1 Importance, Distribution, Botany and Genetics

Sudhakar Pandey and Shubhra Natasha Kujur

Abstract

Cucumber (*Cucumis sativus* L.) is one of the important vegetable crop indigenous to India grown for its immature fruits eaten raw as salad and also can be cooked as vegetable or processed. Demand of fresh market cucumber is very high due to consumption preference as compared to pickling cucumber. Monoecious or gynoecious are dominant sex forms in cucumber, whereas androecious, andromonoecious hermaphroditic and tri-monoecious forms are also found. Five of the cucumber's seven chromosomes arose from fusions of ten ancestral chromosomes after divergence from *Cucumis melo*. The morphological diversity is mainly exhibits in fruit colour, sex type and plant growth habit. Several new genes (73) has been listed in new gene list includes major-effect QTLs bringing total number of genes to 199. Knowing the gene action of qualitative and quantitative traits governed by QTLs and single gene is very important for the improvement of the cucumber. The present article attempts to provide comprehensive information on significance, origin, botany and genetics of cucumber for further research.

1.1 Introduction

Cucumber belongs to family Cucurbitaceae family having 825 species of 118 genera. In total production of vegetable in India, cucurbits contribute about 5.6% and cultivated in 76.6 thousand hectare area and production is about 9516 thousand tons (FAO 2018). Worldwide area under cucumber and Gherkins is 198000 ha with an annual production of 75,219,000 tons (FAO 2018). In India, total cultivated area under cucumber and Gherkins is 31 thousand hectare with an annual production of 195 thousand tons (FAO 2018). Among the cucurbits, cucumber (*Cucumis sativus* L.) is precious vegetable crop grown for its immature fruits. It is commonly grown under open field as well as protected conditions and now available round the year for fresh consumption as well as export. After watermelon, cucumber is cultivated more widely than any other cucurbit crops. Usually, cucumber are eaten raw as salad, but it can also be eaten cooked as vegetable. Pickling cucumber is used as pickled. Cucumber is also beneficial in preventing constipation, jaundice and indigestion. Cucumber is a good source of valuable nutrients, i.e. vitamin C (2 mg/100 g), iron (1.5 mg/100 g) and also contains 0.4% protien and 2.5% carbohydrate.

S. Pandey (✉) · S. N. Kujur
ICAR-Indian Institute of Vegetable Research,
Varanasi 221305, India
e-mail: sudhakar.pandey@icar.gov.in

S. Pandey et al. (eds.), *The Cucumber Genome*, Compendium of Plant Genomes,
https://doi.org/10.1007/978-3-030-88647-9_1

1.2 Uses

Cucumber is highly useful in both high and low blood pressure alleviation because of its high content of potassium (50–80 mg/100 g) (Kashif et al. 2008). This fruit is rich in polyphenolics and cucurbitacins, which have multiple medicinal properties such as anti-carcinogenic, antioxidant, anti-elastase, anti-hyaluronidase, anti-inflammatory, diuretic, anti-hyperglycemic, amylolytic, antimicrobial and analgesic effects (Uthapala et al. 2020). Besides, cucumber is extensively used in the beauty products worldwide which include soap, face cream, shampoo, etc. Cucumber seeds are used in a variety of ways for human consumption and also for oil extraction.

1.3 Cultivar Group Based on Market Segment

Based on the market segment, cucumber is classified into two groups, i.e. slicing cucumber (for fresh consumption) and pickling cucumber (for processing purpose). Pickling cucumber is generally smaller in size in relation to length and diameter, has a light green rind colour with prominent tubercles at the immature stage. Slicing cucumber is used mostly for fresh consumption. The fruit colour of processing cucumber is creamy, light green with white tinge and dark green. The consumer preference for colour of fruit varies from region to region. Slicing as well as pickling cucumber has one more segment called parthenocarpy primarily grown under the protected structure. The development of fruit with or without pollination but without fertilization is called parthenocarpy. The parthenocarpy cucumber lines also linked with gynoecious gene, bears only female flowers. Lietzow et al. (2016) detected seven QTLs related to the parthenocarpy fruit set. The parthenocarpic cucumber varieties/hybrids are now grown commercially due to more yield and better quality.

1.4 Origin and Distribution

The cucumber (*Cucumis sativus* L.) has been domesticated from its progenitor *Cucumis sativus* var. *hardwickii* (Qi et al. 2013) about 3,000 years ago in India and spread quickly for cultivation in south and east Himalayas. The primary centre of origin of cucumber is India (Whitaker and Davis 1962; Jeffrey 1980; de Candolle 1886; Robinson and Decker-Walters 1997). China is considered as secondary diversity centre as it spread to China ~2000 years ago and to European countries 700–1500 years ago (Keng 1974; Paris et al. 2012). In the second century, Romans brought cucumber to Greece and Italy. The cucumber introduced to Haiti in 1494 by Spanish, and in Montreal, Canada by Cartier, in Florida, U.S., by Desoto, and in Virginia, U.S., by Amidas and Barlow in 1535, 1539 and 1584, respectively (Whitaker and Davis 1962; Robinson and Decker-Walters 1997). Swiader et al. (1992) confirmed based on record that cucumber cultivation in France and England started in the ninth and fourteenth centuries, respectively.

1.5 Crossability and Domestication

The *Cucumis sativus* has four botanical varieties, which are cross compatible, i.e. *Cucumis sativus* var. *hardwickii* (wild cucumber), *Cucumis sativus* var. *xishuangbannesis* (semi-wild Xishuangbanna cucumber), *Cucumis sativus* var. *sikkimensis* (Sikkim cucumber) and *Cucumis sativus* var. *sativus* (cultivated cucumber). Among these botanical varieties, *C. sativus* var. *hardwickii* possesses a multiple branching and fruiting habit (Horst and Lower 1978) and have considerable variability in *C. sativus* germplasm (Dijkhuizen et al. 1996), thus has better prospect for generating genetic variation in cultivated cucumber (Staub et al. 1992).

The genus *Cucumis* has about 66 species, and only chromosome in cucumber is $2n = 2x = 14$. While its sister species, *C. hystrix*, have

2n = 2x = 24 chromosomes. The wild species *C. hystrix* is found only in the Yunnan Province of Southern China which has distinctive genetic attributes that make its taxonomic determination complex (Chen et al. 1995; 1997a and b). Through dysploid chromosome reduction, cucumber evolved from its extinct 2n = 24 ancestor, in which several chromosome reorganization process includes inversions, fusions and translocations takes place with the exclusion of cucumber chromosome 7, which remained largely uninterrupted during the evolution of *Cucumis* species (Weng 2021). Other distinct species of *Cucumis* is *Cucumis melo* which include annual and perennial species with chromosome number $2n = 24$ (Kirkbride 1993).

