Breeding for Climate Resilient Parthenocarpic Vegetables

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A B S T R A C T

The development of fruits without fertilization is known as parthenocarpy. Parthenocarpy improves the fruit quality, processing attributes, production and productivity of vegetable crops like tomato, cucumber, watermelon etc. Absence of seeds can enhance the shelf life of the fruits, allowing a better conservation, fruit set in adverse climatic conditions, early and off-season production of vegetable crops. Therefore, it is important to ensure yield stability regardless of environmental conditions. Breeding of new cultivars with the ability to develop fruits without pollination or any artificial stimuli is a promising approach. Parthenocarpic vegetables can be natural or can be induced artificially by various methods like, use of plant growth regulators, distant hybridization, mutation, use of irradiated pollen, alternation in chromosome number, gene silencing, gene modifications and genome editing tools. Therefore, present review is focused on genetics, nature of gene action, mapping of QTLs and various breeding methods to induce parthenocarpy in vegetable crops.

Key words
Chromosomal Changes, Genome Editing Tools, Growth Regulators, Parthenocarpic, Vegetables

Introduction

The development of fruits without fertilization is known as parthenocarpy. A plant is known to be parthenocarpic plant when its fruits are completely devoid of seeds or contain a very minute number of seeds or present aborted seeds. Consumers appreciate the seedless fruits by both in fresh consumption (e.g., watermelon, grape, citrus and banana) as well as in processed fruits (e.g., frozen eggplant, tomato sauce) (Pandolfini, 2009). Seedless fruits can be obtained through parthenocarpy and by stenospermocarpy (seeds abort after fertilization) (Voraquaux et al., 2000). Pollen production activity is very sensitive to temperature in most of the vegetable crops including tomato. It requires a narrow range of temperature for pollination (i.e.30°C–35°C/15°C–21°C day/night). Severianin is a parthenocarpic cultivar of tomato which produces a higher yield and fruit set in colder temperatures (night temperature, 12°C) than seeded cultivars (Hassan et al., 1987). In bell pepper, there is a blossom drop, if day temperature is 33°C or above or night temperature remain above 26.5°C or drop below 10°C. Brinjal require long and warm
temperature (17-25°C) for better growth and yield. If temperature falls below 17°C vegetative growth is arrested and pollen deformity at bud stage occurs. High temperature stress (35/20°C day/night) during anthesis in common bean reduces pollen germination, pollen tube growth, fertilization, pod and seed set.

In cucurbits viz., cucumber, gherkin, pumpkin, summer squash, musk melon, water melon and bitter gourd pollination and fruit set take place at optimum temperature range of 13-18°C. On the other hand, fruit set in bottle gourd and ridge gourd takes place relatively at higher temperature (above 25°C). Therefore, parthenocarpy could be potentially utilised for production of several vegetable crops in winter months (Tomes, 1997) or more generally, to ensure yield stability in case of unfavourable pollination conditions.

Moreover, it has been observed that seed development in fruits restricts the marketable yield in cucumber (Tiedjens, 1928; Denna, 1973) and tomato (Falavigna and Soressi, 1987). In the case of brinjal, the absence of seeds avoids browning and texture reduction of the pulp (Maestrelli et al., 2003). Some of the desirable quality parameters of parthenocarpic vegetables compare to seeded vegetables mentioned in Table 1. Furthermore, seeds can produce substances that accelerate the deterioration of the fruit (watermelon and eggplant). In this regard, the absence of seeds can enhances the shelf life of the fruits, allowing a better conservation. Parthenocarpy can be exploited for increasing winter and early production of horticultural crops (Ficcadenti et al., 1999 and Acciarri et al., 2002); there by increases the availability of horticultural products round the year. In addition, low temperatures during winter and early spring decreases the amount of fertile pollen. These factors reduce yields and fruit quality and delayed harvest due to lengthen the cultivation period. Green house cultivation of cucurbits (summer squash) not only allows offseason production but also protects from virus infestation.

The most important consideration during greenhouse cultivation is selection of variety and it should have ability to set fruits parthenocarpically. Much variation for parthenocarpic tendency has been observed in Cucurbita pepo (zucchini) germplasm (Martinez et al., 2014). Therefore, it is important to maintain fruit production regardless of environmental conditions. Breeding of new cultivars with the ability to develop fruits without pollination or any artificial stimuli is a promising approach (Yoshioka et al., 2018).

