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Parthenocarpy : "A Potential Trait to Exploit in Vegetable Crops"

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ABSTRACT

The fruit gives a suitable climate to seed creation, security and dispersal. Pollination and fertilization are needed for fruit set and growth and fertilized fruits possess seeds. Parthenocarpy is the term for the production of fruits without pollination or fertilization. Parthenocarpy improves the quality of the fruit, as well as its processing characteristics, performance, public perception and productivity of vegetable crops such as tomato, cucumber, watermelon. The absence of seeds will extend the shelf life of fruits, allowing for better preservation, fruit set in unfavourable climatic conditions, and early and offseason vegetable crop production. This trait has proven to be extremely useful in developing fruits in environments where successful pollination and fertilization are difficult to achieve, such as in greenhouse cultivation (Yin, *et al.* 2006). Consumers, on the other hand, prefer seedless fruits for fresh consumption, processing and canning (e.g., watermelon, cucumber and bitter gourd). Parthenocarpy and stenospermocarpy (seeds abort after fertilization) are two ways to obtain seedless fruits (Voraquaux *et al.* 2000). When a plant's fruits are entirely devoid of seeds, or contain very small seeds or aborted seeds, it is referred to as parthenocarpic. A promising methodology is the creation of new cultivars with the ability to produce fruits without pollination or artificial stimuli. Parthenocarpy can be induced naturally or artificially using a variety of techniques including the use of plant growth regulators, distant hybridization, mutation, use of irradiated pollen, alternation in chromosome number, gene transfer, gene silencing and genome editing tools (Rao *et al.* 2018). In India, more research is required to use advanced breeding methods such as MAS, it will improve the accuracy and speed of generation, and genome editing techniques such as CRISPR/Cas 9, a relatively new trending technique for quick breeding of parthenocarpic vegetables.

Keywords Growth regulators, Genome editing tools, Parthenocarpy, Pollination, Vegetables.

INTRODUCTION

The natural or artificial induction of fruit production without pollination and fertilization, or the process of fruit development without fertilization, is known as parthenocarpy (Parthenos, virgin; karpos, fruit). When a plant's fruits are entirely devoid of seeds, or

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contain very small seeds or aborted seeds, it is referred to as parthenocarpic. Parthenocarpic fruit growth has been identified when phytohormones from sources other than the developing seeds are applied to the ovary (Abad and Monteiro 1989, Garcia-Martinez and Hedden 1997, Gillaspy *et al*. 1993). This perception recommends that parthenocarpic gene/s can primarily influence hormone production, transport, and/or metabolism in the ovary, resulting in ovary sensitivity or increased hormone levels having the ability to promote fruit growth even in the absence of pollination and fertilization (Vivian-Smith *et al*. 2001).

The phytohormones are involved in seed and fruit production, synchronizing and controlling the processes (Pandolfini 2009). Thus, signalling processes are needed for the initiation of seed and fruit production, as well as the development of the fertilization products that play a key role in seed and fruit development (Raghavan 2003). Among the different phytohormones, gibberellins, cytokinins and auxins, are involved in the signaling processes that follow pollination and fertilization and these are the primary requirements for additional growth and development of seeds and the fruit (Fos *et al.* 2001). When pollen development, germination and fertilization are not possible due to environmental conditions, fruit production and quality are adversely affected. As a result, parthenocarpy is regarded as the most effective method of producing fruits in the absence of pollination and/or fertilization. Developing seeds have been reported as a source of phytohormones and thus stimulates the fruit growth and development (Ozga *et al.* 2002). Seeds in fruit are not suitable in certain vegetables because of their rough or leathery texture, unpleasant taste and presence of toxic compounds, allergens and effect on palatability (Dalal *et al.* 2006). Parthenocarpic fruits such as cucumber, eggplant, watermelon, and tomato are examples of vegetables, which are desirable for enhancing the quality of both fresh and processed fruits (Denna, 1973, Varoquaux *et al.* 2000, Yin *et al.* 2006). As a result, replacing the seeds and seed cavities with eatable fruit tissue is both a consumer-friendly offer and a research challenge.

Parthenocarpy, including stenospermocarpy and apomixes, is a genetically regulated trait in which fruit set is independent of the sequence of events that occurs after pollination and fertilization. Typical pollination and fertilization occurs in stenospermocarpy, which is distinct from parthenocarpy and fruit production begins, but early embryo abortion results in seedless fruits as reported in grapes and watermelon (Ledbetter and Ramming 1989). Apomixis is the growth of embryos and seeds without fertilization, and as a result, apomictic species grow fruit without fertilization, as seen in oranges, blackberries, walnuts and mangoes (Hanna and Bashaw 1987, Koltunow and Grossniklaus 2003, Nybom 1986).

