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Parthenocarpy in vegetable crops: Inheritance, hormonal signalling and prospects for crop improvement

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Abstract
Parthenocarpy, the development of fruits without fertilization, is an important phenomenon in vegetable crops, contributing to improved fruit quality, stable fruit set and enhanced marketable yield under unfavourable environmental conditions. This review highlights the genetic inheritance, hormonal regulation, molecular mechanisms and induction approaches of parthenocarpy in vegetable crops. Its expression is governed by diverse genetic mechanisms, including single-gene and polygenic inheritance, along with the coordinated regulation of phytohormones such as auxins, gibberellins and cytokinins. Various approaches, including plant growth regulators, hybridization, mutation breeding, chromosome manipulation, gene silencing and genome editing, have been explored to induce parthenocarpy. Its application in tomato, cucumber, eggplant, sweet pepper and muskmelon offers promising opportunities for seedless fruit development and improved productivity. Integration of conventional breeding with modern biotechnological approaches could facilitate the development of stable parthenocarpic cultivars for sustainable vegetable production.

Keywords: Parthenocarpy, genetic inheritance, molecular mechanisms, seedless fruits, crop improvement

Introduction

Parthenocarpy, defined as fruit development in the absence of fertilization, is an important reproductive phenomenon in vegetable crops that contributes to improved fruit quality and consistent yield under environmental conditions unfavourable for pollination and fertilization (Maupilé *et al.*, 2024) [1]. In major vegetable crops, including tomato, cucumber, eggplant, watermelon and chilli, it promotes fruit set under inadequate pollination conditions, improves fruit quality and processing characteristics, and enhances marketable productivity (Su *et al.*, 2021; Sharif *et al.*, 2022; Guan *et al.*, 2024; Kondo *et al.*, 2021) [2, 3, 4, 5]. Parthenocarpy can occur naturally due to genetic variations or be induced artificially through several approaches, such as plant growth regulator application, mutation breeding, chromosome manipulation, gene silencing and genome editing (Pal *et al.*, 2021; Indian *et al.*, 2023) [7, 6]. At the molecular level, this phenomenon involves complex regulatory networks comprising genes associated with hormone biosynthesis, transport, perception and signal transduction pathways (Susila *et al.*, 2013) [8].

Types of parthenocarpy

1. **Natural or genetic parthenocarpy**: Natural or genetic parthenocarpy may occur spontaneously, without external stimulation, or may be expressed under environmental conditions that are unfavourable for pollination and fertilization (Patel *et al.*, 2022; Baddigam *et al.*, 2024) [10, 9]. It is often associated with increased endogenous hormone levels in the ovary, which promote fruit development even in the absence of pollination and fertilization (Patel *et al.*, 2022; Baddigam *et al.*, 2024) [10]. This type of parthenocarpy has been reported in several vegetable crops, including tomato, eggplant, cucumber and sweet pepper (Dhatt & Kaur, 2016; Patel *et al.*, 2022; Indian *et al.*, 2023; Chaudhari *et al.*, 2024) [11, 12, 13, 6].
2. **Artificial parthenocarpy:** Artificial parthenocarpy involves the stimulation of ovary development and subsequent fruit formation in the absence of pollination and fertilization through human-directed interventions (Patel *et al.*, 2022; Indian *et al.*, 2023; Chaudhari *et al.*, 2024) [10, 6, 11].

Genetics of parthenocarpy

Parthenocarpy is a heritable trait; however, its genetic control varies considerably among vegetable crops and does not follow a uniform inheritance pattern. In tomato, the trait is associated with several recessive genes (Fos *et al.*, 2001; Gorguet *et al.*, 2005) [14, 15], whereas in *Capsicum annuum* L., it is governed by a

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single recessive gene (Tiwari *et al.*, 2011) [16]. In cucumber, parthenocarpy exhibits a more complex inheritance pattern involving two major genes with additive, dominance and epistatic effects, along with additive-dominant polygenes in both monoecious and gynoecious forms (Yan *et al.*, 2010) [17].

In tomato, the *pat* gene is a recessive mutation associated with pleiotropic effects on fruit development. It promotes rapid ovary growth during the first 10 days after anthesis, accompanied by early initiation of pericarp cell division and increased auxin, gibberellin and DNA levels in the ovary (Mapelli *et al.*, 1978) [18]. Furthermore, three alleles, namely *pat*, *pat*-2 and *pat*-3/*pat*-4, have been identified as genetic sources of facultative parthenocarpy due to their influence on the hormonal balance of the ovary compared with wild-type plants (Fos *et al.*, 2001) [14]. In cucumber, genetic variation associated with parthenocarpy has also been reported, with polymorphism ranging from 3–8% among cultivated varieties and 10–25% among botanical cultivars (Behera *et al.*, 2011) [19].

Scientific suggestion: Keep the gene symbols (*pat*, *pat*-2, *pat*-3 and *pat*-4) in italics throughout your manuscript. Also, verify the exact interpretation of the cucumber polymorphism percentages against the original Behera *et al.* (2011) [19] publication before submission.

