Vol. 4 Issue- 12, August 2024 (e-ISSN: 2582-8223)

Recent Advances in Parthenocarpy and Its Applicationsin Vegetable Crops

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ARTICLE ID: 34

Abstract

Parthenocarpy, the development of seedless fruits without fertilization, offers significant benefits in vegetable crop production, including enhanced fruit quality, extended shelf life and improved adaptability to diverse growing conditions. This review paper explores the recent advancements in parthenocarpy, detailing its types, genetic basis, methods of induction and applications in vegetable crops. The paper also includes insights from leading scientists in the field and discusses future prospects for parthenocarpic research. The development of parthenocarpic varieties through plant growth regulators, genetic manipulation and hybridization has shown promising results in improving yield and marketability, meeting the increasing demand for high-quality, seedless produce.

Introduction

Parthenocarpy, derived from the Greek words "parthenos" (virgin) and "karpos" (fruit), refers to the formation of fruit without the fertilization of ovules. This phenomenon can occur naturally or be induced through various techniques and it has significant implications for agriculture, particularly in the production of seedless vegetable crops (Nancy, 2015). Seedless fruits are highly valued for their convenience, improved quality and longer shelf life. This paper reviews the types of parthenocarpy, the genetic mechanisms underlying it, methods to induce parthenocarpy and its applications in vegetable crops, with additional insights from scientific literature.

Reasons for occurrence of parthenocarpy

- Fruit development without pollination
- Fruit development due to stimulus received by pollination followed by unsuccessful fertilization

- Degradation of pollen mother cell (PMC) or fertilized ovule
- Abortion of embryos
- Chromosomal irregularities
- Male sterility and self-incompatibility

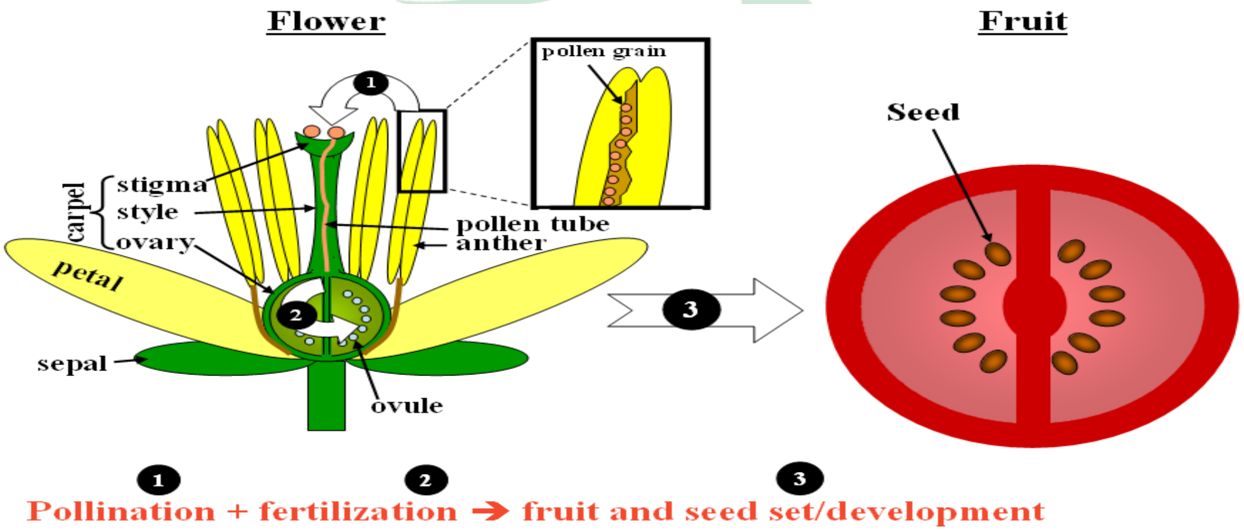
Types of Parthenocarpy

Parthenocarpy is classified into two main types:

1. **Natural Parthenocarpy**: Occurs spontaneously in some plant species, such as bananas and certain fig varieties (Tiwari *et al*., 2011).