Advantages of parthenocarpic vegetable crops

i. Pollination and fertilization are negatively affected by environmental stresses such as low/high temperatures, but parthenocarpic vegetables produce fruits in absence of pollination and fertilization, resulting in stability in development and productivity.

ii. Seedless fruits such as parthenocarpic cucumber, seedless watermelon and seedless pickled gherkin are preferred by consumers (Baker *et al*. 1973).

iii. Parthenocarpy prompts creation of novel vegetables like seedless tomato, parthenocarpic cucumber and seedless water melon.

iv. Parthenocarpy increases quality and shelf life in brinjal because seeds are linked to fruit bitterness (Dalal *et al.* 2006).

v. Parthenocarpy improves taste, total soluble solid content in vegetables e.g. seedless tomato (Falavigna, *et al*. 1978, Lukyanenko 1991).

vi. It increases profitability for processing industries because seedless fruits do not need seed removal during processing. For example, a seedless tomato (Lukyanenko 1991).

vii. Avoid horizontal gene transfer, which is a major source of transgenic approval issues (Varoquaux *et al.* 2000).

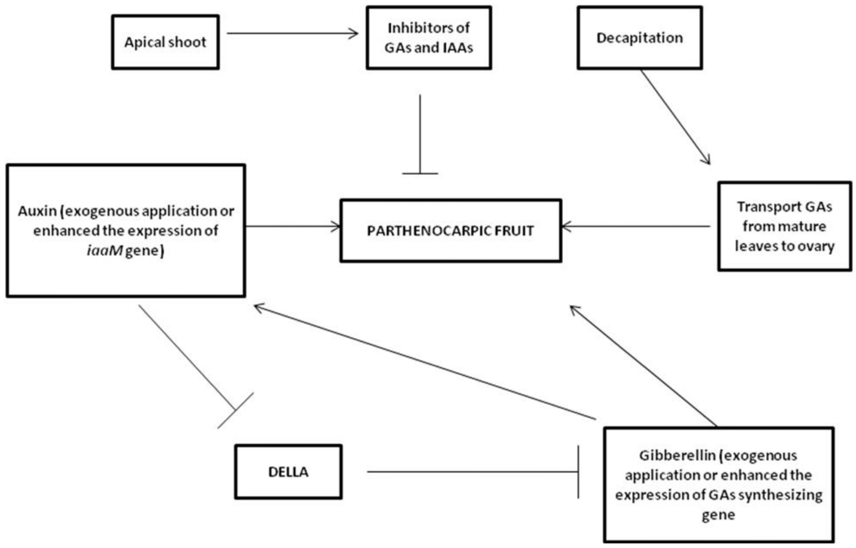


Fig. 1. Role of phytohormes in parthenocarpic fruit development (Arrows denote the positive regulation and lines ending in a bar denote negative regulation).

viii. Protect genetically modified crops: tying a transgene to seedlessness will prevent the transgene from being unfairly appropriated by simply crossing the transgenic plant with another commercial variety (Varoquaux *et al.* 2000).

ix. Parthenocarpic fruits, such as parthenocarpic cucumbers, are early yielders.

x. Vertical fruit harvesting- by growing parthenocarpic cucumbers in green houses, more gains can be realized by continuous fruit set on vine. This will reduce the cost and time spent on pollen vibrators and manual pollination, both of which are needed in the production of greenhouse vegetables.

Table 1. Different examples of plant growth regulators used for parthenocarpic fruit development.

Vegetable	Plant growth regulator	Stage of treatment	Remarks	Reference
Watermelon	CPPU @ 0.5 ml/L	At the time of anthesis	Complete seedless fruits	Kawamura *et al*. 2018
Pumpkin	GA_3 @ 150 ppm		96.9% parthenocarpic fruits	Sharif Hossain 2015
Muskmelon	CPPU @ 10 mg/L and BA			Hayata *et al*. 2000
Bottlegourd	CPPU @ 10-100 mg/L	After or 2 days before anthesis	100% seedlessness	Jing 1999
Kakrol	2,4-D @ 50 ppm	At the time of anthesis	90.0% parthenocarpy	Chowdhury *et al* 2007
Pointed gourd	2,4-D, NAA, CPPU, Fulmet, GA_3 and TIBA at (25, 50, 100 and 200 ppm)	At the time of anthesis	NAA at 200 ppm- Abnormal seeds GA_3 at 200 ppm Empty seeds	Hassan J and Miyajima I 2019
Sweet pepper	0.05% NAA	Prior to anthesis	86% seedless	Heuvelink and Korner 2001

Table 2. Different examples of parthenocarpic lines/cultivars of vegetables developed through distant hybridization.