The relationship among the *Cucumis* species has been worked out based on morphology, crossability and protein analysis (Deakin et al. 1971; Staub et al. 1987 and 1992; Perl-Treves and Galun 1985) to know the biosystematics and phylogeny which have been mainly established by nuclear DNA analysis (Jobst et al. 1998; Zhuang et al. 2004). Garcia-Mas et al. (2004) demonstrated the phylogenetic relationships among *Cucumis* species utilizing ribosomal internal transcribed spacer sequences and SSR markers. Earlier report obtained using isozyme and restriction fragment markers (Staub et al. 1992; Perl-Treves and Galun 1985; Jobst et al. 1998) to study the genetic relationships did not agree with the previous findings. It is believed that wild species of *Cucumis* has originated from Africa. On the other hand, Southern Asia was primary sites of domestication for cucumber and germplasm of same origin have been utilized for transfer of several traits in breeding programme (Dane et al. 1980; McCreight et al. 1993; Staub et al. 1999).

1.6 Botany

(1) Habit: It is annual in nature and viny in growth. Plants are climbing herb and can be trail through support.

(2) Root: Plant has strong tap root system penetrate in the soil up to 50–100 cm. Secondary root system is profusely branched having superficial growth in the upper 50 cm of the soil.

(3) Stem: The stem is herbaceous, hairy, angled and stout. Plant has primary as well as secondary branches with simple tendril. The internodal length depends upon the growth habit of the plant. Some plant has small internodal length due to compact growth habit.

(4) Leaf: Leaves are simple with deeply cordate base and acuminate apex. The shape is triangular, ovate has 7–20 cm length. The petiole length is 5–15 cm and unbranched tendril developed at every leaf axil.

(5) Inflorescence: Solitary, female flowers born in leaf axil and male with large peduncle.

(6) Flower: Cucumber was originally monoecious, subsequently gynoecious and andromonoecious cultivar bred. Other sex forms such as androecious, hermaphroditic and tri-monoecious are also reported. In monocious, male and female flowers are born at different nodes on same plant. The number of male flowers are much high as compare to female flowers in monoecious plant. The gynoecious plants beard only pisttilate flowers at every node.

(7) Calyx and Corolla: Sepals are five lobed and five partite petals, yellow, round, 3–4 cm in diameter fused at the base.

(8) Staminate flower: Staminate flowers are predominant (more numerous) in axillary clusters and have three stamens. Anthers of two stamens are bilocular and the third is unilocular. Each stamen has stalk called filaments and it is free to each other, while all stamens are approximately united by their anthers.

(9) Pistillate flower: The arrangement of the pistillate flowers on the plants is generally solitary, axillary and borne on short thick pedicels. Multi-pistillate flowers are also reported in cucumber. The female flowers are epigynous (other floral parts are above the ovary) and hermaphrodite flowers are perigynous (having the stamens and other floral parts at the same level as the carpels). The pistil consists of one to five (but usually

three) carpels which in turn, produce ovaries with a corresponding number of locules. The pistillate flowers contain up to five stigmas. The ovary of pistillate flower has vestiture either white or black on its surface.

(10) Fruit: The fruit shape is generally oblong, cylindrical, oval and elongated and called many seeded pepo. The blossom end fruit shape is acute, obtuse and round, whereas peduncle end fruit shape is generally obtuse. The fruit is many seeded pepo having pale green flesh. The colour of fruit skin at edible stage is varied from yellow, mottled light green to dark green. At immature fruit stage, suture (slightly depressed in relation to the fruit surface) is present on fruit surface. Undulation of the surface of the fruit independently on the position of the carpel is knows as creasing, generally found in Japanese genotypes. Small raised growth on fruit surface is known as wart also present in few genotypes. The colour of fruit skin at ripening (seed harvest) stage is generally brown or yellow.

(11) Seed: The seeds are flat in shape, white in colour, 8–10 cm × 3–5 mm in size and approximately 1000 seeds are counted in 20–23 g. The number of seeds in a single fruit varies from 75 to 250.

1.7 Floral Biology

The floral biology of cucumber crop is very important for the researchers and breeders. Flowering starts after 20–30 days of sowing depending upon the cultivars. The ratio of male and female flower varies from 7:1 to 17:1 in monoecious lines (Ekeke 2018). The anthesis of flower takes place between 5.30 am and 7.00 am, whereas the anthers dehisce from 4.30 am to 5.00 am. The temperature and other environmental conditions influenced the anther dehiscence in cucumber. The optimum temperature for anthers dehiscence is 20.5–21.5 °C. Pollen remains viable up to 2.00 pm after anther dehiscence and become unviable by the evening. Receptivity of stigma starts 12 h before opening of flower and continues to be till 6–7 h after that. Due to short duration stigma receptivity, pollination should be done within two hour after anthesis. Early drying of stigmatic secretion occurs due to increase in temperature. Lack of pollination is the major causes of fruit abortion, deshaped fruit and poor fruit setting particularly in monoecious lines. Most important pollination agent is insects (bees). It is advisable to have at least one beehives per acre for getting better yield and quality fruits. Under protected condition growing of parthenocarpic cultivars of cucumber are suitable.

1.8 Genetic Resources and Variability

Genetic diversity in the accessions of any crop species is the key of improvement programmes. Several thousand accessions of cucumber are being maintained at different location worldwide (Weng and Sun 2011). Assessment of diversity based on morphological traits has limitations, since most of them are influenced by the environmental factors. Therefore, molecular approaches are more important to assess of genetic diversity. The morphological traits which have major diversity are immature fruit skin colour (creamy white, mottled light green, mottled dark uniform green to dark green), fruit ribbing (ribbed and non-ribbed), ovary colour of vestiture (white and black), spine size (large, intermediate, small), fruit wart number (absent, few, many), fruit glossiness (dull, glossy) and fruit strips (absent, present). The information on the extent and makeup of genetic variability of a crop is important for framing the strategies to conserve and utilize of biodiversity.

Reduction in genetic diversity is major bottleneck in the populations of cultivated cucumber. Previous studies suggested that cultivated cucumber has a much narrower genetic base as compared to wild cucumber (Weng et al. 2010; Li et al. 2011; He et al. 2013). Qi et al. (2013) re-sequenced the 115 accessions of cucumber and reported about 3.6 million nucleotide variants. The targeted 115 cucumber accessions were grouped in 4 clusters, i.e. the Indian, the XIS (Xishuangbanna), the Eurasian and the East Asian group. In compared to the other three groups, Indian group had the significantly higher nucleotide diversity and the large numbers of private variants (Qi et al. 2013). The genetic diversity of Indian collection using EST-SSR was assessed by Pandey et al. (2018). Wang et al. (2018) used SNP to assess the population structure of 1234 cucumber accession comprising India, East Asia and Eurasia collection. The Indian, south Asia and East Asia group had the highest level of diversity, while collection of North America, Turkey Europe, central/west Asia and Africa have less diversity (Wang et al. 2018).

In India, two cucumber lines IC 257296 (IGNR No. 18030) and IC 420405 (IGNR No. 18029) have been identified for bearing two female flower per node with small fruit size and high caroteniod content with orange flesh colour, respectively (Pragya et al. 2019). Several other germplasm either indigenous or exotic contributed to in the improvement of cucumber (Tatlioglu 1993). Indian origin germplasm PI 183056 (large root size), PI 183967 (nematode resistance, sequential fruiting, multiple lateral branching) and PI 197087 (downy mildew and gummy stem blight resistance) used widely for cucumber improvement programme worldwide. Other important introduced lines are PI 200815 (resistant to downy mildew and gummy stem blight), PI 200818 (bacterial wilt), PI 212233 (powdery mildew resistance), PI 220860 (gynoecious), PI 418962, PI 419008, PI 419009 and PI 419135 (multiple disease resistance) used for specific breeding programme (Stoub et al. 2008).