- **Vegetative Parthenocarpy**: Fruit development without pollination stimulus (e.g., seedless cucumbers) (Yan *et al.*, 2010).
- **Stimulative Parthenocarpy:** Requires pollination stimulus, but seeds do not develop (e.g., seedless watermelons).
- **Steno-spermoparthenocarpy**: This condition often results from incomplete fertilization or abortion of embryos during seed development (e.g., Seedless Grapes, watermelon)
- **Facultative parthenocarpy:** occurs when seedless fruits develop only when pollination is prevented (e.g., Tomato, Brinjal)
- **Obligatory:** Parthenocarpy could be defined as a process by which fruits are produced without the process of fertilization of ovules (e.g., Ivy gourd)

2. **Artificially Induced Parthenocarpy**: Achieved through human intervention using techniques such as: Irradiated pollen, Auxin – IAA, Gibberellins – GA_3



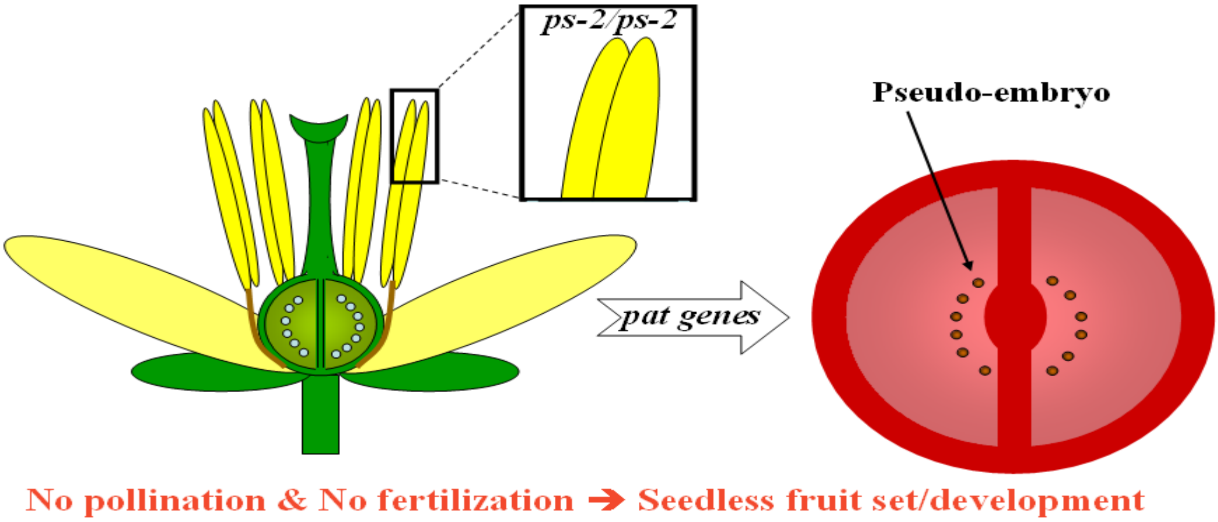


Fig 1. Schematic representation of fertilization and parthenocarpy

Importance of parthenocarpy in Vegetable crops

Seedless fruits, Improved quality, Increased shelf life, Protected cultivation, Increased production under adverse environment, off season production can be done.

Table 1: Quality parameters of parthenocarpic vegetables compare to seeded vegetables

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	High sugar content in seedless watermelon	Kawamura *et al.*, 2018
Cucumber	A mild flavour, thin peel, high yield and fruit quality	Li *et al.*, 2014
Gherkin	Seedless pickled gherkins are more crunchy, firm and fleshier than its seeded variety	Baker *et al.*,1973
Tomato	Seedless tomato fruits are tastier, more dry-matter, contain more sugars, less acidity	Lukyanenko, 1991
Eggplant	Reduced browning, 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

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Genetic Inheritance of Parthenocarpy

Understanding the genetic mechanisms underlying parthenocarpy is crucial for breeding programs. The inheritance patterns vary among different crops:

- Tomato: Several single recessive genes (pat-2, pat-3/pat-4 and pat-6) control parthenocarpy. In Brinjal (Eggplant): A single major gene is responsible for parthenocarpy.
- Cucumber: An incompletely dominant gene (Pc) governs this trait (Dalal *et al.*, 2006).

Table 2: Plant growth regulators used for parthenocarpic fruit development

Plant	Growth regulator	Stage of Vegetable treatment	Remarks	Reference
Watermelon	CPPU @ 0.5 ml/L	At the time of anthesis	Complete seedless fruit	Kawamura *et al.*, 2018
Pumpkin	GA3 @ 150 ppm		96.9% parthenocarpic fruits	Sharif Hossain, 2015
Pointed gourd	2,4-D, NAA, CPPU, Fulmet, GA3 and TIBA at (25, 50 and 100 ppm)	At the time of anthesis	NAA at 200 ppm Abnormal seeds GA3 at 200 ppm Empty seeds	Hassan and Miyajima, 2019
Kakrol	2, 4-D @ 50 ppm	At the time of anthesis	90.0 % parthenocarpy	Chowdhury *et al.* (2007)
Sweet pepper	0.5% NAA	Pre- anthesis sprays	86% seedless	Heuvelink and Korner (2001)

Distant hybridization:

It involves mating individuals from different species or genera to combine divergent genomes into a single nucleus. This process overcomes species barriers to gene transfer, improving genotypes and phenotypes in progeny. Traditional breeding involves two main steps:

- Creating a breeding population segregating for one parental genotype's parthenocarpy phenotype.
- Selecting progeny with parthenocarpy and desirable traits from the non-parthenocarpic parent.