Crop	Parthenocarpic line/cultivar	Cross involved	Remarks	Reference
Tomato	Line RP 75/79	Multiple cross between Atom × Bubjekosoko and Heinemanns Jubilaum × Priora (developed by R. Reimann-Philipp)	Normal appearance of fruits	Philouze and Maisonneuve 1978
Brinjal	SA002-02 × *S. torvum* and SMA003-03 × *S. torvum*	3 wild relatives (*S. torvum*, *S. aethiopicum, S. anguivi*) of brinjal× 7 cultivated accessions	Development of normal seedless fruits	Afful *et al.* 2018
Tomato	Severianin	*L. esculentum* and *L. hirsutum*	80-110g fruit size with completely filled locules	Philouze and Maisonneuve 1978, Lin *et al.* 1984
Spine gourd and Pointed gourd		Utilized pollens of related taxa *M. charantia* & *L. leucantha*	Highest set (66% in Spine gourd & 85% in Pointed gourd	Singh, 1978

Types of parthenocarpy

Natural or genetic parthenocarpy

Natural occurring parthenocarpy can be obligate orfacultative. When the expression of the parthenocarpic trait is not affected by external influences, it is called obligatory genetic parthenocarpy. In the presence or absence of fertile pollen, genotypes with obligate parthenocarpy are unable to produce viable seeds (George *et al.* 1984). Plants with this condition are believed to be defective during the growth of female gametophytes and require manual vegetative propagation, such as the Ivy gourd. When the parthenocarpic growth of fruit occurs only in the absence of pollination and fertilization, such as in tomatoes and brinjal, it is reffered to as facultative parthenocarpy. The natural parthenocarpy is caused by an increase in endogenous hormones in the ovary in the absence of pollination and fertilization (Gillaspy *et al.* 1993). Genetic parthenocarpy can solve the issue of low pollen viability and poor pollen release, which often

Table 3. Seedless fruit production by using irradiated pollens.

	Crop	Treatment	Dosage	Remarks	Reference
	Soft X- irradiation	800-1000 Gy in 'Fujihikari- TR' 400-1000 Gy in 'Benikodama'	Slightly higher sugar content in fruits	Sugiyama and Morishita (2000)	
Watermelon	ray – irradiation	Doses of 600 and 800 Gy	Significant increase in total sugar and carotenoid contents	Moussa and Salem (2009)	
	Soft X-irradiation	Irradiated pollen with 600 Gy , packed in vacuum as well as N_2 and stored at 4 C^{o} and 25 C^{o} for 14, 28 and 90 days for producing seedless watermelons	100 percent fruit set obtained	Akutsu (2018)	

Table 4. Parthenocarpy related with variation in ploidy levels of vegetables.

Vegetable	Species	Other changes	Ploidy no.	Reference
Tomato	*Solanum esculentum* (2n = 2x = 24)	Increase in dry matter, TSS content	Triploid (2n = 3x = 36)	Habashy *et al.* 2004, Habashy *et al.* 2004
Cucumber	*Cucumis sativus* (2n = 2x = 14)		Triploid (2n = 3x = 21)	Chen *et al.* 2003
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

occurs under low light, low or high temperatures in open and greenhouse conditions.

Artificial Parthenocarpy

It entails the same stimulation processes as pollination and fertilization for the development of a fruit. There are many methods available to produce parthenocarpic fruits in many crops. They are

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

1. Use of plant growth regulators

It is an efficient method to initiate parthenocarpy in vegetables by exogenous use of plant growth regulators to the stigma or the carpels. Among the plant growth regulators ethylene and abscisic acid are known to induce the fruit development; while as, gibberellins, auxins and cytokinins induced parthenocarpy (Ozga and Reinecke 2003). The exogenous use of plant growth hormones, such as auxins, cytokinins and GAs, can influence a variety of plant growth and development processes. The use of these plant growth hormones causes parthenocarpic fruits to develop in vegetable crops (Table 1). The first report of exogenous auxin application to flowers for induction of parthenocarpy was published by Gustafson (1936), although later studies on the effects of various growth regulators parthenocarpy initiation were conducted in a variety of horticultural crops. Auxin stimulates the expression of auxin-biosynthetic genes in the ovaries and ovules to induce parthenocarpy when used exogenously (Carmi *et al*. 2003, Mezzetti *et al*. 2004). Auxin is the primary inducer of fruit set and it works in part by instigating gibberellin biosynthesis (Fig. 1). Interestingly, gibberellin does not appear to play a significant role in final fruit size, but it appears to be critical in preventing flower and fruit abscission (Tiwari *et al*. 2012). Therefore, it may be concluded that gibberellin along with auxin seems to be playing an important role in parthenocarpy. Gibberellins are produced by pollen and exogenous use of gibberellins raises the level of auxin in the ovary of an unpollinated blossom, causing fruit to set without fertilization. The rate of cell division in contiguous fruit tissue is controlled by the developing embryo. As previously mentioned, developing seeds aid cell expansion inside the fruit by serving as a source of auxin.

