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Classical Genetics and Traditional Breeding in Cucumber (*Cucumis sativus* L.)

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Abstract

Rapid progress has been made in classical genetics and traditional breeding in cucumber for various quantitative and qualitative traits which greatly benefited the development of superior varieties suitable for open field and protected cultivation. The different breeding methods like plant introductions, hybridizations, pedigree selection, recombination breeding and marker assisted selection have been employed successfully in developing superior varieties and F₁ hybrids. The development of new varieties with earliness, high-yield and resistance to diseases (powdery mildew, downy mildew and tolerant to virus) through selection of superior parental lines followed by hybridization and marker assisted introgression of desired genes was a game changer in cucumber breeding. The exploitation of gynoeceous sex along with parthenocarpic traits in traditional breeding has made revolution in cucumber cultivation throughout the world which enabled the adoption of cucumber crop by farming community on large scale. Molecular markers technology could be exploited to overcome the obstacle of traditional breeding by accelerating the breeding cycle and selection of desirable traits. The high density genetic maps for various traits have been constructed in cucumber to detected quantitative traits loci (QTLs) for genetic enhancement in different market classes of cucumber. Therefore, this chapter highlighted the concepts of genetic foundations for advancement made in cucumber breeding.

Keywords: cucumber, traditional breeding, classical genetics, molecular breeding

1. Introduction

Cucumber (*Cucumis sativus* L) is an important vine species of the Cucurbitaceae family. Cucumber is the fourth most important vegetable crop worldwide and is a model system for other Cucurbitaceae family which is used for studying several significant biological processes [1]. Cucumber is originated from India, particularly southern foot-hills of Himalayan region. It was domesticated in India from its wild relative, *Cucumis sativus* var. *hardwickii* 3000 years ago [2, 3]. It is commercially grown in the tropical and subtropical regions of the world. The fruits are widely consumed as salad at immature stage. Cucumber is high in water content and low in calories, fat, cholesterol, and sodium [4] and good source of mineral nutrients (Ca, Mg, P & K) and medicinal properties such as antioxidant, anti-inflammatory, and

anti-cancer benefits. Cucumbers are also used for digestive benefits and mood stability when modulating stress. Cucumbers fortify cells so they may retain hydrated and work at the highest levels, and may slow age-related cellular deteriorations [5]. The available genetic diversity within the cultivated cucumber is very low [2, 6–9] which is the major impediment in the genetic improvement of various cucumber market classes [10]. Thus, increasing the genetic diversity of cultivated cucumber is an important task for public sector research [11]. The cultivated cucumber has narrow genetic base with 3–8% polymorphism within the cultivated genotypes, and 10–25% between botanical varieties [12]. Earliness, high yield, uniform fruit shape, size, color and better quality are prerequisites for the release of the cucumber varieties and F_1 hybrids for open field condition. In addition to these characters, gynoeceous and parthenocarpic traits are desirable for green house cucumber production. Identification of genotypes tolerance to drought is also one of important breeding objective in cucumber [13]. Cucumber is a monoecious vegetable crops species. However, several gynoeceous varieties and F_1 hybrids have been developed by introgression of F locus (gynoeceous gene) in the background of different market classes of the cucumber for commercial production. The utilization of gynoeceous lines are economical and easier for hybrid seed production by reducing the cost of male flower pinching and hand pollination [14]. The present day cucumber F_1 hybrids for open field production derived from the cross between gynoeceous $\times$ monoecious and monoecious $\times$ monoecious where as green house grown F_1 hybrids are the result of the cross of gynoeceous $\times$ gynoeceous lines with parthenocarpic traits. The evaluation and selection of the genotypes only based on phenotype characters for high yield and stability of gynoeceous sex form require many years in multiple environments which is very expensive and time consuming process. The whole genome sequencing in cucumber [15] have opened the way to utilize the DNA markers viz. simple sequence repeats (SSRs) for gene mapping, marker assisted selection and marker trait association for several economic traits in cucumber [16–18]. With the development of high density linkage map several traits have been mapped in cucumber including, flowering time [19] fruit quality [20], diseases [17, 21], yield [22], fruit spines [23], fruit color [8], chromosomal mapping and QTL analysis of resistance to downy mildew [24–26], yellow fruit flesh [27], pleiotropic andromonoecy and carpel number [28, 29]. QTLs have been identified in Sikkim cucumber (*Cucumis sativus* var. *sikkimensis*) for important horticultural traits including flowering time, fruit size, flesh thickness, fruit spines, fruit color [30].