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Two types of hybridization are used: interspecific (between different species) and intraspecific (within the same species). Intraspecific hybridization has produced parthenocarpic tomato lines suitable for various climates and eggplant lines (Serrani *et al*., 2007). Examples include Oregon T5-4, Oregon Cherry, IVT-line 2 and Talina2/1. IVT-line 1 in tomato resulted from crossing *S. habrochaites* and *S. lycopersicum*, while obligate parthenocarpy in aneuploid tomatoes came from crossing *Solanum esculentum* and *S. peruvianum*. Interspecific hybridization, such as in watermelon, is also used to alter ploidy and obtain parthenocarpic fruits. Triploid plants, often sterile due to meiosis failure, are key in parthenocarpy. Chemical mutagenesis, notably using EMS, has produced parthenocarpic mutants in Arabidopsis and tomatoes.

Table 3: Parthenocarpic lines/cultivars of vegetables developed through distant hybridization

Parthenocarpic Crop	Parthenocarpic line/cultivar	Cross involved
Tomato	Line RP75/79	Multiple cross Atom × Bubjekosoko and Heinemanns Jubilaum × Priora
Tomato	Severianin	*L. esculentum* and *L. hirsutum* (bred by N. Soloviova)
Tomato	P-26 and P-31	*L. esculentum* and *L. pennellii*
Tomato	Line RG	L. *esculentum* and *L. cheesmanii* var. minor
Tomato	IVT 1	*L esculentum* and *L. hirsutum*
Tomato	IVT 2	*L. esculentum* and *L. peruvianum*
Spine gourd and Pointed gourd	Utilized pollens of related taxa *M. charantia* & *L. leucantha*	Highest set (66% in Spine gourd & 85% in Pointed gourd

Mutation

The limited natural genetic diversity in the gene pool can be addressed by mutation breeding. A mutation, which is a heritable change in somatic or germ cells, is distinct from standard genetic recombination and segregation. While specific mutations can now be induced and selected, random mutations have traditionally been the main source of genetic variation. Spontaneous mutations occur naturally and are used in traditional breeding. For instance, the

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parthenocarpic shapat mutants in the tomato line Montfavet 191 exemplify this. When natural genetic variation is low, mutations can be induced chemically or through radiation. Effective methods include helium accelerated ions in tomatoes, soft X-rays in watermelon, and gamma irradiation in Citrullus lanatus. Chemical mutagens such as ethyl methane sulphonate (EMS), ethyl ethane sulphonate (EES), 5-bromouracil and 2-aminopurine are also used. EMS is particularly notable for its efficacy and convenience, having been used to produce parthenocarpic mutants in Arabidopsis and tomato (e.g., stock 2524: short anther mutant, sha).

Alteration in Chromosome Number

In the 1940s, Kihara's group developed a method to produce seedless triploid watermelon. The process involves:

1. **Tetraploid Line Production**: Applying colchicine (0.2%-0.4%) to young seedlings for 2-3 days.
2. **Triploid Seed Production**: Hand-pollinating tetraploid females with diploid males or growing them in fields with tetraploid females and diploid males.
3. **Triploid Seed Germination**: Germinating the poorly germinating triploid seeds under controlled conditions before field transplantation.
4. **Triploid Fruit Production**: Growing triploid plants with diploid pollinators.

Colchicine, a toxic alkaloid from the autumn crocus (*Colchicum autumnale*), inhibits mitosis and doubles chromosomes. Challenges include identifying tetraploid plants, reduced pollen fertility, and difficulties in producing and germinating tetraploid lines. Triploid plants have inhibited ovule growth, resulting in seedless fruits.

Gene Transfer

To reduce the negative effects of exogenous plant growth regulators (PGRs), scientists have developed transgenic methods that mimic their application. Expressing auxin biosynthesis genes, such as iaaM (Tryptophan monooxygenase) or iaaH (Indoleacetamide hydrolase) from Agrobacterium T-DNA under the ovule/placenta-specific promoter defh9, induces parthenocarpic fruit development in crops like tobacco, eggplant, tomato, cucumber and strawberry.