In the absence of pollination or application of gibberellic acid in pea, apical shoot has been

Table 5. Parthenocarpic vegetable production by using gene silencing, transgenic and RNA interference approaches.

Gene	Function	Gene modification	Crop	Reference
SEP1/TM29	Cytokinin	Antisense or co-suppre-ssion; MADS-box	Tomato	Ampomah-Dwamena *et al.,* (2002)
SlIAA9	Auxin signalling	Antisense down regu-lation	Tomato	Wang *et al.,* 2005
AtARF8	Auxin signalling	Expression of Mutant AtARF8-4 gene	Tomato	Goetz *et al.* 2007
SlDELLA	Gibberellin signalling	Antisense down regu-lation	Tomato	Marti *et al.* 2007
SlChs	Flavonoid biosynthesis	RNAi-mediated silencing	Tomato	Schijlen *et al*. 2007
SlTPR1	Ethylene signa-lling	Over expression	Tomato	Lin *et al.* 2008
SlARF7	Auxin signalling	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	Garcia- Hurtado *et al.* 2012
ARFs	Auxin response	RNA interference	Brinjal	Du *et al*. 2016

identified as a source of inhibitors that inhibit fruit development (Rodrigo and Garcia-Martinez 1998). Even in derooted plants, decapitation stimulated parthenocarpic development, which was counteracted by applying indole acetic acid (IAA) or abscisic acid (ABA) in agar blocks to the severed stump (Rodrigo and Garcia-Martinez 1998). The GAs are diverted from mature leaves to the unpollinated ovary by decapitation, resulting in parthenocarpic ovary formation (Garcia-Martinez *et al.* 1991). Serrani *et al.* (2010) also demonstrated that applying auxin transport inhibitor (NPA; N-1-naphthylphthalamic acid) to unpollinated tomato ovaries induced parthenocarpic fruit set, which was accompanied by increased indole-3-acetic acid (IAA) content, which was counteracted by inhibitor of gibberellins biosynthesis (Paclobutrazol). A family of DELLA nuclear factors, specifically RGA, GAI, RGL1, RGL2 and RGL3 are negative regulators of the GA reaction (Wen and Chang 2002). Auxin promotes GA-dependent degradation of DELL A proteins and upregulates gibberellin biosynthesis (Fu and Harberd 2003), as DELLA silencing also induces facultative parthenocarpy in tomato fruits (Marti *et al.* 2007). Moreover, GA biosynthesis inhibitors inhibited fruit development, which is switched by GA application (Santes and Garcia-Martinez 1995).

2. Distant hybridization

Close or near hybridization occurs between varieties of the same species or subspecies, while distant hybridization occurs between distant species. Wide or distant hybridization or mating between individuals of different species orgenera, is a method for bringing diverged genomes together in a single nucleus. Wide hybridization overcomes what is known as the species hindrance to gene transfer, allowing for the transfer of a genome of one species to another, resulting in improvements in genotypes and phenotypes in progenies. There are two basic steps in traditional; i) Creating a breeding population that segregates for one parental genotype's parthenocarpy phenotype and ii) Selecting progeny from a segregating population with parthenocarpy and the attractive traits of the non-parthenocarpic parent (Table 2). Two types of crosses are used to create a breeding population : Inter- specific and intra-specific hybridization.

Intraspecific hybridization was used for the first time in tomato to produce a facultative parthenocarpic line suitable for a hot and dry climate (normal fruit at moderate temperature) (Hawthorn 1937). Following that, intraspecific hybridization was used to build various other parthenocarpic lines, such as

Oregon T5-4, Oregon Cherry, Oregon 11, 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). IVT-line 1 in tomato was created from a cross between *S. habrochaites* and *S. lycopersicum* (Zijlstra 1985), while as Obligate parthenocarpy in aneuploid tomato was created from a cross between *Solanum esculentum* and *S. peruvianum* (Lesley and Lesley 1941). Interspecific hybridization to alter ploidy is a popular method for obtaining parthenocarpic fruits, as stated in banana, watermelon and citrus (Fortescue and Turner 2005). Triploid plants are usually sterile because they are unable to pass through meiosis. Despite the fact that the mechanisms of fruit initiation in triploid plants are largely unknown, perceptions suggest that sterility is an important requirement for parthenocarpy to manifest.