1.9 Genetics and Gene Action

The whole genome of cucumber is first time sequenced (Huang et al. 2009). This study indicated that out of seven chromosomes, five chromosome of cucumber is derived from merging of ten ancestral chromosomes after speciation from *Cucumis melo*. The *sequenced* cucumber genome is useful in the study of traits, i.e. sex expression, biosynthesis of cucurbitacin, disease resistance and 'fresh green' odour. The genomic information may be used for breeding better cultivar, studying the function and development process of the plant vascular system. After release of genome draft of cucumber, significant development has been made in improving genetic resources of cucumber. Several mutants have been reported and many genes or QTLs have been identified, which offers an improved understanding of the inheritance and genetic basis of commercially important traits. The mutant genes are related to cotyledon, hypocotyl, stem, leaf, flower and fruit. Several single-gene mutants affect sex expression in cucumber. Cucumber gene catalog (2017 version) is an updated form of cucumber gene list 2010 (Call and Wehner 2010). In 2017 cucumber gene catalog, major revisions have been made and only cucumber mutations having distinct, noticeable phenotypic variations or of horticultural significance were included. Genes related to isoenzymes were eliminated from the list. QTL with large effects and qualitatively inherited genes for disease resistances and other agriculturally important traits are included (Weng and Wehner 2017). In 2017 version, 73 new genes or major QTLs were included, which brings overall number of genes to 199. For a more comprehensive list of cucumber genes and sources, see the Cucurbit Genetics Cooperative (CGC) 2016–2017 (http://cuke.hort.ncsu.edu/cgc). Newly added gene/ major effect-QTL are briefly described trait wise.

1.9.1 Flower-Related

Many mutants have been isolated and several genes/ QTLs have been identified to understand the inheritance pattern and genetic mechanisms of essential traits in cucumber. Although monoecious or gynoecious are main sex type, but androecious (only staminate flowers), andromonoecious (staminate and perfect flowers), hermaphroditic (perfect flowers) and tri-monoecious (staminate, perfect and pistillate flowers) sex types also found in cucumber. Due to this great variation of sex types, cucumber serves as a prototype for studies of sex determination. The main mechanism of sex determination is proposed to be controlled by three major genes *F, M* and *A* (Kubicki 1969a and b; Li et al. 2008; Yamasaki et al. 2001; Tan et al. 2015). The degree of female flower expression is governed by *F/f* gene, whereas the gene controlling bisexual flower expression is *M/m.* Dominant *F* allele, suppresses *A/a* gene; however, the recessive *a* allele produces staminate flowers (Kubicki 1969b). Another male flower promoting gene *CsACO2* (*a-1*), encoding ACC oxidase gene is identified by Chen et al. (2016). Subgynoecious (with exclusively female flowers at later stage) is a type of monoecious cucumber. Two subgynoecious gene, i.e. *Mod-F1* and *Mod-F2*, independent of *F* and *M* loci, enhances the intensity of femaleness in cucumber by producing high proportion of female to male flowers were identified by Chen et al. (2011). Time of flowering is an important trait, it plays critical role in the environmental adaptation of most crops during domestication. The Xishuangbanna cucumber (XIS), a semi-wild cucumber is a useful resource of novel genes that could be used in cucumber improvement. Four QTLs, i.e. *qFt1.1, qFt5.1, qFt6.1* and *qFt6.2* for flowering time are identified using a Xishuangbanna (XIS) cucumber (Qu et al. 2014; Pan et al. unpublished data; Bo et al. 2015). A major effect QTL, *qEf1.1* for early flowering was tagged by Lu et al. (2014) in a population derived by crossing early flowering genotype, Muromskij and late flowering genotype 9930.

1.9.2 Leaf-Related

Hair-like structure present all over the above ground parts of the plant is called trichome. Plants trichomes may play a significant part to tolerate from biotic and abiotic stresses like high and low temperature, high UV rays and also from insects and herbivorous animals (Wagner 1991). Three new glabrous mutants, i.e. *Glabrous 1* (*gl-1, csgl1*), *Glabrous-2* (*gl-2, csgl-2*) and *Glabrous-3 (gl-3, csgl-3)* are identified by different workers and were added to the new gene list (Weng and Wehner 2017). The three mutants were morphologically different and controlled by dissimilar genetic mechanisms. Cucumber mutant, *csgl1* exhibited trichomes only on hypocotyls and emerging leaves, present on chromosome 3 (Cao et al. 2001; Li et al. 2015b). Mutant *csgl-2* is showing trichomes on the flower sepals, fruits and fruit peduncle, however, leaf, petiole and stem were mostly glabrous, mapped on chromosome 2 (Yang et al. 2011).While *csgl3* was located on chromosome 6 and having trichome-free plant morphology (Cui et al. 2016). *CsGL3* was epistatic to *CsGL1* and encode a class IV and I HDZIP transcription factor, respectively; however, function of *CsGL2* is unknown. Another glabrous mutant identified as trichome-less (*tril*), CGN19839 derived from European greenhouse cucumber, showing completely glabrous phenotype, inherited by single recessive gene (Wang et al. 2016). Most of the cucurbits are having bitter foliage due to the presence of cucurbitacin. Shang et al. (2014) identified a gene for bitter leaf (*Bl*), located in chromosome 5, which regulates biosynthesis of bitterness in leaves of cucumber by triggering transcription of *Bi* that regulates cucurbitacin biosynthesis. Leaf colour mutants are commonly used to understand the chlorophyll biosynthesis pathways and chloroplast development mechanism. A cucumber virescent leaf mutant 9110Gt conferred by the *v-1* gene, was identified and mapped in chromosome 6 showing yellowish green leaves at seedling stage and turned into normal green at later stage of plant growth. *CsaCNGCs* encoding channel protein is identified as putative candidate gene for *v-1* gene (Miao et al. 2011 and 2016). Yellow plant (*yp*) mutant is identified by Abul-Hayja and Williams (1976), mutant plant is having light yellow-green leaves and showing slow growth habit. A similar golden leaf mutant C528, having chlorophyll deficiency is isolated by EMS-induced mutagenesis (Li et al. 2015a; Gao et al. 2016). Photosynthesis efficiency is critically affected by leaf area and it is a major trait affecting crop yield.

A major QTL, *ll2* (*littleleaf-2)* is mapped in wild cucumbers (*Cucumis sativus* var. *hardwickii*) for bearing little leaves, located in chromosome 7 (Shi et al. 2014).