Rotino et al., (1999) suggested the ideotype of parthenocarpic trait, to improve the productivity of vegetable crops, has to satisfy the following three features: 1) production of marketable fruits without pollination, 2) percentage of fruit setting under adverse conditions is similar to that obtained under favourable growth conditions and 3) phenotypic expression of the trait should not display any negative effect on both intrinsic and extrinsic fruit quality. In addition to these three traits 4) multi-pistillate parthenocarpic (eg. cucumbers) is also most productive trait which has to be exploited at commercial level. C. pepo subsp. texana produce more than one female flower bud per leaf axil, introgression of this trait into cocozelle and zucchini germplasm and could result in increased yields (Paris, 2010).

Advantages of parthenocarpic vegetable crops

1. Stability in production and productivity as pollination and fertilization were adversely affected by environmental stresses like low/high temperatures but parthenocarpic
vegetables does not require pollination and fertilization to set fruits.

2. Consumer acceptance will increases - parthenocarpic cucumber, seedless water melon and seedless pickled gherkin (Baker et al., 1973).

3. Novelty- seedless tomato, parthenocarpic cucumber and seedless water melon.

4. Improved quality and shelf life in brinjal as seeds are associated with bitter ness of fruit (Dalal et al., 2006).

5. Improved taste, high TSS - seedless tomato (Falavigna, et al., 1978; Lukyanenko, 1991).

6. Increase profitability for processing industries- seed less tomato (Lukyanenko, 1991)

7. Vertical fruit harvest- by growing of parthenocarpic cucumbers in green houses, continuous fruit set on vine will give more profits. This will cut down the cost and time to spend on pollen vibrators and manual pollination as these are necessary in green house grown vegetables.

8. No effect of “crown set inhibition” in parthenocarpic cucumbers so, fruits are continues.

9. Early yielder- parthenocarpic cucumbers.

10. Avoid the horizontal gene transfer, as major problem in transgenic approval (Varoquaux et al., 2000).

11. Protect genetically modified crops: linking a transgene with seedlessness would prevent unfair appropriation of the transgene by simply crossing the transgenic plant with another commercial variety (Varoquaux et al., 2000).

Majorly parthenocarpic vegetables can be broadly divided based on nature of their origin in to two types’ i.e. natural parthenocarpy and artificial induction of parthenocarpy.

**Natural parthenocarpy**

Naturally coccinia and some genotypes of cucumber produce seedless fruits.

**Artificial induction of parthenocarpy**

1. Use of plant growth regulators
2. Distant hybridization
3. Mutation
4. Use of irradiated pollen
5. Alternation in chromosome number
6. Gene silencing
7. Gene modifications
8. Genome editing tools

**Use of plant growth regulators**

The exogenous applications of plant growth hormones, like auxins, cytokinins and GAs, can influence many processes in plant growth and development. Application of these plant growth hormones may leads to development of parthenocarpic fruits in vegetable crops (Table 2).
Distant hybridization