3. Mutation

The lack of natural genetic diversity in the genepool, which can be minimized by mutation breeding, is a major limitation in traditional breeding. A heritable alteration in sporophytic (i.e. somatic cells) or gametophytic tissue (i.e. germ cell line from where gametes arise) is known as a mutation and standard genetic recombination and segregation do not cause this. While specific mutations can now be induced and selected (Cooper *et al*. 2008), random mutations have traditionally been the most common source of genetic variation. Spontaneous mutations occur in nature and are utilized in traditional breeding methods. The parthenocarpic sha-pat mutants in the tomato line 'Montfavet 191' are a good example of this (Pecaut and Philouze 1978). Mutations have been caused chemically or by radiation therapy when genetic variation in natural populations is reduced. Various radiation therapies, such as helium accelerated ions in tomatoes (Masuda *et al.* 2004), soft–X-ray in watermelon (Sugiyama and Morishita 2000), and gamma irradiation in *Citrullus lanatus* (Sugiyama and Morishita 2001) have been utililized effectively to produce parthenocarpic mutants. Alkylating agents, such as ethyl methane sulphonate (EMS) and ethyl ethane sulphonate (EES) and base analogs, such as 5-bromouracil and 2-aminopurine, are available for chemical mutagenesis. The most well-known mutagen is EMS, which is both powerful and convenient. It has been utilized to produce Arabidopsis (*fwf*) and tomato (stock 2524 : short anther mutant, *sha*) parthenocarpic mutants (Bianchi and Soressi 1969 ; Soressi, 1970 ; Vivian-Smith *et al.* 2001).

4. Use of irradiated pollen

Pollens irradiated with soft-X-rays or γ- rays are used for pollination in the irradiation process to grow seedless fruits. Seedless watermelon (*Citrullus lanatus*) cultivars have been developed using soft X-ray irradiated bottle gourd pollen. The rate of fruit set was 57.1% when bottle gourd pollen was used to pollinate female watermelon flowers (with watermelon pollen 65.0%) Table 3. The pollination with bottle gourd pollen resulted in formation of deformed (triangular or oblong shaped) parthenocarpic fruits, but other characteristics such as fruit weight, rind thickness, flesh color and Brix were nearly identical to control fruit. After pollination with bottle gourd pollen, the fruit produced tiny, white empty seeds.

5. Alternation in chromosome number

This method was first developed by Kihara's group in the fourties primarily for watermelon, to raise triploids plants that created seedless fruits with just leftover integuments (Kihara 1951). In wide crosses, chromosome elimination can result in the development of haploids, which are of great interest to breeders. Parthenogenesis is the term used to describe the development of haploids as a result of interspecific hybridization (Rowe 1974) (Table 4).

There are several steps in producing triploid watermelon

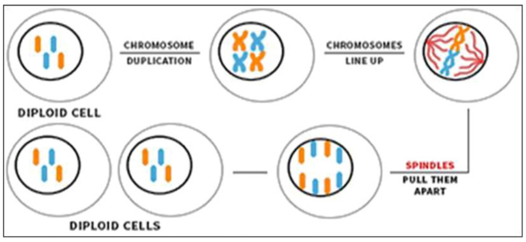
i. Production of tetraploid line through colchicine treatment : Application of colchicine 0.2% - 0.4% to the growing point of young seedlings at 1 to 2 true – leaf stages for 2 to 3 days successively is generally practiced.

ii. Production of 3x seeds : This is done by either hand pollinating the tetraploid female with diploid male or in open fields with adjacent rows of 4x female and 2x male and pinching of male buds in 4x plants.

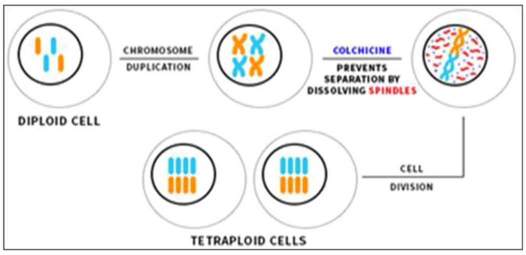
iii. Germination of 3x seeds : Triploid seeds are poor in germination and hence the seeds are to be germinated under controlled conditions followed by transplantation to field.

iv. Production of 3x fruits : Triploid plants are raised along with diploid plants, which serve as pollinators.

Colchicine mode of action



Normal Mitosis



Mitosis with Colchicine

Colchicine is a highly toxic alkaloid derived from the bulbs (0.1-0.5%) and seeds (0.2-0.8%) of autumn crocus or meadow saffron (*Colchicum autumnale*). Colchicine is sometimes referred to as a doubling agent. It acts as a mitotic inhibitor and prevents the development of spindle fibers.

Some shortcomings of this approach include the difficulty in identifying tetraploid plants and the decreased fertility of their pollen, as well as the difficulty in producing tetraploid parental lines. Tetraploid fruits produce less seeds and the techniques needed to successfully germinate triploid seeds have made this approach much less practical. The growth of ovules is inhibited in triploid plants during the early stages of fruit development. As a result of high ploidy level, embryo development is affected and triploid plants produce fruits with rudimentary integuments and no seeds.