1.9.3 Fruit-Related

Bitterness in cucumber fruit occurs due to cucurbitacin, which is a cucumber beetle attractants and an undesirable property for consumption purpose but it act as protectants against most of the pests. However, cucumber cultivar having low cucurbitacin content in the fruit is preferred by the breeders. Several genes have been identified which control the bitterness/non-bitterness in cucumber, such as recessive gene *bi (bi-1)* producing bitter-free fruit and foliage and dominant gene *Bt (Bt-1*) making highly bitter fruit. Zhang et al. (2013) identified recessive *bi-3* gene and *bi-1* gene is recessive and epistatic to the *bi-3* gene, which produce cucumber plants having non- bitter fruit and foliage. Fruit length is an important agronomic trait in cucumber that affects yield as well as consumer preference. Cucumber exhibits tremendous variation in fruit size, from 5 to 60 cm in length (Yang et al. 2012). Commercially, there are different standard for fruit length of cucumber, for example, pickling cucumbers of the U.S. have short and blocky fruits, while slicing cucumbers have relatively long fruits. Longer cucumber are preferred by Chinese fresh market, while Beit Alpha types popular in the Mediterranean region are thin and shorter ((Robinson and Decker-Walters 1997). To understand the underling genetic mechanism of fruit length, several investigations has been made. Jiang et al. (2015) identified gene *fl-1(fruit length-1*) governing fruit length by using two near-isogenic lines, 408 and 409 having difference in fruit length. Two EMS-induced mutant, *long fruit* (*lfr*) and *short fruit (sfr)* were isolated by Wang et al (2014) from cucumber line “Shannong No. 5”. The appearance of fruits of cucumber is one of the essential aspects of cucumber breeding due to the processing purpose and consumer acceptance. Thick tough skin in cucumber is dominant to thin tender skin (Strong, 1931) small spine size (*ss*) is linked with tender fruit (*te*) (Fanourakis and Simon 1987). Fruit ribbing in cucumber is studied by Miao et al. (2011) and they revealed that fruit ribbing is controlled by single, dominant gene *Fr* and four fruit epidermal trait associated genes, *u* (fruit colour), *d* (glossiness), *H* (fruit netting) and *fr* (no ribbing) were found to be strongly linked loci in chromosome 5. Spine density in cucumber fruit is a major quality attribute for marketing. Zhang et al. (2016) isolated recessive mutant, *few spines 1* (*fs1*) from CNS2 cucumber line. Spontaneous mutant line, 06–2 named as microtrichome (*mict*), is derived from the North China inbred line 06–1, is having spineless fruit (Zhao et al., 2015a). The colour of cucumber fruit also largely influences consumers’ preference. Colour of cucumber fruit is determined by the content of chlorophylls. Two mutants, light *green fruit* (*lgf, CsYcf54*) and *light green peel (lgp*) for fruit colour in cucumber were isolated by different researchers using EMS-induced mutation from cucumber line 406. Lun et al. (2016) identified a recessively inherited mutant, *CsYcf54* having light green fruits and foliage. Mutation in CsaARC5 gene results into the recessive mutant, *lgp* exhibiting light green exocarp (Zhou et al. 2015b). Orange endocap in ripe fruits of Xishuangbanna (XIS) cucumber is due to the presence of high level of *ß*-carotene, a metabolic precursor of vitamin A, which is recessive to white endocarp (no *ß*-carotene); the *ore* locus governing orange endocarp, encodes β-carotene hydroxylase gene is located on chromosome 3 (Bo et al. 2011). The presence of fragrance is a value added trait in many food crops like rice, soybean and sorghum. A few cucumber cultivars with pandan-like fragrance in their fruits and leaves were found in Thailand. Pramnoi et al. (2013) identified a single recessive gene, *fgr* responsible for pandan-like fragrance in the fruits and leaves of PK2011T202. *fgr* is located on chromosome 1 and encodes betaine aldehyde dehydrogenase 2 (BADH2) (Yundaeng et al. 2015). Cucumber is a highly perishable crop and postharvest losses of crop are of great concern to farmers. Improved shelf life of cucumber helps to reduces postharvest deterioration susceptibility.

Chemically induced mutant identified by Dirks et al. (2013), controlled by single recessive gene (*res*), showing less sensitive ethylene mutant, which maintains fruit firmness consequently resulting in longer shelf life after fruit harvest.

1.9.4 Growth Habit

Breeding cucumber plant with compact (short) structure is an important trait. As the dwarf plant architecture needs less labour intensive cultivation while providing more fruits per plant. Regulatory molecular mechanisms of plant growth and development can be interpreted by dwarf plant mutants. Genes underlying dwarf mutations in a number of plant species have been studied by several researchers. In cucumber, gene catalog 2017, Weng and Wehner added four new mutants having dwarf or compact plant height including *Compact-3 (cp-3)* (Crienen et al. 2009), *Super compact-1 (scp-1)* (Wang et al. 2017), *Super compact-2 (Scp-2)* (Li Zheng unpublished data) and *Short internode (Si)* (Lin et al. 2016). The *cp-3, scp-1* and *scp-2* have extremely reduced plant height. Mutant, *scp-1* and *scp-2* are produce by mutation in genes of brassinosteroid (BR) biosynthesis pathway. Dwarfism in mutant, *si* is associated with truncated F-Box protein, exhibiting short internode (*si*), smaller fruit and more wrinkled leaves. Hypocotyl elongation is affected by environmental conditions in commercial cucumber cultivars. Sometimes high temperature or low light intensity may cause increased hypocotyl length, causing poor quality seedling for transplanting. Short hypocotyl in semi wild Xishuangbanna (XIS) cucumber is controlled by a recessive allele, *sh1*, which is insensitive to UVB-free light and temperature fluctuation. *sh1* encodes a human SMARCA3-like chromatin remodelling factor (Bo et al. 2016). The *tendrilless (ten)* mutation that forms branches instead of tendrils is isolated from a cucumber landrace, CG9192. The affected gene *TEN* encodes a TCP (*TB1*, *CYC*, and *PCF*) transcription factor (Wang et al. 2015). Another mutant, *tendrilless-1* (*td-1*) has been tagged on chromosome 6, exhibits tendril less, dwarf trichome-free plant BM007 (Li YH personal communication). Strong association was observed among branches per plant and yield in cucumber (Carmer and Wehner 2000). However the development of many lateral branches escalates the compactness of the plants, which decreases ventilation and can causes diseases. Non-lateral branch (*nlb*) gene, was mapped on the chromosome 1 of cucumber in F_2 population derived from the crossing of non-lateral branch line 419 and branch line SB-2 (Jiang et al. 2008; Ren et al. 2013). Darker green colour in cucumber is an indicator of extended shelf life. Haaring (2014) invented new cucumber plant having dark green stem (*Gs*) in the seedling stage, which is indicator of a darker green fruits. Dark green stem (*Gs*) is simply inherited trait and dominant or incomplete dominant over regular green stem.

1.9.5 Disease Resistance

Major diseases of cucumber include powdery mildew (PM), downy mildew (DM), target leaf spot (TLS), angular leaf spot (ALS), Fusarium wilt (FOC), anthracnose (AR), scab and various viral diseases like cucumber mosaic virus (CMV), zucchini yellow mosaic virus (ZYMV), papaya ringspot virus (PRSV) and watermelon mosaic virus (WMV). Several investigations have been done for resistances to these economic important diseases of cucumber.