2. Classical genetics in cucumber

2.1 Genetics of quantitative and qualitative characters

The deep understanding about cucumber crops biology was only possible due to mendelian's classical genetics which have made possible for the cucumber breeders to develop improved varieties and F_1 hybrids. The knowledge about different genes which affects economic traits facilitated breeders to develop proper genetic resources for the development of trait specific genetic stock for further use for genetic improvement of cucumber. For example, the size of the population will be much smaller if a breeder is selecting for a trait controlled by a single gene, than if the trait is controlled by multiple genes with a large environmental influence. The application of Mendelian genetics using classical techniques in cucumber has facilitated the discovery of a number of genes for yield, quality, plant architecture, and disease and pest resistance in both slicing and pickling cucumber. The yield in

cucumber is enhanced by utilizing gynoecious as one of the parent in breeding programme which promote higher female to male sex ratio. Sex ratio (female: male), fruit weight and fruit size are the direct yield components in cucumber breeding.

2.2 Sex expression

In commercial cucumber cultivars, the type of sex forms (gynoecious or monoecious) and the amount of their expression is important because these have a direct effect on harvesting date, production and productivity of this crop. Flowering time in cucumber played a critical role in fetching early market price and increase in fruit yield for the growers. In cucumber, the type of sex form (gynoecious or monoecious) and the amount of their expression have direct effect on harvesting time, production and productivity. The sex expression also played a vital role in seed production as well as development of new plant types. The flowering traits like node number at which first female flower appear, days to first pistillate flower opening, and male: female ($\sigma^{\circ}:\text{♀}$) flower ratio (sex ratio) are the important traits for determination of earliness and fruit yield. The sex expression in cucumber is controlled by three genes, *F*, *M*, and *A* [31]. The degree of female flower expression is controlled by *F/f* gene [31, 32]. The *F* locus determines the amount of femaleness ($FF > Ff > ff$). Gynoecious sex expression in F_1 hybrid of cross of gynoecious $\times$ monoecious is governed by partial dominance ([33]; Perl-Treves and Rajagopalan [34] where as in gynoecious $\times$ subandroecious, it was governed by multiple genes [35]. single gene with dominant or incomplete dominance [36], single dominant gene [8, 37–39] and oligogene with some modified genes [40], three major QTLs conferring subgynoecy in cucumbers [41]. Seven gynoecious QTLs were detected on chromosomes 5 and 6 in backcross population [42]. These studies suggested that gynoecious is an important economic trait for determinant of earliness and yield in cucumber.

2.3 Parthenocarpy

The discovery of parthenocarpy in cucumber has led to the development of seedless fruit in combination with gynoecious trait. Gynoecy coupled with parthenocarpy is a yield and quality related parameter and a high value vegetable crop suited for protected cultivation because these varieties do not require pollination for fruit setting. The fruits of greenhouse parthenocarpic cucumber varieties are also mild in flavor, seedless and have a thin skin that does not require peeling. Still the genetics of parthenocarpy is not well understood in cucumber which is utmost important for efficient breeding procedure. Pike and Peterson [43]; Kim et al. [44] and Jat et al. [38] suggested that an incomplete dominant gene is responsible for parthenocarpic fruit development. Single recessive gene is responsible for parthenocarpy in cucumber [45]. The growing environmental conditions and epistatic interactions influence the parthenocarpy trait [46, 47] and two additive dominant epistatic major genes and additive dominant polygenes [35]. Seven QTLs for parthenocarpy were detected on chromosome 5 and 7 (*parth5.1* and *parth7.1*) and two on chromosome 6 (*parth6.1* and *parth6.2*) [48]. One major effect QTL (*parth 2.1*) was identified controlling parthenocarpy [49, 50]. The identification of QTLs is a valuable resource for cucumber breeders for development of parthenocarpic cultivars.