6. Gene transfer

In order to reduce the harmful effects of the exogenous application of PGRs, scientists have developed transgenic methods that imitate their exogenous application. It has been reported that expressing the auxin biosynthesis genes *iaaM* (*Tryptophan monooxygenase*) or *iaaH* (*Indoleacetamide hydrolase*) from *Agrobacterium* T-DNA under the influence of the ovule/placenta specific promoter defh9 results in parthenocarpic fruit development in tobacco (Bavrina *et al.* 1999), eggplant (Rotino *et al.* 1997), tomato (Ficcadenti *et al.* 1999), cucumber (Yin *et al.* 2006), and strawberry (Mezzetti *et al.* 2004). The *DefH9-iaaM* gene contains the coding region of the *iaaM* gene from *Pseudomonas syringae* pv. *savastanoi* which is regulated by the *Anthirrhinum majus* placental and ovule-specific *DefH9* promoter. The *iaaM* gene codes for the enzyme tryptophan monoxidase which converts tryptophan to indolacetamide, which is then converted to indole-3-acetic acid (IAA) either chemically or enzymatically. The *DefH9-iaaM* transgene causes parthenocarpic fruits to form without pollination or fertilization and seeds to form within the fruit after pollination. Similarly, obligate and facultative parthenocarpy in tomato has been identified when the *Agrobacterium rhizogenes*-derived *rolB* gene, which confers auxin sensitivity, is expressed under a fruit-specific promoter (Carmi *et al.* 2003).

The transgenic fruits tend to be identical to seeded fruits in size and morphological appearance e.g., tomato (Pandolfini *et al.* 2002). Transgenic parthenocarpic plants have also been shown to have lower processing costs, better flavor (high soluble solids, high brix) and higher total yield than non-transgenic plants (Barg and Salts 2000 ; Carmi *et al.* 2003; Salts *et al.* 1992). Despite transgenic approach may provide a valuable method for obtaining parthenocarpic varieties with additional benefits, the difficulties in creating transgenic plants, as well as consumer fear, have raised concerns about its commercial viability

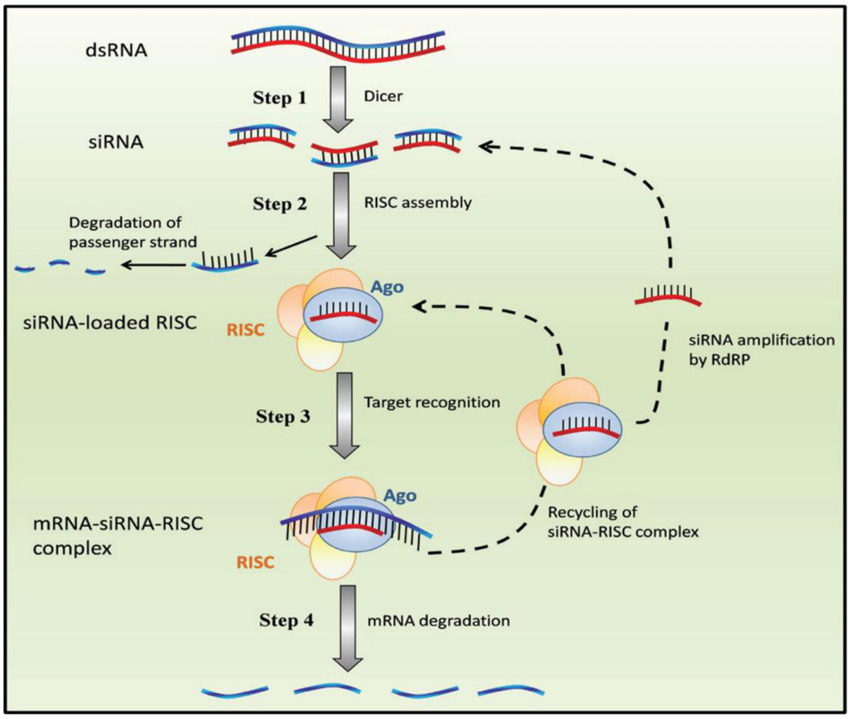


Fig. 2. Schematic representation of RNAi (Figure source : Cuccato *et al.* 2011).

(Acciarri *et al*. 2002; Donzella *et al.* 2000; Ficcadenti *et al*. 1999 ; Rotino *et al.* 1997).