1.9.5.1 Simply Inherited Disease Resistance Genes

Three recessive gene, *cca-1*, *caa-2* and *caa-3* governing resistance to *Corynespora cassiicola* causing target leaf spot (TLS) in cucumber have been tagged on Chromosome 6. A molecular marker, CSFR33 linked with *cca-1* locus has been identified in TLS-resistant cucumber line, Q5 by Wang et al. (2010). Yang et al. (2012) found a single recessive gene *cca-2,* governing TLS resistance in PI 183967. Resistance in D31 cucumber line for TLS is governed by *cca-3* gene, Csa6M375730, a CC-NB-ARC type resistance gene analog is identified as putative candidate gene for *cca-3* (Wen et al. 2015). Earlier investigations suggested that in cucumber there is strong linkage between resistances genes of three potyviruses including PRSV, WMV and ZYMV, as all these resistance genes are located on chromosome 6. Resistance in Chinese inbred line, '02245' for papaya ring spot virus (PRSV) and watermelon mosaic virus (WMV) are governed by a single recessive gene $prsv^{02245}$ and wmv^{02245}, respectively (Tian et al. 2015, 2016). Zucchini yellow mosaic virus (ZYMV) resistance in cucumber inbred lines 'A192-18' is controlled by a single recessive gene $zym^{A192\text{-}18}$. VPS4-like protein encoding gene is putative candidate for the $zym^{A192\text{-}18}$ (Amano et al. 2013). Resistance to Zucchini yellow fleck virus (ZYFV), was found in inbred lines developed from cucumber genotype, Taichung Mou Gua' (TMG). Resistance to ZYFV was determined to be governed by a single recessive gene, *zyf* (Gilbert-Albertini et al. 1995; Kabelka and Grumet 1997).

1.9.5.2 QTLs Providing Resistance to Following Diseases and Abiotic Stress

Powdery mildew resistance in cucumber line, Jin5-508 is governed by major QTL *Pm1.1,* mapped in chromosome 1 by Xu et al. (2015). *Pm1.1* is dominantly inherited *QTL*. However, Nie et al. (2015) identified a recessively inherited QTL, *pm5.1,* for PM resistance on chromosome 5. de Ruiter et al. (2008) identified resistance in PI 250,147 for cucurbit yellow stunting disorder virus (CYSDV) and mapped three QTL. Major QTL, *qCYSDV5.1* for CYSDV resistance was located in chromosome 5; this QTL is near to the QTL conferring resistance to powdery mildew (de Ruiter et al. 2008). Zhang et al. (2014) identified one major QTL *Foc2.1* governing resistance from fusarium wilt on chromosome 2. Resistance to fusarium stem and root rot was identified in cucumber line URS 189 by de Milliano et al. (2012). Two linked QTLs for FW resistance is mapped on chromosome 6. Weng and Wehner 2017 designated these two QTLs as *qFoc6.1* and *qFoc6.2*. A cross between *C. hystrix* and *C. sativus* produced three gummy stem blight (GSB) resistant introgression lines (ILs), i.e. HH1-8–1-2, HH1-8–5 and HH1-8–1-16. Three QTLs, *qGsb1.1*, *qGsb4.1* and *qGsb6.1* were identified for GBS resistance (Lou et al., 2013). QTLs conferring resistance to MYSV (melon yellow spot virus) were identified in F_2 population developed by crossing 27,028,930 (resistant) and Tokiwa (susceptible) genotypes. Resistant parent 27,028,930 contributes two major QTLs, *qMYSV1.1* (*qSwf1.1*) and *qMYSV3.1* (*qSwf3.1*) and one minor QTL, *qMYSV7.1* (*qSwf7.1*) present on 1, 3 and 7 chromosome, respectively, while susceptible parent Tokiwa also contribute one minor QTL *qMYSV4.1* (*qSwf4.1*) present on chromosome 4 (Sugiyama et al. 2015). One abiotic stress resistance (waterlogging tolerance) QTLs was also included in 2017 gene list (Weng and Wehner 2017). More hypocotyl-derived adventitious roots (AR) were produced by Zaoer-N, a waterlogging tolerant cucumber cultivar under waterlogging condition. QTL analysis revealed that AR number (ARN) is controlled by a major QTL, *ARN6.1* and two minor effect QTLs *ARN3.1* and *ARN 5.1* (Xu et al. 2016).

1.10 Conclusion

The biotic and abiotic factors are the major environmental stresses constantly reducing the crop yield and fruit quality of cucumber. The white fly, aphid, thrips and mites are becoming new challenges for growing of cucumber under protected conditions. Among biotic stress, vector borne viral diseases such as Tomato Leaf Curl New Delhi Virus (ToLCNDV) and Zucchini yellow mosaic virus (ZYMV) are becoming the challenges for the researchers. Other important diseases are gummy stem blight, powdery mildew, downy mildew, wilt and root knot nematode. There is need to develop the cucumber lines for better adoptability, which has capacity to set the fruit under high temperature (heat set) and can tolerate wet condition. There are two major segments in cucumber for consumer point of view. First is for fresh market and second one is for processing. Cucumber is grown under open-field conditions and under protected conditions (glass house). Partehnocarpy cucumber is only varieties which can be grown under glass house production as it does not requires pollination for fruit setting and have very high yield potential. Development of stable parthenocarpy cucumber variety in different segment (based on skin colour) is very important because liking of colour varies from one region to other region.

Screening of germplasms for various abiotic and biotic stress and using those identified resistance lines in a breeding programme is one of the way to combat the new challenges particularly climate change. For developing multiple disease resistant lines, available molecular markers needs to be validated to check the feasibility. Conventional breeding as well as molecular approaches are used for development of new varieties/lines. CRISPR-Cas9 and gene editing new technology are being used for development of new lines with targeted gene particularly for complex traits.

References

Abul Hayja Z, Williams PH (1976) Inheritance of two seedling markers in cucumber. Hort Science 11:145

Amano M, Mochizuki A, Kawagoe Y, Iwahori K, Niwa K, Svoboda J, Maeda T, Imura Y (2013) High resolution mapping of *zym*, a recessive gene for Zucchini yellow mosaic virus resistance in cucumber. Theor Appl Genet 126:2983–2993

Bo K, Ma LZ, Chen JF, Weng Y (2015) Molecular mapping reveals structural rearrangements and quantitative trait loci underlying traits with local adaptation in semi-wild Xishuangbana cucumber (*Cucumis sativus* L. var. *Xishuangbannanesis* Qi et Yuan). Theor Appl Genet 128:25–39

Bo K, Song H, Shen J, Qian C, Staub JE, Simon PW, Lou Q, Che J (2011) Inheritance and mapping of theoregene controllingthe quantity ofb-carotene in cucumber (*Cucumis sativus* L.) endocarp. Mol Breeding. https://doi.org/10.1007/s11032-011-9624-4

Bo KL, Wang H, Pan YP, Behera TK, Pandey S, Wen CL, Wang YH, Simon PW, Li YH, Chen JF, Weng Y (2016) Cucumber *Short Hypocotyl1* (*Sh1*) encodes a human SMARCA3-like chromatin remodeling factor regulating hypocotyl elongation. Plant Physiol 172:1273–1292

Call AD, Wehner TC (2010) Gene List 2010 for Cucumber. Cucurbit Genet Coop Rep 33–34:69–103

