai, midhills and higher hills under poly-house condition, two genotypes of parthenocarpic cucumber, namely Pant Parthenocarpic Cucumber-2 and Pant Pant Parthenocarpic Cucumber-3, were identified and released by Uttarkhand State Variety Release Committee during May 2011 for commercial cultivation at farmers' poly-house. The programme on the development of parthenocarpic gynoecious varieties for protected cultivation was undertaken during 2010 at the Division of Vegetable Science ICAR-IARI, New Delhi. In the winter of 2014–15, 17 breeding lines which were advanced to F_8 and showing true gynoecious and parthenocarpic behaviour were evaluated under low-cost poly-house. The line DPaC-6 was observed as most promising as it expressed 25.0% and 16.7% higher yield than check Pant Parthenocarpic Cucumber-2 and Asma, respectively. Though its yield (122.5 t/ha) was less than the best check F_1 hybrid Kion (127.0 t/ha) it was statistically at par. The yield obtained by DPaC–6 (122.5 t/ha) can be considered quite high since it was obtained during the off-season (winter season) under low-cost poly-house without using any energy. On the basis of its consistent superior performance, DpaC-6 was identified by IARI Variety Identification Committee in 2016. The inheritance studies of fruit skin colour and parthenocarpy were also conducted by crossing DPaC-6 and monoecious cucumber variety PusaUday. The F_1 progeny showed intermediate colour between dark green DPaC-6 and light green Pusa Uday. The F_1 progeny showed true gynoecious parthenocarpic behaviour as its fruits were seedless and developed without pollination which suggested that the gynoecious parthenocarpic trait is governed by a single dominant gene. The F_1 progenies were advanced to F_2 and also simultaneously backcrossed with parthenocarpic line DPaC-6 to confirm the monogenic dominant nature of parthenocarpy.

12.6   Conclusion

Tremendous progress has been made in unravelling genetic architecture and basic understanding of cucumber genetic improvement through classical genetics and traditional breeding in the past many decades. Classical genetics has helped in understanding the heritability of different quantitative and qualitative traits in cucumber. Much progress has been made in elucidating the genetics of disease resistance, taxonomy and phylogenetic relationships. Numerous genes controlling various monogenic, oligogenic and polygenic traits have been identified, and subsequently, the breeding programmes for the genetic improvement of cucumber have been initiated. Based on the traditional breeding for the past ten decades, different commercial hybrids/cultivars have been released in cucumber. However, the improvement in quantitative traits is limited by traditional breeding; hence in this context, the advent of molecular breeding and genomics have played a significant role in cucumber. The integration of traditional breeding programmes with advanced molecular tools will certainly accelerate the cucumber genetic improvement in the era of climate change.

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