7. Gene silencing

Gene silencing (GS) is a molecular and highly efficient reverse genetic tool that inhibits the function of particular genes (Dash *et al.* 2015). Gene silencing, in general, is an epigenetic method of gene regulation that depicts the 'switching off' of a gene by a mechanism other than changes in DNA sequence. The degradation of RNA molecules is included in GS, which has been well preserved over time (Chen and Rajewsky 2007). Since, the GS phenomenon is linked to RNA activity within the cell, it is also known as RNA silencing. The transcriptional and post transcriptional stages are the two key stages where gene silencing can be used. The target DNA sequences are made unreliable for transcription by transcriptional gene silencing methods (Dash *et al.* 2015 ; Pathak and Gogoi, 2016). The changes in promoter and enhancer sequences efficiencies, methylation patterns, histone modifications, addition or deletion of specific sequences and so on are examples of transcriptional gene silencing methods. Post transcriptional gene silencing methods, on the other hand, focus on the targeted mRNA molecule produced after transcription. It might include the function of ribozymes, antisense RNAs and interfering RNA (RNAi). PTGS (Post transcriptional gene silencing) is a common phenomenon. RNA interference (RNAi) and Antisense RNA technology, among other methods of PTGS, have been used to induce parthenocarpy in vegetables by interfering with gene expression (Table 5).

Mechanism of RNAi/PTGS

The involvement of small RNAs (21-26 nucleotides) is a peculiar feature of this phenomenon that acts as a marker for gene expression down regulation (Waterhouse *et al.* 2001 ; Hannon 2002 ; Pickford and Cogoni, 2003). This process necessitates the use

Table 6. Genetic inheritance of parthenocarpy in vegetable crops.

Vegetable	Target genes	Genome editing tool	Remarks	Reference
Tomato	AGL6, AGAMOUS-like	CRISPR-Cas 9	Under heat stress conditions, seedless fruits with normal weights and shapes were formed	Klap *et al.* 2017
Tomato	IAA9, auxin-induced 9	CRISPR-Cas 9	Change in leaf shape in parthenocarpic phenotypes were observed	Ueta *et al.* 2017

of proteins from the Argonaut family (Hammond *et al.* 2000).

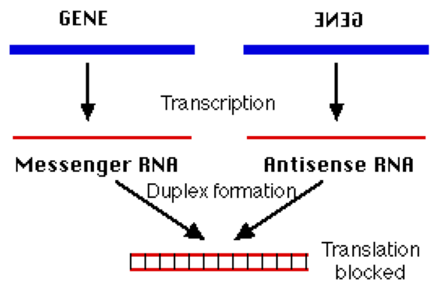
Steps involved in mechanism of RNAi

I. The operation of long dsRNA intermediates triggers RNAi, which is then digested by Dicer enzyme (a ribonuclease III enzyme) into small dsRNA of 21-24 nucleotides with 3'- dinucleotide overhang, a 5' monophosphate and a 3'- hydroxyl group. RNAi stimulates the activity of dsRNA intermediates, which are converted into RNA duplexes of 21-24 nucleotides by Dicer, a ribonuclease III-like enzyme called Dicer (Fire *et al.* 1998 ; Bernstein *et al*. 2001).

II. Dicer's processed product, small dsRNA, is solely responsible for gene silencing; as a result, small dsRNA are also known as small interfering RNAs and abbreviated as siRNA.

III. After the formation of small interfering dsRNA, the two strands of this dsRNA are isolated. One of the isolated strands from the siRNA, the guide or antisense strand that is complementary to the target sequence, is coordinated towards the assembly of RISC (RNA induced silencing complex), while the other is digested (Hammond 2000 ; Tang 2003).

IV. The RISC is made up of guide RNA (one strand of siRNA) and a few Argonaute family proteins. The guide RNA checks the host genome for complementary messenger RNAs (mRNAs) and when RISC arrives at the target site, the endonuclease action of the Argonaute family protein slashes the sequence, rendering the target gene inactive.



Antisense RNA technology. Figure source: Kimball, 2002

Antisense RNA technology. Figure source: Kimball, 2002

The schematic representation of the RNAi process is presented in the Figure 2.

Antisense RNA technology

In Antisense technology, artificially – produced complementary molecules search out and tie to messenger RNA (mRNA), obstructing the last stage of protein development. The basic idea is that if a complementary oligonucleotide (a short) RNA or DNA molecule is inserted into a cell, it will precisely bind to its target mRNA through the exquisite specificity of complementary base pairing, the same mechanism that ensures fidelity of DNA replication and RNA transcription from the gene. As a result of this binding, RNA dimmer is formed in the cytoplasm and ends protein synthesis.

8. Genome editing tools

Use of genome editing tools for induction of parthenocarpy is a very recent and advanced method and it includes TALENs, ZFNs and CRISPR/Cas9.