Intraspecific hybridization have been utilized for producing a facultative parthenocarpic line suitable for a hot and dry climate (normal fruit at moderate temperature) was first introduced in tomato (Hawthorn, 1937). Different facultative parthenocarpic tomato lines/cultivars developed through distant hybridization mentioned in Table 3. After that, various other parthenocarpic lines have been generated by using intraspecific hybridization e.g. Severenien, Oregon T5-4, Oregon Cherry, Oregon 11, Line 75/79, Line P-26, Line P-31, Line RG and IVT-line 2 in tomato (Baggett and Frazier, 1978; Philouze and Maisonneuve, 1978; Zijlstra, 1985) and ‘AE-P’ lines and ‘Talina2/1’ in eggplant (Kikuchi et al., 2008). Obligate parthenocarpy in aneuploid tomato developed from a cross between *Solanum esculentum* and *S. peruvianum* (Lesley and Lesley, 1941), IVT-line 1 was developed from a cross between *S. habrochaites* and *S. lycopersicum* (Zijlstra, 1985). Altered ploidy through interspecific hybridization is a common approach to obtain parthenocarpic fruits in various crops such as banana, watermelon and citrus (Fortescue and Turner, 2005). Afful *et al.*, (2018) crossed three wild relatives of brinjal with seven cultivated accessions and the crosses, SA002-02 × *Solanum tovum* and SMA003-03 × *Solanum tovum* devoid of seeds (parthenocarpic). This may be attributable to allelic incompatibility at fertilization (Behera and Singh, 2002). Singh (1978) reported the induction of parthenocarpary in *Momordica dioica* (spine gourd) and *Tichosanthes dioca* (pointed gourd) with pollen of related taxa (*M. charantia* and *Lagenaria leucantha*) and the parthenocarpic fruit setting was higher with the pollen mixture of these two *sps.* (66% against 36% in *M. dioica*), (85% against 58% in *T. dioca*) compared to natural pollination. Some cowpea lines developed from wild × cultivated crosses have also been discovered to be parthenocarpic. Emasculated, unpollinated flowers on these lines do not abscise but produce seedless pods. Mature parthenocarpic pods are of normal size but contain only small shrivelled and poorly developed 'seed'. The 'seeds' within a single pod typically differ in size and apparent stage of development and are strongly attached to the pod. This suggests that partial development of some ovules occurs (Ehlers and Hall, 1997).

Mutation

Spontaneous mutations occur naturally and are used in classical breeding programmes. Good example of this is the parthenocarpic sha-pat mutants in the tomato line ‘Montfavet 191’ (Pecaut and Philouze, 1978). Various radiation treatments, such as helium accelerated ions in tomato (Masuda *et al.*, 2004), soft–X-ray in watermelon (Sugiyama and Morishita, 2000; Kawamura *et al.*, 2018) and gamma irradiation in *Citrullus lanatus* (Sugiyama and Morishita, 2001) have been used successfully to generate parthenocarpic mutants. Alkylating agents (EMS and EES) has been used to generate parthenocarpic mutants of Arabidopsis (fwf) and tomato (stock 2524; short anther mutant, sha) (Bianchi and Soressi, 1969; Soressi, 1970; Vivian-Smith *et al.*, 2001).

Use of irradiated pollen

As parthenocarpy concern, the major advantage of using soft X-ray irradiated bottle gourd pollen is production of seedless watermelon (*Citrullus lanatus*) with diploid cultivars. When the pollen of bottle gourd was used to pollinate pistillate watermelon flowers, the rate of fruit set was 57.1% (with watermelon pollen 65.0%). All parthenocarpic fruits produced by pollination with bottle gourd pollen were deformed (triangular or oblong shaped) however, fruit weight, rind
thickness, flesh color and Brix in the parthenocarpic fruit were almost the same as control fruit. There were no normal seeds except for small, white empty seeds in the fruit obtained from pollinating with bottle gourd pollen. Bottle gourd pollen tubes did not reach the ovules of watermelon ovaries. Therefore, it was concluded that parthenocarpy resulting from pollination with bottle gourd pollen was stimulative parthenocarpy, not pseudo parthenocarpy (pseudogamy) (Sugiyama et al., 2014).

Another interesting study revealed the mechanism behind the production of seedless watermelon fruits after pollinating with soft X-ray (600 Gy) irradiated pollen of watermelon. The results indicated that, soft X-ray irradiation did not damage the cell walls of the watermelon pollen and leading to normal pollination and fertilization. However, the chromosomal double helix of the watermelon pollen were damaged, thereby inhibiting embryotic developmental processes, leading to abortion of the embryo and degeneration of endosperm, which lead to the production of seedless watermelon (Qu et al., 2016).

**Alteration in chromosome number**

Unbalanced development of embryo and endosperm in triploid background has been utilized to yield parthenocarpic fruit. In watermelon seedless fruits with only residual integuments are obtained from F1 hybrid plants derived from cross between tetraploid and diploid parents (Kihara, 1951). Chromosome elimination in wide crosses may lead to the production of haploids, which are of enormous interest to the breeders. Haploid formation following interspecific hybridization is usually interpreted as parthenogenesis (Rowe 1974). Some of the parthenocarpic vegetables associated with various ploidy levels mentioned in Table 4.