2.4 Fruit characters

The improvement in fruit traits including shape, size, and color is an important target in cucumber breeding. The fruit traits like fruit weight, length diameter and

number of fruit per plant are directly related to yield. The other traits like shape index (length: diameter and length/stalk ratio), fruit skin (size of spines, dull or uniform fruit color) and fruit bitterness decides the market value of fruits which are important particularly for slicing cucumber [51]. A single recessive gene controls fragrance in cucumber [52], fruit color traits were controlled by two major genes, single recessive gene, (*w*), was identified that controls white immature fruit color [53], single recessive gene controlled the inheritance of quantity of beta-carotene [54]. Green flesh color is one of the most important and commercial trait of cucumber fruit was controlled by a major effect QTL [55]. The bent characters of the fruit were quantitative inheritance controlled by multiple genes and major genes [56]. Twin fused fruits were controlled by single recessive gene [57]. Two loci controlling fruit bitterness in cucumber [24–26]. The QTLs were also identified in cucumber for several economic traits including fruit spine, skin colors, fruit netting, fruit size, hollow size, flesh thickness variation [58], fruit carpel number, sex expression, fruit length, fruit diameter, fruit shape, fruit number, and powdery mildew resistance [28, 29].

2.5 Inheritance for resistance to diseases

Several diseases infect cucumber which results in huge yield losses in production. The common disease infecting cucumber is powdery mildew, downy mildew, anthracnose, scab, angular leaf spot and virus diseases (cucumber mosaic virus (CMV), papaya ring spot virus, (PRSV), zucchini yellows mosaic virus). The management of these diseases increase the cost of production because of increasing use of chemicals for control of diseases which also has adverse implication on environment and ecology. The development of resistant sources and breeding of resistant varieties are economical, healthier and eco-friendly approach. There are different approaches for breeding resistance against different kinds of stresses which involve both conventional and modern tools. Achieving the goal of development of a resistant variety also needs attention on the durability of resistance for which the knowledge of resistance on the inheritance, expression and interaction with related genes and environment aspects are required.

2.6 Powdery mildew

It is one of the most severe foliar diseases in cucumbers but the inheritance of its resistance still remains unclear which is the major bottle-neck in the development of improved cucumber cultivars. Several fungicides are available to control this disease but their application increases environmental burdens and financial pressures on growers [59]. Therefore, development of the suitable genotypes resistance to powdery mildew is need of the hours. Several resistant cucumber cultivars have been identified, are only resistant to powdery mildew, such as PI 250147 [60], S06 [61], and SSSL0.7 [62]. The resistance in the Puerto Rico 37 variety was controlled by multiple recessive genes [63], PM resistance in the PI 197087 variety was controlled by 1–2 major and 1–2 minor genes [64], one and two recessive genes in PI 2008151 and Natsufushinari, respectively [65], major recessive gene (*s*) and a dominant gene (*R*) and a dominant suppressor gene (*I*) in P1212233 and P123514, [66, 67]. The genetic loci conferring resistance to PM have been gradually identified *pm-1*, *pm-2*, *pm-3* and *pm-h* loci [60]. A dominantly inherited PM resistance gene, *Pm1.1* present in Chinese Long line Jin5–508, which has been mapped. Most resistant cucumber cultivars become susceptible to PM at low temperatures. Collectively, the inheritance of cucumber PM resistance is complex and affected by temperature and region.

2.7 Downy mildew

Understanding the inheritance of downy mildew is fundamental to successful cucumber breeding programs. Downy mildew resistance is controlled by a single recessive gene [68, 69], pair of dominant and recessive interacting genes [70], two recessive genes in PI 197088 and a single recessive gene in 'Poinsett' [71], three recessive genes, *dm-1*, *dm-2* and *dm-3* [72], two incompletely dominant genes [73], inheritance for downy mildew resistance is quantitative [24–26, 74], number of genes, dominant, partially dominant, or recessive are responsible for resistance [75], multiple recessive genes [76]. The cucumber accession PI 197087 from India and its derivatives like Gy14 are resistant to downy mildew that is conferred by *dm-1*. The *dm-1* conferred DM resistant was less effective since 2004 when new DM pathogen strains emerged. The different results for inheritance of downy mildew resistance may be due to some factors like pathogen variability, environmental factors (temperature, relative humidity, inoculum movement etc.), mechanism of resistance and source of resistance. Recently, two major-effect QTLs for resistance to DM strain (*dm4.1* and *dm5.2*) were identified from PI 197088 and PI 330628.

2.8 Virus diseases

Chemical treatments against cucumber mosaic virus (CMV) are not effective; therefore genetic resistance is considered the primary line of defense. Genetic analysis revealed that CMV resistance in cucumber is quantitatively inherited [77] whereas in *Cucumis sativus* var. *hardwickii* (wild relative) is controlled by single recessive gene [78]. The inheritance of resistance to zucchini yellow mosaic virus in cucumber is controlled by single recessive gene (*zmv-1*). The genes resistant to viruses has been mapped on chromosome 6 including *psrv* for PSRV, *wmv* for WMV and *cmv6.1* for CMV [77, 79, 80]. Recently, cucurbit aphid-borne yellows virus (CABYV) has been reported in cucumber from India [81].