Table 7. 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 Parth 2.1 and six minor-QTLs	SSR 133 (total 1335) and InDel 9 (total 173). EC1 × 8419 s-1 cross, 145 F2:3 population	Seven novel QTLs were reported 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 were identified in cucumber.	Sun *et al.* 2006b
Tomato	Pat		Situated on the long arm of chromosome 3	Beraldi *et al.* 2004

The CRISPR/Cas9 method is the most widely used genome editing technology. The creation of sequence-specific nuclease based technologies such as Zinc Finger Nucleases (ZFNs) (Kim *et al.* 1996), Transcriptional Activator-Like Effect or Nucleases (TALENs) (Bogdanove and Voytas 2011) and Clustered Regulatory Interspaced Short Palindromic Repeat (CRISPR) Associated Protein System (CRISPR/Cas9) (Doudna and Charpentier 2014) has allowed site-directed genome modification. Among the genome editing tools, only CRISPR/Cas9 allows for the rapid growth of new parthenocarpic vegetable cultivars (Table 6).

Genetics of parthenocarpy

The mode of inheritance for parthenocarpic fruit set has been investigated in some species and it has been found to vary from a single gene to multiple quantitative trait loci (QTLs) (Table 6). The following genes have been reported to be capable of maintaining parthenocarpic traits in tomato (*Lycopersicum esculentum* L.) : *pat*, *pat*-2, *pat*-3 and *pat*-4 (Philouze 1983). Parthenocarpy is dominated by a few genes in eggplant that have an additive effect (Hennart 1996). Parthenocarpic mutants have been used to grow cultivars for greenhouse cultivation in cucumber, which is one of the plant species where parthenocarpic mutants have been used more seriously. A single gene (*Pa*) expressing incomplete dominance and modifier genes appear to regulate the parthenocarpic phenotype (Pike and Peterson 1969). Parthenocarpy in gynoecious and parthenocarpic cucumber lines is under the influence of an incomplete dominant gene, according to F_2 population segregation and test crosses for parthenocarpic fruit production (Jat *et al.,* 2017).

Molecular markers and mapping of parthenocarpy

Beraldi *et al.* (2004) were the first to map the parthenocarpy gene, *pat*, in tomato. The genetics of parthenocarpy were investigated in two tomato lines, IL5-1 and IVT-line-1, both of which carried *Solanum habrochaites* chromosome segments and it was reported that parthenocarpy is dominated by two QTLs in tomato (Gorguet *et al.* 2008). In IL5-1, one QTL is located on chromosome 4 (*pat* 4.1) and other is situated on chromosome 5 (*pat* 5.1), whereas, one is on chromosome 4 (*pat* 4.2) and one is on chromosome 9 (*pat* 9.1) in IVT-line^{-1}. *Pat* 4.1 from IL 5^{-1} and *pat* 4.2 from IVT-line-1, both situated near the centromere of chromosome 4 are possibly allelic. The discovery of these QTLs will aid in the understanding of tomato fruit set, as well as the production of parthenocarpic fruits in other economically important solanaceous vegetable crops. In eggplant, an intraspecific linkage map for parthenocarpy was developed (Barchi *et al*. 2010). Using co-dominant simple sequence repeat and single nucleotide polymorphism markers, a quantitative trait locus (QTL) study of eggplant revealed that two QTLs regulating parthenocarpy have been found, one on chromosome 3 (Cop 3.1) and other on chromosome 8 (Cop 8.1), respectively (Miyatake *et al.,* 2012). Micro synteny between tomato and Arabidopsis revealed ARF8 as a possible candidate gene for these two QTLs. In Arabidopsis without pollination or fertilization, ARF8 is known to function as an inhibitor of additional carpel growth. Tomatoes with an aberrant form of the Arabidopsis ARF8 gene have also developed parthenocarpy (Gorguet *et al*. 2008) (Table 7).

CONCLUSION

Parthenocarpy is an important trait for improving vegetable crop production, quality and processing traits. This trait is especially useful in the cultivation of cross-pollinated vegetable crops in greenhouses. Several methods to engineer genetic parthenocarpy in transgenic plants have been developed and made available as a result of different approaches providing a conceptual basis. As a result, genetically modified parthenocarpy will soon increase the quality and yield of many horticultural crop plants. Although it is well known that phytohormones play an important role in fruit set, their genetic manipulation can result in seedlessness. Simultaneously, molecular approaches based on microarrays would enable researchers to track changes in gene expression patterns during fruit production in both parthenocarpic and pollinated fruits. Furthermore, the application of biotechnological techniques will improve the efficiency and detection of parthenocarpic genes in crops for the benefit of mankind. Advanced breeding methods such as MAS, can improve the accuracy and speed of generation, whereas genome editing techniques, such as CRISPR/Cas9, are a newer trending technique for quick breeding of parthenocarpic vegetables. As a result, the need to improve fruit quality and productivity in order to meet our society's needs may depend on novel technologies, which may also help us better understand fruit production.

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