**Gene silencing**

Parthenocarpy in cucumber may be promoted by a ‘parallel switch,’ namely, hormone dependent and hormone independent pathways. During hormone independent parthenocarpy, fruit set was promoted by hormone insensitive regulatory proteins, such as the NP-specialized proteins in ‘EC1.’ In the presence of sufficient hormones, young fruits formed through both hormone dependent and independent pathways could continuously grow to maturity. In the absence of hormones, the development of hormone sensitive fruits proceeds to fruit abortion, whereas the hormone insensitive fruits remain in a dormant state because of the increasing expression of abortion inhibiting proteins. However, the expansion of dormant fruits and their further promotion are unknown. Although the accurate regulation of parthenocarpy in cucumber remains unclear, Li et al., (2017) provide a theoretical framework for understanding the mechanism of parthenocarpy for its application in agricultural production.

**Gene modifications**

Auxin, gibberellin and cytokinins or mixtures of these hormones have all been proven to be effective in inducing fruit development in the absence of fertilization in several crop species, for instance tomato and eggplants (Gillaspy et al., 1993). The role of plant hormones in fruit set and genetic methods for obtaining seedless fruits by manipulating hormones action extensively reviewed by Pandolfini (2009). Martinez et al., (2014) observed the parthenocarpy of zucchini accessions is associated with down regulation of ethylene production in unpollinated fruits during the first days post anthesis (DPA) especially at 3 DPA.
Biotechnology offers a wide range of opportunities and easier ways of obtaining parthenocarpic varieties than conventional breeding (Rotino et al., 1997 and Varoquaux et al., 2000). The processes of seed and fruit development which are intimately connected and synchronized, are controlled by phytohormones (Gillaspy et al., 1993). The regulatory region(s) of the gene represents the most important genetic information to control temporal and spatial expression of the gene of interest. These two parameters are relevant both to obtain parthenocarpy and to ensure an optimal expressivity of the parthenocarpic trait without affecting the vegetative plant growth. An excess or a defect in the expression of a phytohormone-synthetizing gene might cause the development of morphologically altered parthenocarpic fruits or an inefficient fruit set and growth, respectively (Falavigna and Rotino, 2006). Transgenic approach, gene silencing by RNA interference (RNAi) and by antisense RNA technology are powerful tools to interfere with the expression of genes. Rotino et al., (1997) reported that, transgenic tobacco and eggplants containing the DefH9-iaaM transgene produce parthenocarpic fruits in the absence of pollination and that seeds are generated inside the fruit following pollination. Parthenocarpy has also been achieved in transgenic tomato plants carrying the DefH9-iaaM construct (Ficcadenti et al., 1999 and Pandolfini et al., 2002). The parthenocarpy produced by the introduction of the DefH9-iaaM construct is facultative. Carmi et al., (2003) also obtained parthenocarpy in tomato via specific expression of the rolB gene in the ovary. Here some of the examples are quoted for parthenocarpic fruit development by genetic modifications (Table 5).

**Genome editing tools**

Genome editing technologies include TALENs, ZFNs and CRISPR/Cas9. CRISPR/Cas9 system is the most popular among the genome editing technologies. The site-directed genome modification has been realized through development of sequence-specific nuclease based technologies that include Zinc Finger Nucleases (ZFNs) (Kim et al., 1996), Transcriptional Activator-Like Effector Nucleases (TALENs) (Bogdanove and Voytas, 2011) and most recently, Clustered Regulatory Interspaced Short Palindromic Repeat (CRISPR) Associated Protein System (CRISPR/Cas9) (Doudna and Charpentier, 2014). For rapid development of new parthenocarpic vegetable cultivars is possible only through CRISPR/Cas9 (Table 6).