Cao CX, Zhang S, Guo HY (2001) Genetic relationship between glabrous foliage character and warty fruit character of cucumber. Acta Hort Sinica 28:565–566

Chen H, Sun J, Li S, Cui Q, Zhang H, Xin F, Wang H, Lin T, Gao D, Wang S, Li X, Wang D, Zhang Z, Xu Z, Huang S (2016) An ACC oxidase gene essential for cucumber carpel development. Mol Plant 9:1315–1327

Chen HM, Tian Y, Lu XY, Liu XH (2011) The inheritance of two novel subgynoecious genes in cucumber (*Cucumis sativus* L.). Scie Horti 127:464–467

Chen JF, Isshiki S, Tashiro Y, Miyazaki S (1995) Studies on a wild cucumber from China (*Cucumis hystrix* Chakr.). I. Genetic distances between *C. hystrix* and two cultivated *Cucumis* species (*C. sativus* L. and *C. melo* L.) based on isozyme analysis. J Jpn Soci Horti Scie 64:264–265

Chen JF, Isshiki S, Tashiro Y, Miyazaki S (1997) Biochemical affinities between *Cucumis hystrix* Chakr. and two cultivated *Cucumis* species (*C. sativus* L. and *C. melo*. L.) based on isozyme analysis. Euphytica 97:139–141

Chen JF, Staub JE, Tashiro Y, Isshiki S, Miyazaki S (1997) Successful interspecific hybridization between *Cucumis sativus* L. and *Cucumis hystrix* Chakr. Euphytica 96:413–419

Cramer CS, Wehner TC (2000) Path analysis of the correlation between fruit number and plant traits of cucumber populations. Hort Sci 35:708–711

Crienen J, Reuling G, Segers B, van de Wal M (2009) New cucumber plants with a compact growth habit. Patent, International publication number WO2009/059777 A1.

Cui JY, Miao H, Ding LH, Wehner TC, Liu PN, Wang Y et al (2016) A new glabrous gene (c*sgl3*) identified in trichome development in cucumber (*Cucumis sativus* L*.*). PLoS ONE 11: e0148422

Dane F, Denna DW, Tsuchiya T (1980) Evolutionary studies of wild species in the genus *Cucumis*. Z Pflanzenzucht 85:89–109

de Candolle A (1886) Plants Cultivated for Their Seeds. Origin of Cultivated Plants, 2nd Edition, International Scientific Series, vol XLIX. Kegan Paul Trench & Co., London, pp 376–384

de Milliano MJK, Folkertsma RT, van Paassen MQM, de Vries JS, Sela MB (2012) *Fusarium* resistant cucumber plants. US Patent US 2012(0066790):A1

de Ruiter W, Hofstede R, de Vries J, van den Heuvel H (2008) Combining QTL for resistance to CYSDV and powdery mildew in a single cucumber line. In: Proc 9th EUCARPIA meeting on genetics and breeding of Cucurbitaceae (Pitrat, M., ed), INRA, Avignon (France), pp 181–188

Deakin JR, Bohn GW, Whitaker TW (1971) Interspecific Hybridization in Cucumis. Eco Bot 25:195–211

Dijkhuizen A, Kennard WC, Havey MJ, Staub JE (1996) RFLP variability and genetic relationships in cultivated cucumber. Euphytica 90:79–89

Dirks RHG, van Dun CMP, Vel Terop JS, Kloet JW (2013) Resistance to post harvest deterioration in cucumber. US Patent # US 2013/0074223 A1

Ekeke C, Ogazie CA and Agbagwa IO (2018) Breeding biology and effect of pollinators on the fruit characteristics of cucumber (*Cucumis sativus* L.), cucurbitaceae. Nigerian J Botany 31(2):325–344

Fanourakis NE, Simon PW (1987) Analysis of genetic linkage in the cucumber. J Hered 78:238–242

FAOSTAT Data (2018) Available at: http://www.faostat.fao.org.

Gao ML, Hu LL, Li YH, Weng Y (2016) The chlorophyll-deficient golden leaf mutation in cucumber is due to a single nucleotide substitution in *CsChlI* for magnesium chelatase I subunit. Theor Appl Genet 129:1961–1973

Garcia-Mas J, Monforte AJ, Arus P (2004) Phylogenetic relationships among *Cucumis* species based on the ribosomal internal transcribed spacer sequence and microsatellite markers. Plant Syst Evol 248:191–203

Gilbert-Albertlni F, Pltrat M, Lecoq H (1995) Inheritance of resistance to zucchini yellow fleck virus In *Cucumis satiuus* L. Hort Sctence 30:336–433

Haaring C (2014) New cucumber plant of species *Cucumis sativus* carrying genetic determinant that leads to darker green stem in seedling stage that is predictive of darker green color of fruits compared to isogenic cucumber plant not carrying determinant. European patent # EP2777386-A1

He XM, Li YH, Pandey S, Yandell BS, Pathak M, Weng Y (2013) QTL mapping of powdery mildew resistance in WI 2757 cucumber. Theor Appl Genet 126:2149–2161

Horst EK, Lower RL (1978) *Cucumis hardwickii*, a source of germplasm for the cucumber breeder. Cucurbit Genet Coop Rep 1:5

Huang S, Li R, Zhang Z, Li S (2009) The genome of the cucumber, *Cucumis sativus* L. Nature Genet 41 (12):1275–1283

Jeffrey C (1980) A review of the Cucurbitaceae. Bot J Linn Soci 81:233–247

Jiang L, Yan SS, Yang WC, Li YQ, Xia MX, Chen ZJ, Wang Q, Yan LY, Song XF, Liu RY, Zhang XL (2015) Transcriptomic analysis reveals the roles of microtubule-related genes and transcription factors in fruit length regulation in cucumber (*Cucumis sativus* L.). Sci Rep 5:8031

Jiang S, Yuan XJ, Pan JS, He HL, Cai R (2008) Quantitative trait locus analysis of lateral branch–related traits in cucumber (*Cucumis sativus* L.) using recombinant inbred lines. Sci. China Ser. C - Life Sci. 51:833–841

Jobst J, King K, Hemleben V (1998) Molecular evolution of the internal transcribed spacers (ITS1 and ITS2) and phylogenetic relationships among species of the family Cucurbitaceae. Mol Phylo Evol 9:204–219

Kabelka E, Grumet R (1997) Inheritance of resistance to the Moroccan watermelon mosaic virus in the cucumber line TMG-1 and cosegregation with zucchini yellow mosaic virus resistance. Euphytica 95:237–242

Kashif W, Kamran QM, Jilani MS (2008) Effect of different nitrogen levels on growth and yield of cucumber (*Cucumis sativus* L.). J Agril Res 46 (3):259–266

Keng H (1974) Economic plants of ancient north China as mentioned in Shih Ching (Book of Poetry) Econom. Botany 28:391–410

Kirkbride JHJr (1993) Biosystematic Monograph of the Genus *Cucumis (Cucurbitaceae).* Parkway Publishers, Boone, North Carolina

Kubicki B (1969) Investigations on sex determination in cucumber (*Cucumis sativus* L.). Genet Poland 10:3–143

Kubicki B (1969) Investigation of sex determination in cucumber (*Cucumis sativus* L.). VII Trimonoecism. Genet Pol 10:123–143

