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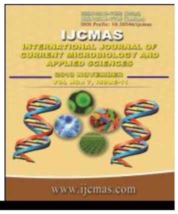

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Breeding for Climate Resilient Parthenocarpic Vegetables

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ABSTRACT

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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 enhances the shelf life of the fruits, allowing a better conservation, fruit set in adverse climatic conditions, early and offseason 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.

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., water melon, 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^{o}C–35^{o}C/15^{o}C–21^{o}C (day/night). Severianin is a parthenocarpic cultivar of tomato which produces a higher yield and fruit set in colder temperatures (night temperature, 12^{o}C) than seeded cultivars (Hassan *et al.*, 1987). In bell pepper, there is a blossom drop, if day temperature is 33^{o}C or above or night temperature remain above 26.5^{o}C or drop below 10^{o}C. Brinjal require long and worm 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.

Naturalparthenocarpy

Naturally coccinia and some genotypes of cucumber produce seedless fruits. Parthenocarpy is also regulated by environmental factors. Low temperature (freezing temperature ≤ 5°C)in bell pepper causes the parthenocarpic fruit development.Breeders started to use natural parthenocarpy at the end of the 1980’s in brinjal (Prohens and Nuez, 2008). This trait is facultative as it is expressed only in cold conditions; as soon as the temperatures are favourable to pollination, normal fruit and seed set occurs. According to Fuzhong *et al.*, (2005) the temperatures that induce parthenocarpy range from 7 to 10°C in brinjal. The elimination or cut of the stigmas of flowers bud is an easy way for getting the expression of parthenocarpy during a breeding process (Daunay, 1981/82; Fuzhong *et al.*, 2005). Manik *et al.*, (2000) investigated parthenocarpic fruiting behavior and fruit characteristics in different kakrol genotypes and concluded that only 'Rangpuri' genotype produced parthenocarpic fruits naturally with high number of flowers per plant, less vegetative growth, successive bearing of fruits and longer harvesting period.

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 parthenocarpy 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 F_1 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 F_2 population and test crosses for parthenocarpic fruit development suggested that parthenocarpy in gynoecious 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	GA_3 @ 2700 ppm; 2-4-D@2.5 ppm	Foliar spray/cut end styles at freshly opened flower stage	GA_3 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 @100mg/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@100mg/L	Pre-anthesis sprays		Choudhury and Phatak, 1958
Pickling cucumber	Methylester chlorflurenol (Morphactine) @ 100ppm	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
Water melon	CPPU @ 0.5 mL/L		parthenocarpy	*Kawamura et al.*,2018
Pumpkin	GA_3 @ 150 ppm		96.9% seedless	Sharif Hossain, 2015
Muskmelon	CPPU @ 10mg/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	*Solanaum esculentum* (2n = 2x = 24)	Increase dry matter, TSS	Triploid (2n = 3x = 36)	Habashy *et al.*, 2004; Mackiewicz *et al.*, 1998
Tomato	*Solanaum 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 co-suppression; MADS-box	Tomato	Ampomah-Dwamena *et al.*, (2002)
rolB	Auxin response	Ovary/ Fruit Specific transgene expression	Tomato	Carmi *et al.*, 2003
SlIAA9	Auxin signaling	Antisense down regulation	Tomato	Wang *et al.*, 2005
AtARF8	Auxin signaling	Expression of Mutant AtARF8-4 gene	Tomato	Goetz *et al.*, 2007
SlDELLA	Gibberellin signaling	Antisense down regulation	Tomato	Marti *et al.*, 2007
SlChs	Flavonoid biosynthesis	RNAi-mediated silencing	Tomato	Schijlen *et al.*, 2007
SlTPR1	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 CRISPAR/CAS-9

Plant Species	**Target genes**	**Editing tool**	**Phenotype**	**Reference**
Tomato	AGL6, AGAMOUS-like	CRISPR-Cas9	Parthenocarpic phenotype. Seedlless 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.* IVTl)	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; Meshcherov 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, pat9.1and 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)

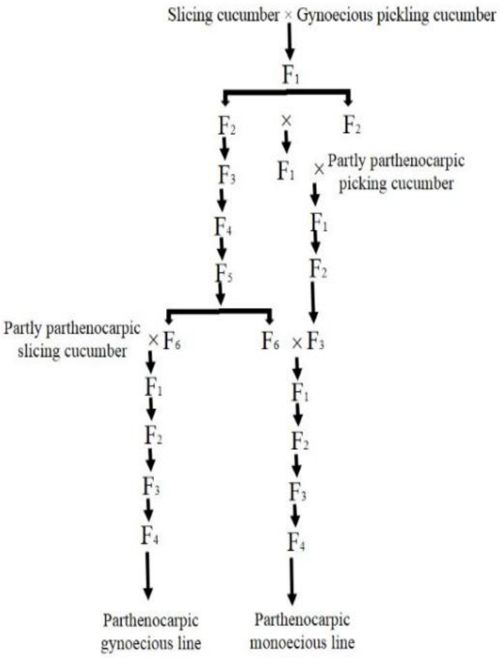
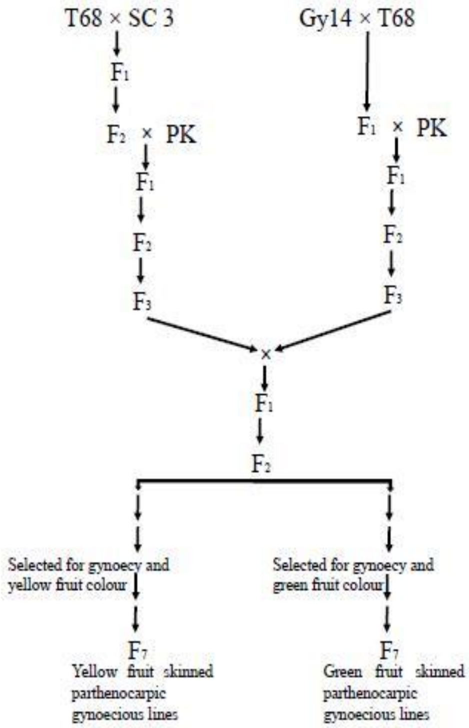


Fig.2 Development of parthenocarpic tropical gynoecious lines in cucumber (More and Budgujar, 2002)



Molecular markers and mapping of parthenocarpy

The first attempt of mapping of parthenocarpy gene, *pat*, in tomato was done by Beraldi *et al.,* (2004). Recently, four QTLs associated with parthenocarpy were identified and mapped in tomato (Gorguet *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 *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 *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 *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 likeCRISPR/Cas9 is very recent trending technique following for fast breeding of parthenocarpic vegetables.

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