3. Traditional breeding

3.1 Traditional breeding objectives and achievements

The development of high yielding cultivars with better fruit quality is the major goal of cucumber breeding programs across the globe. Due to the introgression of gynoeocious sex form in the background of different cucumber market classes, the development of varieties with earliness characters along with high female: male flowers ratio is also an important objective for cucumber breeding. Therefore, rapid advancement has been made in the development of gynoeocious and parthenocarpic cucumber lines/varieties suitable for green house cultivation. Cucumber breeders have developed several genetic stocks for pest and disease resistance. The introgression of pest and disease resistance gene from available sources should be the prime goal for most of the cucumber breeding programmes in future for the development of multiple disease resistance (MDR) varieties including virus resistance. The various fruit quality traits have been selected in cucumber depending on regional preference of the consumers. These quality traits include fruit size, shape (length and diameter), color (light green, dark green), shelf life, seediness and nutritional quality. Cucumber breeders have combined several sex expression and fruit quality genes to develop desirable genotypes. Many pickling cucumber hybrids were developed by crossing gynoeocious lines with monoecious lines. These hybrids are predominantly gynoeocious in nature which provides pollens for fruit set which enhances

total yield in pickling cucumber. Breeding technique for achieving these goals differ among breeders as does his/her definition of quality fruits. Gynoecious sex has also been combined with parthenocary trait to set fruit without pollen particularly for green house cultivation, since it eliminates the need for pollination and produces superior quality fruits. Gynoecious sex expression has been commercially exploited for the hybrid seed production since the female plants do not produce male flowers. Recently, the cucumber breeders have been interested in the development of carotene rich (yellow cucumber) lines. Several cucumber varieties have been developed for early characters, high yield, and resistance to diseases using heterosis breeding. The most commonly used breeding methods for the improvement of cucumber is inbreeding, single plant selection from segregating populations, heterosis breeding and presently marker assisted selection (MAS). The most common breeding procedure followed in cucumber is the selection from a local cultivar. Several F₁ hybrids have been developed in cucumber both from public and private sector through hybridization across the globe. Cucumber is easily grown, indeterminate plant types, offer plenty of large flowers to work with over a long period of time where a large variation is observed for quantitative and qualitative characters. The use of gynoecious lines as one of the parent in breeding programme has made possible to enhance the area under hybrid cultivation. Recent QTL mapping and cloning studies in cucumbers for many quantitative traits will present a complete picture on the genetic architecture of these traits. The identification of molecular markers (SNPs and SSRs) for earliness, yield and quality traits would be directly useful in genome selection to expedite cucumber breeding in different market classes. The cloning of QTLs and genome wide association studies (GWAS) for important quantitative traits will be more innovative and future-focused for trait specific breeding of cucumber.

3.2 Breeding methods

Several breeding methods have been employed for the genetic improvement of cucumber depending on the specific breeding objectives. Single plant selection, single seed descent method, mass selection, simple backcross breeding, pedigree selection, hybridization, use of sex inheritance and chemicals in breeding, and population improvement and extraction of inbred lines are the most common methods used. In recent time, marker assisted selection derived lines have been developed for the improvement of quantitative and qualitative traits in different cucumber market classes. Simple backcross breeding is quite useful for transferring characters governed by single genes e.g. disease resistance or quality traits from donor lines to more stable recurrent parents. Often, six generations of selection and backcrossing to the recurrent parent are required to recover the desired genotypes (recurrent parent + additional trait). Single seed descent method is useful for the development of inbred lines by self pollination. In chemical breeding the gynoecious lines are treated with Silver nitrate/silver thiosulphate to induce hermaphrodite flowers for pollination. The population improvement method is based on recurrent selection and aims at long term gains for the characters having low to moderate heritability. The exploitation of hybrid vigor in cucumber is desirable due to high heterosis for earliness, yield and disease resistance. Heterosis breeding can exploit the genetic diversity present in cucumber for various growth and yield characters. In Western countries almost 90% of the area of cucumber is under F₁ hybrids.