Li Q, Cao CX, Zhang CJ, Zheng XX, Wang ZH, Wang LN, Ren ZH (2015) The identification of *Cucumis sativus Glabrous 1* (*CsGL1*) required for the formation of trichomes uncovers a novel function for the homeodomain-leucine zipper I gene. J Expt Bot 65:4943–4958

Li WQ, Gao B, Yang J, Chen P, Li YH (2015) Physiological characterization of a new yellow leaf mutant. Acta Agri Boreal Occident Sin 24:98–103 (in Chinese)

Li YH, Yang LM, Pathak M, Li DW, He XM, Weng Y (2011) Fine genetic mapping of *cp*, a recessive gene for compact (dwarf) plant architecture in cucumber, *Cucumis sativus* L. Theo. Appl. Genet. 123:973–983

Li Z, Pan J, Guan Y, Tao Q, He H, Si L, Cai R (2008) Development and fine mapping of three co-dominant SCAR markers linked to the M/m gene in the cucumber plant (Cucumis sativus L.). Theor Appl Genet 117:1253–1260

Lietzow CD, Zhu H, Pandey S, Havey MJ, Weng Y (2016) QTL mapping of parthenocarpic fruit set in North American processing cucumber. Theor Appl Genet 129:2387–2401

Lin T, Wang SH, Zhong Y, Gao DL, Cui QZ, Chen HM, Zhang ZH, Shen HL, Weng Y, Huang SW (2016) A truncated F-box protein confers the dwarfism in cucumber. J Genet Genomics 43:223–226

Lou LN, Wang HY, Qian CT, Liu J, Bai YL, Chen JF (2013) Genetic mapping of gummy stem blight (Didymella bryoniae) resistance genes in *Cucumis sativus-hystrix* introgression lines. Euphytica 192:359–369

Lu HF, Lin T, Klein J, Wang SH, Qi JJ, Zhou Q, Sun JJ, Zhang ZH, Weng Y, Huang SW (2014) QTLSeq identifies a major early flowering QTL corresponding to the *FT* locus in cucumber. Theor Appl Genet 127:1491–1499

Lun YY, Wang X, Zhang CZ, Yang L, Gao DL, bChen HM, Huang SW (2016) A *CsYcf54* variant conferring light green coloration in cucumber. Euphytica 208:509–517

McCreight JD, Nerson H, Grumet R (1993) Melon, *Cucumis melo* L. In: Kalloo G, Bergh BO (eds) Genetic Improvement of Vegetable Crops. Pergamon Press, New York, pp 267–294

Miao H, Zhang SP, Wang M, Wang Y, Weng Y, Gu XF (2016) Fine mapping of virescent leaf gene *v-1* in cucumber (*Cucumis sativus* L.). Int J. Mol Sci 17:1602

Miao H, Zhang SP, Wang XW, Zhang ZH, Li M, Mu SQ et al (2011) A linkage map of cultivated cucumber (*Cucumis sativus* L.) with 248 microsatellite marker loci and seven genes for horticulturally important traits. Euphytica 182:167–176

Nie JT, He HL, Peng JL, Yang XQ, Bie BB, Zhao JL, Wang YL, Si LT, Pan JS, Cai. R (2015) Identification and fine mapping of *pm5.1*: a recessive gene for powdery mildew resistance in cucumber (*Cucumis sativus* L.). Mol Breed 35:7

Pandey S, Ansari WA, Pandey M, Singh B (2018) Genetic diversity of cucumber (*Cucumis sativus*) estimated by EST-SSR markers and morpho-physiological traits. Physiol. Mol. Biology Plants 24 (1):135–146

Paris HS, Daunay MC, Janick J (2012) Occidental diffusion of cucumber (*Cucumis sativus*) 500–1300 CE, two routes to Europe. Ann Bot 109:117–126

Perl Treves R, Galun E (1985) The *Cucumis* plastome: physical map, intragenic variation, and phylogentic relationships. Theor Appl Genet 71:417–429

Pragya R, Pandey A, Munshi AD, Bhardwaj R, Gangoupadhyay KK, Malav PK, Pandey CD, pradeep K, Tomar BS, Kumar A (2019) orange-fleshed cucumber (*Cucumis sativis* var. *sativus* L.) germplasm from North east India: agro-morphological, biochemical and evolutionary studies. Genet Resour Crop Evol 66: 1217-1230

Pramnoi P, Somta P, Chankaew S, Juwattanasomran R, Srinives P (2013) A single recessive gene controls fragrance in cucumber (*Cucumis sativus* L.). J Genet 92:147–149

Qi JJ, Liu X, Shen D, Miao BY (2013) A genomic variation map provides insights into the genetic basis of cucumber domestication and diversity. Nat Gene 45:1510–1515

Qu SP, Pan YP, Weng Y (2014) QTL Mapping of flowering time and fruit shape in Xishuangbana cucumber (*Cucumis sativus* L. var. *xishuangbannanesis* Qi et Yuan). Proc Cucurbit pp 54–56

Ren GL, Yang XQ, He HL, Cai R, Pan JS (2013) Molecular mapping of non-lateral gene in cucumber. Acta Hort Sinica 40:1375–1381

Robinson RW, Decker-Walters D (1997) Cucurbits. CAB International, Wallingford, England, p 226

Shang Y, Ma YS, Zhou Y, Zhang HM, Duan LX et al (2014) Biosynthesis, regulation, and domestication of bitterness in cucumber. Science 346:1084–1088

Shi TT, Wang SH, Lin T, Yang Q, Huang SW (2014) Genetic mapping of *little leaf 2* (*ll2*), a major QTL controlling leaf area in cucumber (*Cucumis sativus* L.). J Agri Biotech 22:415–421

Staub JE, Fredrick L, Marty T (1987) Electrophoretic variation in cross-compatible wild diploid species of *Cucumis*. Canad J Bot 65:792–798

Staub JE, Knerr LD, Holder DJ, May B (1992) Phylogenetic relationships among several African *Cucumis* species. Canad J Bot 70:509–517

Staub JE, Serquen FC, Horejsi T, Chen JF (1999) Genetic diversity in cucumber (*Cucumis sativus* L.): IV. An evaluation of Chinese germplasm. Genet Res Crop Evol 46:297–310

Strong WJ (1931) Breeding experiments with the cucumber (*Cucumis sativus* L.). (Sci Agr) 11:333–346

Sugiyama M, Kawazu Y, Fukino N, Yoshioka Y, Shimomura K, Sakata Y, Okuda M (2015) Mapping of quantitative trait loci for Melon yellow spot virus resistance in cucumber (*Cucumis sativus* L.). Euphytica 205:615–625

Swiader JM, Ware GW, McCollum JP (1992) Producing vegetable crops . Danville, Illinois : Interstate, 626p

Tan JY, Tao QY, Niu HH, Zhang Z, Li D, Gong ZH, Weng Y, Li Z (2015) A novel allele of monoecious (*m*) locus is responsible for elongated fruit shape and perfect flowers in cucumber (*Cucumis sativus* L.) Theor Appl Genet 128: 2483–2493