**Genetics of parthenocarpy**

In several species, the mode of inheritance for parthenocarpic fruit set has been observed and it varies from a single gene to multiple quantitative trait loci (QTLs) (Table 7). In tomato (Lycopersicum esculentum L.) the following genes have been identified which are able to sustain the parthenocarpic traits: pat, pat-2, pat-3, pat-4 (Philouze 1983). However study lead to the conclusion that pat-2 gene plays the major role and mp gene, in the homozygous state, influences the phenotypic expression of pat-2 in both homozygous and heterozygous states (Vardy et al., 1989). In eggplant, a genetic tendency to parthenocarpy seems to be controlled by few genes with additive effect (Hennart, 1996). Cucumber is one of the plant species where parthenocarpic mutants have been more intensively used to breed cultivars for greenhouse cultivation. The parthenocarpic trait appears to be controlled by a single gene (Pa) expressing incomplete dominance and by modifier genes (Pike and Peterson, 1969). The segregation of F2 population and test crosses for parthenocarpic fruit development suggested that parthenocarpy in gynoeicous and parthenocarpic cucumber line is under the control of incomplete dominant gene (Jat et al., 2017).
Table 1: Quality parameters of parthenocarpic vegetables compare to seeded one

| Crop         | Parthenocarpic                                                                 | Reference          |
|--------------|-------------------------------------------------------------------------------|--------------------|
| Watermelon   | The shape, flavour and yield are as good as seed-producing cultivars and have a longer shelf life | Kihara, 1951      |
| Watermelon   | No significant differences in sugar contents between seeded and seedless watermelon | Kawamura et al., 2018 |
| Cucumber     | Total sugar content of parthenocarpic fruits to be significantly lower than that of the pollinated fruits, with significant negative effects in the sweet taste of fruit | Li et al., 2014 |
| Gherkin      | Seedless pickled gherkins are more crunchy, firmer and fleshier than its seeded variety | Baker et al., 1973 |
| Tomato       | Seedless tomato fruits are tastier, more dry-matter (up to 1%), contain more sugars less acidity and less cellulose | Lukyanenko, 1991 |
| Tomato       | More soluble solids                                                           | Falavigna, et al., 1978 |
| Tomato       | The fruit size, morphology and jelly fill in the locules of seedless fruits were comparable with seeded fruits of the parental line | Carmi et al., 2003 |
| Eggplant     | High yield and fruit quality                                                  | Donzella et al., 2000 |
| Sweet pepper | Parthenocarpic fruit growth reduces yield fluctuation and blossom-end rot (BER) | Heuvelink and Körner, 2001 |

Table 2: Use of plant growth regulators for parthenocapic fruit development

| Crop         | Growth regulator                               | Stage of treatment | Types of parthenocarpy                                      | Reference                      |
|--------------|-----------------------------------------------|--------------------|-------------------------------------------------------------|--------------------------------|
| Brinjal      | GA₃ @ 2700 ppm; 2-4-D @ 2.5 ppm               | Foliar spray/cut end styles at freshly opened flower stage | GA₃ induced the completely seedless fruits during all seasons. 2,4-D, induced the development of degenerated seeds | Nothmann and Koller, 1975 |
| Kokrol       | 2-4-D/2-4-5-T @ 100 mg/L                      | Pre-anthesis sprays | Complete parthenocarpy                                      | Vijay and Jalikop, 1980        |
| Kokrol       | 2, 4-D @ 50 ppm                               | At the time of anthesis | 90.0% parthenocarpy                                        | Chowdhury et al., 2007         |
| Cucumber     | GA @ 100 mg/L                                 | Pre-anthesis sprays | Complete parthenocarpy                                      | Choudhury and Phatak, 1958     |
| Pickling cucumber | Methylester chlorflurenol (Morphactine) @ 100 ppm | 3 weeks after flowering | Parthenocarpy (13 fruits per plant and 23g each fruit wt.) | Wiebosch and Berghoef, 1974 |
| Bottle gourd | CPPU @ 10–100 mg/L                            | 2 days before or after anthesis | Complete parthenocarpy                                      | Jing, 1999                     |
| Watermelon   | CPPU @ 0.5 mL/L                               |                    | parthenocarpy                                               | Kawamura et al., 2018          |
| Pumpkin      | GA₃ @ 150 ppm                                 |                    | 96.9% seedless                                              | Sharif Hossain, 2015           |
| Muskmelon    | CPPU @ 10 mg/L and BA                         |                    |                                                              | Hayata et al., 2000            |
Table 3: Development of facultative parthenocarpy in tomato by distant hybridization