3.3 Heterosis breeding

Cucumber is a monoecious and cross pollinated crop, there is a great scope for exploitation of heterosis. High level of hybrid vigor could be obtained with the

involvement of diverse parents. Several studies have been conducted to identify the best heterotic combination for earliness, yield and quality traits in cucumber. Appreciable heterosis was observed over better parent and top parent for many economic traits like node number of first female flowers, number of fruits per plant, days to fruit set, days to first fruit harvest, yield per plant [82–89]. Significant heterosis has also been reported for earliness characters using gynoecious lines [82, 83, 90] and quality characters [88]. The hybrid combinations of gynoecious × gynoecious and gynoecious × monoecious showed maximum heterosis followed by monoecious × monoecious hybrids for earliness and yield per plant [83, 90]. Therefore yield of the cucumber can be enhanced by using gynoecious line as one of the parent in future breeding programme. Hence breeder should concentrate mainly number of fruits rather than the fruit size to increase yield in cucumber.

3.4 Limitations of traditional breeding

Traditional breeding has the major limitations of its dependency only on selection of traits based on morphological markers (leaf characters, flowering traits including sex ratio, fruit color, fruit size, shape etc.) from a segregating population. Traditional breeding has been effectively utilized for the improvement of qualitative characters. Traits like beta carotene containing cucumbers (linked to orange flesh) and parthenocarpy (linked to seedless) are the classical examples of selection using morphological markers. Traditional breeding has also been exploited for major changes in important quantitative characters including early maturity, fruit size, free from bitterness and fruit yield. Further genetic improvement in quantitative traits using traditional strategies will be more time consuming. For examples, selection for parthenocarpy will be difficult using visual appearance as was done in the past. It is fairly straight forward to select cucumber genotypes containing high beta carotene from a segregating population, but it is difficult to distinguish levels of carotene based on color.

The most effective method for selecting a multiple allele trait is to utilize multiple markers to identify a majority of the alleles. This is especially true to the cucumber crop, which requires a large amount of space to evaluate. However, phenotypic markers will have an intrinsic disadvantage if the trait is influenced by the environmental factors. Development of disease resistance lines are often challenging for cucumber crop. Many disease resistance traits are quantitative; their expression is affected by environmental factors and requires complex inoculation procedure. Cucumber mosaic virus, downy mildew and powdery mildew are the good examples of diseases where development of new cultivar with high level of resistance has thus far proven difficult. Host plant resistance strategy should be utilized for control of these diseases. For these diseases several resistant sources have been identified [91] across the world but these genotypes do not withstand with high disease pressure under multiple locations.

3.5 Rationale for molecular breeding

Molecular markers have the potential to overcoming the limitations of traditional selection methods, since they are non-destructive, eliminate environmental variation associated with disease resistance and can be evaluated for multiple traits simultaneously. However, the molecular breeding requires the development of segregating populations for the traits of interest and the trait must be properly identified during marker identification. Recently, due to the advance technologies of genome sequencing, genome wide association study (GWAS) or Linkage disequilibrium (LD) mapping have gained popularity which is a powerful and alternative

genetic mapping approach for the identification and dissecting important QTL regions which harbor candidate genes of interest in plants [92]. When, GWAS performed on large set of diversity panel, it provides the higher resolution mapping of traits associated variants because it exploits historical recombination events. GWAS study identifies genomic regions harboring loci controlling different traits. The sequencing data will help in the development of desirable genotypes in the form of cultivar which will help the farmers to receive higher returns on their investments. The potential of molecular breeding to save money is in their long term utilization in combination with multiple markers for a wide variety of traits; this will allow cucumber breeder to select for multiple traits from the large populations.

4. Conclusion

Classical genetics and traditional breeding techniques have made great contribution in better understanding and genetic improvement of cucumber crop for several qualitative and quantitative traits, understanding of phylogenetic relationship and taxonomy. Using traditional breeding methods, cucumber breeder have identified a number of genes associated with economic traits and used this information to develop early and high yielding cultivars. Advancement of some quantitative characters using traditional methodology is difficult and time consuming process. Therefore molecular markers technology offers an avenue to overcome the hurdles associated with traditional breeding. Molecular breeding has played a significant role in better understanding of cucumber genetics, and has been directly responsible for some of the improvement made in modern cucumber cultivars in different market classes. Classical breeders have said “Anything is possible using traditional approaches; it is just that the world is not large enough to hold the populations needed to find the variation required for some traits. As we move forward with molecular breeding in cucumber, it is important that we understand the need to maintain traditional breeding programs, and that the skill set required for classical breeding is not lost.

Conflict of interest

The authors declare no conflict of interest.

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