Tatlioglu T (1993) Cucumber *Cucumis sativus* L. In: Kalloo G, Bergh BO (eds) Genetic Improvement of Vegetable Crops. Pergamon Press Ltd., Tarrytown, New York, pp 197–234

Tian GL, Miao H, Yang YH, Zhou J, Lu HW, Wang Y, Xie BY, Zhang SP, Gu XF (2016) Genetic analysis and fine mapping of watermelon mosaic virus resistance gene in cucumber. Mol Breed 36:131

Tian GL, Yang YH, Zhang SP, Miao H, Lu HW, Wang Y, Xie BY, Gu XF (2015) Genetic analysis and gene mapping of papaya ring spot virus resistance in cucumber. Mol Breed 35:110

Uthapala TGG, Marapana RAUJ, Lakmini KPC, Wettimuny DC (2020) Nutritional bioactive compounds and health benefits of fresh and processed cucumber (Cucumis sativus L.). Sumerianz J Biotech 3(9): 75-82

Wagner GJ (1991) Secreting glandular trichomes - More than just hairs. Plant Physiol 96(3):675–679

Wang H, Li W, Qin Y, Pan Y, Wang X, Weng Y, Chen P, Li Y (2017) The cytochrome P450 gene *CsCYP85A1* is a putative candidate for *super compact-1* (*scp-1*) plant architecture mutation in cucumber (*Cucumis sativus* L.). Front Plant Sci https://doi.org/10.3389/fpls.2017.00266

Wang HZ, Li SJ, Yang RH, Guan W (2010) EST-SSR marker linked to cucumber target leaf spot resistance-related gene. Acta Hort 871. ISHS 871:49–53

Wang LN, Zhang B, Li JR, Yang XY, Ren ZH (2014) Ethyl Methane sulfonate (EMS)-mediated mutagenesis of cucumber (*Cucumis sativus* L.). Agri Sci 5:716–721

Wang S, Yang X, Xu M, Lin X, Lin T, Qi J, Shao G, Tian N, Yang Q, Zhang Z, Huang S (2015) A rare

SNP identified a TCP transcription factor essential for tendril development in cucumber. Mol Plant 8:1795–1808

Wang X, Bao K, Reddy UK, Bai Y, Hammer SA, Jiao C, Wehner TC, Ramirez A, Madera, Weng Y, Grumet R, Fei ZJ (2018) The USDA cucumber (*Cucumis sativus* L.) collection: genetic diversity, population structure, genome-wide association studies and core collection development. Hort Res 5:64

Wang YL, Nie JT, Chen HM, Guo CL, Pan J, He HL, Pan JS, Cai R (2016) Identification and mapping of *Tril*, a homeodomain-leucine zipper gene involved in multicellular trichome initiation in *Cucumis sativus*. Theor Appl Genet 129:305–316

Wen CL, Mao AJ, Dong CJ, Liu HY, Yu SC, Guo YD, Weng Y, Xu Y (2015) Fine genetic mapping of target leaf spot resistance gene *cca-3* in cucumber, *Cucumis sativus* L. Theor Appl Genet 128:2495–2506

Weng Y (2021) Cucumis sativus Chromosome Evolution, Domestication, and Genetic Diversity – Implications for Cucumber Breeding (PDF file) Plant Breed., Review 49: 77–111

Weng Y, Johnson S, Staub JE, Huang S (2010) An extended microsatellite genetic map of cucumber, *Cucumis sativus* L. HortScience 45:880–886

Weng Y, Wehner TC (2017) Cucumber Gene Catalog 2017. Cucurbit Genet Coop Rep 39–40:17–54

Weng Y, ZY Sun (2011) Major Cucurbits. In: Genetics, Genomics and Breeding of Cucurbits (YH Wang, TK Behera, C. Kole, eds). CRC Press, ISBN: 157808766X

Whitaker TW, Davis GN (1962) Cucurbits: Botany, Cultivation, and Utilization. Interscience Publishers Inc., New York

Xu X, Ji J, Xu Q, Qi X, Chen X (2016) Inheritance and quantitative trail loci mapping of adventitious root numbers in cucumber seedlings under waterlogging conditions. Mol Genet Genom. https://doi.org/10.1007/s00438-016-1280-2

Xu XW, Yu T, Xu RX, Shi Y, Lin XJ, Xu Q, Qi XH, Weng W, Chen XH (2015) Fine mapping of a dominantly inherited powdery mildew resistance major-effect QTL, *Pm1.1*, in cucumber identifies a 41.1 kb region containing two tandemly arrayed cysteine-rich receptor-like protein kinase genes. Theor Appl Genet 129:507–516

Yamasaki S, Fujii N, Matsuura S, Mizusawa H, Takahashi H (2001) The M locus and ethylene-controlled sex determination in andromonoecious cucumber plants. Plant Cell Physiol 42:608–619

Yang L, Dal-Hoe K, Li Y, Zhang X, Luan F, Harvey MJ, Jiang J, Weng Y (2012) Chromosome rearrangements during domestication of cucumber as revealed by high-density genetic mapping and draft genome assembly. Plant J 71:895–906

Yang SJ, Miao H, Zhang SP, Cheng ZC, Dong SY, Wehner TC, Gu XF (2011) Genetic analysis and mapping of *gl-2* gene in cucumber (*Cucumis sativus* L.). Acta Hort Sinica 38:1685–1692 (in Chinese)

Yundaeng C, Somta P, Tangphatsornruang S, Chankaew S, Srinives P (2015) A single base substitution in BADH/AMADH is responsible for fragranceincucumber (*Cucumis sativus* L.), and development of SNAP markers for the fragrance. Theor Appl Genet 128:1881–1892

Zhang H, Wang L, Zheng S, Liu Z, Wu X, Gao Z, Cao C, Li Q, Ren Z (2016) A fragment substitution in the promoter of *CsHDZIV11/CsGL3* is responsible for fruit spine density in cucumber (*Cucumis sativus* L.). Theor Appl Genet 129:1289–1301

Zhang SP, Liu MM, Miao H, Zhang SQ, Yang YH, Xie BY, Wehner TC, Gu XF (2013) Chromosomal mapping and QTL analysis of resistance to downy mildew in *Cucumis sativus*. Plant Dis 97:245–251

Zhang SP, Miao H, Yang YH, Xie BY, Wang Y, Gu XF (2014) A major quantitative trait locus conferring resistance to *Fusarium* wilt was detected in cucumber by using recombinant inbred lines. Mol Breed 34:1805–1815

Zhao JL, Pan JS, Guan Y, Zhang WW, Bie BB, Wang YL, He HL, Lian HL, Cai R (2015) *Microtrichome* as a class I homeodomain-leucine zipper gene regulates multicellular trichome development in *Cucumis sativus*. J Int Plant Biol 57:925–935

Zhou Q, Wang SH, Hu BW, Chen HM, Zhang ZH, Huang SW (2015) An accumulation andreplication of chloroplasts *5* gene mutation confers light green peel in cucumber. J Integ Plant Biol 57:936–942

Zhuang FY, Chen JF, Staub JE, Qian CT (2004) Assessment of genetic relationships in *Cucumis* species by SSR and RAPD analysis. Plant Breed 123:167–172