| Parthenocarpic line/cultivar | Cross involved                                                                 | Reference                                      |
|-----------------------------|---------------------------------------------------------------------------------|------------------------------------------------|
| **Line RP75/79**            | Multiple cross Atom × Bubjekosoko and Heinemanns Jubilaum × Priora (developed by R. Reimann-Philipp) | Philouze and Maisonneuve 1978                  |
| **Severianin**              | *L. esculentum* and *L. hirsutum* (bred by N. Soloviova)                       | Philouze and Maisonneuve 1978; Lin et al., 1984 |
| **P-26, P-31, etc.**        | *L. esculentum* and *L. pennellii*                                              | Stoeva et al., 1985                           |
| **Line RG**                 | *L. esculentum* and *L. cheesmanii* var. minor                                   | Mikhailov and Georgiev 1987                    |
| **IVT 1**                   | *L. esculentum* and *L. hirsutum*                                               | Zijlstra 1985                                  |
| **IVT 2**                   | *L. esculentum* and *L. peruvianum*                                             | Zijlstra 1985                                  |

Table 4: Parthenocarpic vegetables associated with various ploidy levels

| Vegetable   | Species                              | Other changes                        | Ploidy no.             | reference                                        |
|-------------|--------------------------------------|--------------------------------------|------------------------|--------------------------------------------------|
| **Tomato**  | *Solanum esculentum* (2n = 2x = 24)  | Increase dry matter, TSS            | Triploid (2n = 3x = 36) | Habashy et al., 2004; Mackiewicz et al., 1998    |
| **Tomato**  | *Solanum esculentum* (2n = 2x = 24)  |                                       | Aneuploid              | Lesley and Lesley 1941                           |
| **Cucumber**| *Cucumis sativus* (2n = 2x = 14)     | (Amphidiploid × Diploid)             | Triploid (2n = 3x = 21) | Chen et al., 2003; Habashy et al., 2004; Mackiewicz et al., 1998 |
| **Cucumber**| cv. “Butchers Disease Resisting” (BDR) (2n = 4x = 28) 0.2% colchicine treatment |                                    | Autotetraploid (2n = 4x = 28) | Grimbly, 1973                                   |
| **Watermelon**| *Citrullus lanatus* (2n = 22) (Autotetraploid × Diploid) | High sugar content, more fruits per plant and thin rind | Triploid (2n = 3x = 33) | Kihara, 1951                                    |
Table 5 Seedless fruit production by gene silencing, transgenic and RNA interference approaches

| Gene       | Function         | Gene modification                          | Crop                                           | Reference                                                                 |
|------------|------------------|--------------------------------------------|------------------------------------------------|---------------------------------------------------------------------------|
| DeH9-iaaM  | Auxin synthesis  | Ovule Specific transgene expression        | Tobacco, eggplant, tomato, raspberry, cucumber. | Rotino et al., 1997; Pandolfini et al., 2002; Yin et al., 2006; Mezzetti et al., 2004 |
| SEP1/TM29  | Cytokinin        | Antisense or cosuppression; MADS-box       | Tomato                                        | Ampomah-Dwamena et al., (2002)                                            |
| rolB       | Auxin response   | Ovary/ Fruit Specific transgene expression | Tomato                                        | Carmi et al., 2003                                                        |
| SIIA9      | Auxin signaling  | Antisense down regulation                  | Tomato                                        | Wang et al., 2005                                                         |
| AtARF8     | Auxin signaling  | Expression of Mutant AtARF8-4 gene         | Tomato                                        | Goetz et al., 2007                                                        |
| SIDElla    | Gibberellin signaling | Antisense down regulation                  | Tomato                                        | Marti et al., 2007                                                        |
| SlChs      | Flavonoid biosynthesis | RNAi-mediated silencing                   | Tomato                                        | Schijlen et al., 2007                                                     |
| SITPRI     | Ethylene signaling | Over expression                           | Tomato                                        | Lin et al., 2008                                                          |
| SlARF7     | Auxin signaling  | RNAi-mediated silencing                    | Tomato                                        | De Jong et al., 2009                                                      |
| AUCSIA     | Auxin response   | Gene silencing                             | Tomato                                        | Molesini et al., (2009)                                                   |
| PIN-4      | Auxin            | RNAi                                       | Tomato                                        | Mounet et al., 2012                                                       |
| GA20OX     | Gibberellic acid | Overexpression                             | Tomato                                        | García-Hurtado et al., (2012)                                             |
| ARFs       | Auxin response   | RNA interference                           | Brinjal                                       | Du et al., (2016)                                                         |
| IAA        | Auxin            | Differential expression found in natural parthenocarpic mutant | Brinjal                                       | Chen et al., (2017)                                                       |
| amiSlARF5  | Auxin signaling  | m RNA down regulated                      | Tomato                                        | Liu et al., 2018                                                          |