The DefH9-iaaM gene combines the iaaM coding region from *Pseudomonas syringae* with the DefH9 promoter from *Antirrhinum majus*, leading to the production of tryptophan monooxygenase, which converts tryptophan to indole acetamide and then to indole-3-acetic acid (IAA). This transgene enables the formation of parthenocarpic fruits without pollination but can produce seeds when pollination occurs. Similarly, in tomatoes, expressing the Agrobacterium rhizogenes-derived rolB gene under a fruit-specific promoter induces parthenocarpy by increasing auxin sensitivity. Transgenic parthenocarpic fruits, such as tomatoes, are similar in size and morphology to seeded fruits and offer benefits like lower processing costs, better flavor (high soluble solids and brix) and higher yields. Despite these advantages, the commercial viability of transgenic plants is challenged by difficulties in creation and consumer concerns.

Table 4: gene modification in some crops

Gene	Function	Gene modification	Crop	Reference
DeH9-iaaM	Auxin synthesis	Ovule Specific transgene expression	Eggplant, tomato, cucumber	Yin *et al.*, 2006; Mezzetti *et al.*, 2004
SlDELLA	Gibberellin signaling	Antisense down regulation	Tomato	Marti *et al.*, 2007
ARFs	Auxin response	RNA interference	Brinjal	Du *et al.*, 2016

Gene Silencing

Gene silencing (GS) is an efficient molecular tool used to inhibit specific gene functions without altering the DNA sequence, often referred to as RNA silencing due to its reliance on RNA activity (Pickford *et al.*, 2003). This epigenetic method involves RNA degradation and has been conserved over time.

GS can occur at two key stages: transcriptional and post-transcriptional.

- **Transcriptional Gene Silencing**: This method makes DNA sequences unreliable for transcription through changes in promoter and enhancer efficiencies, methylation patterns, histone modifications, and sequence alterations.
- **Post-Transcriptional Gene Silencing (PTGS)**: This focuses on the targeted mRNA molecules produced after transcription, utilizing ribozymes, antisense RNAs and RNA interference (RNAi).

PTGS, including RNAi and Antisense RNA technology, has been used to induce parthenocarpy in vegetables by interfering with gene expression.

Table 5: Parthenocarpic vegetable production by using gene silencing

Gene	Function	Gene modification	Crop	Reference
ARFs	Auxin response	RNA interference	Brinjal	Du *et al.*, 2016
PIN-4	Auxin	RNAi	Tomato	Mounet *et al.*, 2012
AUCSIA, CHS	Auxin response	Gene silencing	Tomato	Molesini *et al.*, 2009
SlTPR1	Ethylene signalling	Over expression	Tomato	Lin *et al.*, 2008

Genome Editing Tools

Genome editing tools like TALENs, ZFNs, and CRISPR/Cas9 are advanced methods for inducing parthenocarpy. Among these, CRISPR/Cas9 is the most widely used and effective for creating new parthenocarpic vegetable cultivars quickly.

- **TALENs (Transcriptional Activator-Like Effector Nucleases)**: Developed by Bogdanove and Voytas in 2011.
- **ZFNs (Zinc Finger Nucleases)**: Introduced by Kim *et al*. in 1996.
- **CRISPR/Cas9 (Clustered Regulatory Interspaced Short Palindromic Repeat/Associated Protein System)**: Established by Doudna and Charpentier in 2014.

Parthenocarpy in cucumbers, for example, is influenced by an incomplete dominant gene (Pa) and modifier genes, as shown by F2 population segregation and test crosses.

Future Prospects

The future of parthenocarpy in vegetable crops looks promising, with ongoing review focusing on:

- Biotechnological Advances: Continued advancements in genetic engineering and molecular breeding will likely produce more efficient and targeted methods for inducing parthenocarpy.
- Environmental Adaptation: Developing varieties that can withstand extreme environmental conditions and still produce high-quality, seedless fruits.

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- Consumer Preferences: As consumer demand for seedless fruits grows, breeding programs will focus on enhancing other desirable traits such as flavor, nutritional content and storage qualities.

Conclusion

Parthenocarpy represents a significant advancement in horticultural science, offering numerous benefits for vegetable crop production. The development of seedless varieties through various methods, including plant growth regulators, genetic manipulation and hybridization, has improved fruit quality, yield and marketability. Continued research and development in this field will further enhance the sustainability and efficiency of vegetable production, meeting the growing demands for high-quality, seedless produce.

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