Table 6 Developing parthenocarpic tomato using CRISPR/CAS-9

| Plant Species | Target genes           | Editing tool  | Phenotype                                                                 | Reference |
|---------------|------------------------|---------------|--------------------------------------------------------------------------|-----------|
| Tomato        | AGL6, AGAMOUS-like     | CRISPR-Cas9   | Parthenocarpic phenotype. Seedless fruits with normal weights and shapes under heat stress conditions were set. | Klap et al., 2017 |
| Tomato        | IAA9, auxin-induced 9  | CRISPR-Cas9   | Enhancement of parthenocarpic phenotype and change in leaf shape.        | Ueta et al., 2017 |
**Table 7 Genetic inheritance of parthenocarpy in vegetable crops**

| Vegetable          | Gene/QTL                                           | Reference                                      |
|--------------------|----------------------------------------------------|------------------------------------------------|
| Tomato             | Several single-gene recessives                     | Fos *et al.*, 2001; Gorguet *et al.*, 2005     |
| Tomato (cv. Carobeta) | One recessive                                     | Georgiev and Mikhailov (1985)                  |
| Tomato (cv. IVTI)  | One recessive                                      | Zijlstra (1985)                                |
| Tomato (cv. OregonT5-4) | Two recessive genes, complementary gene pairs        | Kean and Baggett (1986)                       |
| Tomato (cv. RP 75/59) | At least three recessive genes                     | Philouze (1989)                                |
| Tomato (cv. MPK-1) | Semi dominant gene (Pat-k) on chromosome-1         | Takisawa *et al.*, 2017                        |
| Tomato (cv. MPK-1) | Only one major QTL, qpat1.1 for PL on chromosome 1 | Takisawa *et al.*, 2018                        |
| Pepino (Solanum muricatum) | Single dominant gene                               | Prohens *et al.*, 1998                         |
| Brinjal             | single major gene                                  | Yoshida *et al.*, 1998; Kuno and Yabe, 2005    |
| Brinjal             | Oligogenically and dominantly inherited            | Daunay *et al.*, (2001)                        |
| Brinjal             | polygenic recessive and strongly dependent on epistatic effects | Tian ShiBing *et al.*, (2003)                  |
| Brinjal             | Two major-effect QTLs                             | Miyatake *et al.*, 2012                        |
| Capsicum annum      | Single recessive gene                              | Tiwari *et al.*, 2011                          |
| Cucumber            | single incompletely dominant gene Pc               | Pike and Peterson 1969                         |
| Cucumber            | Single recessive gene                              | Hawthorn and Wellington, 1930; Meleshchero and Juldasheva, 1974 |
| Cucumber            | Many incompletely recessive genes                  | Kvasnikov *et al.*, (1970)                     |
| Cucumber            | Three independent major genes with equal additive action | de Ponti and Garretsen (1976)                  |
| Cucumber            | Quantitative trait controlled by two major genes and polygenes | Yan *et al.*, 2008 & 2010                     |
| Cucumber            | Two major additive-dominant-epistatic genes and additive-dominant polygene | Yan *et al.*, 2010                            |
| Cucumber            | Seven QTLs with a major-effect QTL, parth2-1 in chromosome 2. | Wu *et al.*, 2015                             |
| Cucumber            | A major-effect QTL Parth2.1 and six minor-effect QTLs | Wu *et al.*, (2016)                           |
| Processing cucumber | Seven QTLs, parth7.1 early parthenocarpic fruit set. | Lietzow *et al.*, 2016                        |
| Summer squash (cv. Whitaker) | Single gene with incomplete dominance             | de Menezes *et al.*, 2005                     |
| Muskmelon           | Recessive genes                                    | Yoshioka *et al.*, 2018                        |
### Table 8: Molecular markers and mapping of parthenocarpy

| Crop       | Gene/QTL     | Type, Number of Markers and Population | Flanking Marker and Distance and Chromosome Number | Reference                        |
|------------|--------------|----------------------------------------|---------------------------------------------------|----------------------------------|
| Cucumber   | A major-effect QTL Parth2.1 and six minor-QTLs | SSR 133 (total 1335) and InDel 9 (total 173). EC1 × 8419 s-1 cross, 145 F_{2:3} population. | Seven novel QTLs were identified on chromosomes 1, 2, 3, 5 and 7. Parthenocarpy 2.1 (Parth 2.1), a QTL on chromosome 2, was a major-effect QTL (flanking markers SSR00684-SSR22083). | Wu et al., (2016) |
| Cucumber   |              | Ten QTLs associated with parthenocarpy distributed across four genomic regions as well as eight linked AFLP markers in cucumber. |                                                   | Sun et al., 2006b |
| Tomato     | Pat          | Localized on the long arm of chromosome 3. |                                                   | Beraldi et al., 2004 |
| Tomato     | pat4.1, pat9.1 and pat5.1 | *S. habrochaites* LYC4, *S. lycopersicum* cv. Moneymaker; Two BC5S1 populations (174 & 183 plants), CAPS and SCAR markers | F2 population (160 plants); IVT-line 1, *S. lycopersicum* cv. Moneymaker. | Gorguet et al., 2008 |
| Eggplant   |              | F2 populations (135 and 93) derived from intraspecific crosses between two non-parthenocarpic lines (LS1934 and Nakate-Shinkuro) and a parthenocarpic line (AE-P03). (324 SSR; 630 SNP) | Two QTLs on chromosomes 3 and 8, which we denoted as Controlling parthenocarpy3.1 (Cop3.1) and Cop8.1, respectively | Miyatake et al., 2012 |
**Fig. 1** Breeding programme applied to select the parthenocarpic pickling cucumber lines (De Ponti, 1976)

**Fig. 2** Development of parthenocarpic tropical gynoecious lines in cucumber (More and Budgujar, 2002)
Molecular markers and mapping of parthenocarpy

The first attempt of mapping of parthenocarpy gene, \textit{pat}, in tomato was done by Beraldi \textit{et al.}, (2004). Recently, four QTLs associated with parthenocarpy were identified and mapped in tomato (Gorguet \textit{et al.}, 2008). The isolation of these QTLs will enhance not only our understanding about fruit set in tomato but also open possibilities to develop seedless fruits in other economically important species solanaceous vegetable crops. Intraspecific linkage map in eggplant for parthenocarpy was developed (Barchi \textit{et al.}, 2010). Quantitative trait locus (QTL) analysis of eggplant by using co-dominant simple sequence repeat and single nucleotide polymorphism markers revealed that two QTLs on chromosomes 3 and 8, which are controlling parthenocarpy 3.1 (Cop3.1) and Cop8.1, respectively (Miyatake \textit{et al.}, 2012). Using these maps, attempts at map-based cloning have been made, and parthenocarpy causing genes may soon be isolated. We mentioned the markers and QTLs of major parthenocarpic vegetables in Table 8.

Breeding methods to develop parthenocarpic vegetables

Parthenocarpy can have a genetic basis or it can be artificially induced. Genetic parthenocarpy is called obligatory when the expression of the parthenocarpy trait is not influenced by external factors and facultative if it occurs only under conditions adverse for pollination and fertilization. Artificially induced parthenocarpy can be observed in several plant species by treating flowers with plant growth factors or by pollination with incompatible pollen or X-rays irradiated pollen (Falavigna and Rotino, 2006). The parthenocarpic trait can be transferred to new types with a few backcrosses from a donor line (Sun \textit{et al.}, 2006a). Breeding of parthenocarpic vegetables and incorporation of additional desirable gene along with parthenocarpy through conventional breeding methods will take very long time and also tedious (Fig. 1 and 2). Using of advanced breeding methods like MAS will enhance the accuracy and rapid advancement of generation and genome editing tools like CRISPR/Cas9 is very recent trending technique following for fast breeding of parthenocarpic vegetables.

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