The inheritance of parthenocarpy is highly variable across crop species and is governed by diverse genetic factors. In tomato, several recessive mutations, particularly *pat*, *pat*-2 and *pat*-3/*pat*-4, have been identified as important genetic determinants of natural parthenocarpy. These alleles modify hormonal regulation within the ovary and stimulate its premature growth before fertilization (Mazzucato *et al.*, 1998; Picarella *et al.*, 2024) [20, 21].

Gene expression studies for parthenocarpy

Auxin plays a significant role in the regulation of parthenocarpic fruit development, with endogenous IAA concentrations influencing its expression. The regulatory role of endogenous auxins in cucumber parthenocarpy was initially documented by Kim *et al.* (1992b) [22]. Subsequently, Su *et al.* (2021) [4] reported enhanced expression of auxin signalling genes, such as AUX22A-like-1, AUX22B-like-2 and AUX28-like, in parthenocarpic cucumber compared with non-parthenocarpic genotypes. Besides auxins, gibberellins are also involved in fruit development, and the GA biosynthesis-associated gene $GA20_{ox}$ was found to be highly expressed in pollinated pear fruits (Wang *et al.*, 2020) [23].

In addition to auxin-related pathways, gibberellin signalling components, particularly DELLA proteins and GID1 (Gibberellin Insensitive Dwarf1), are also involved in the regulation of parthenocarpy. DELLA proteins and GID1 function as negative and positive regulators of gibberellin responses, respectively (Hedden, 2020) [24]. In tomato, the expression of cytokinin biosynthesis-related genes, including $SlIPT_1$, $SlIPT_2$, $SlCYP735A_1$, $SlCYP735A_2$ and $SlLOG_2$, was found to increase in the ovary following anthesis, suggesting their involvement in hormonal regulation during early fruit development (Matsuo *et al.*, 2012) [25].

Several approaches can be used to induce artificial parthenocarpy

Parthenocarpy can be artificially induced through several approaches, including the application of plant growth regulators, distant hybridization, mutagenesis, irradiated pollen, chromosome number manipulation, gene silencing, targeted genetic modification and genome editing (Indian *et al.*, 2023; Baddigam *et al.*, 2024; Chaudhari *et al.*, 2024) [6, 9, 11].

1. **Plant hormone use:** Gibberellins, cytokinins, and auxins are known to promote parthenocarpic fruit development. However, the application of other plant growth regulators, including 2,3,5-triiodobenzoic acid (TIBA), CPPU, and 2,4-D, can result in the formation of hollow seeds surrounded by a thin, soft, and edible outer layer (Hassan & Miyajima 2019 [26]; Cong *et al.* 2020; Baddigam *et al.*, 2024 [9]; Chaudhari *et al.*, 2024 [11]; Maupilé *et al.* 2024; Meng *et al.*, 2024) [27].
2. **Hybridization:** Facultative parthenocarpy can be introduced through interspecific hybridization. Furthermore, interspecific hybridization-mediated modification of ploidy has been widely adopted as a breeding strategy for developing parthenocarpic fruits in watermelon, tomato, and banana (Baddigam *et al.*, 2024; Chaudhari *et al.*, 2024) [9, 11].
3. **Mutation:** Mutations may occur spontaneously under natural conditions or be induced artificially. These genetic alterations can affect various processes, including signaling pathways, hormone biosynthesis, fruit development, and conventional breeding mechanisms, thereby promoting the initiation and development of parthenocarpic fruits (Baddigam *et al.*, 2024; Chaudhari *et al.*, 2024) [9, 11].
4. **Irradiated pollen**: Seedless fruit development can be promoted through the application of pollen treated with different intensities of X-ray and gamma-ray radiation (Baddigam *et al.*, 2024; Chaudhari *et al.*, 2024) [9, 11].
5. **Chromosome number change:** Parthenocarpic fruit development can be achieved by exploiting the disrupted coordination of embryo and endosperm development associated with triploid genetic conditions (Baddigam *et al.*, 2024) [9].
6. **Gene transfer and silencing:** The application of genetic engineering has enabled the development of parthenocarpic fruits through the targeted manipulation of genes involved in phytohormone signaling, auxin biosynthesis, and associated regulatory pathways. Successful induction of parthenocarpy has been reported in genetically modified tobacco (*Nicotiana tabacum* L.), eggplant, and tomato, although unintended changes in plant phenotype have sometimes been observed (Kim *et al.*, 2019; Baddigam *et al.*, 2024) [28, 9].

Factor affecting parthenocarpy

1. **Genetic Factors:** Phytohormone-related genes, particularly those involved in auxin and gibberellin production, play a significant role in regulating fruit initiation and development. Functional alterations in these genes can promote parthenocarpic fruit formation. The $SlAGL_6$ gene, in particular, has been identified as a major genetic regulator of parthenocarpy in tomato, as mutations in this gene result in seedless fruit development (Fos *et al.*, 2001) [14].
2. **Hormonal Factors**: Hormonal regulation is a key factor governing parthenocarpic fruit development. Auxins, particularly indole-3-acetic acid (IAA), stimulate fruit initiation and expansion, while ethylene modulates fruit growth and maturation and can promote parthenocarpy following exogenous application in specific plant species. Other phytohormones, including gibberellins, cytokinins, and abscisic acid, also contribute to the regulation of fruit developmental processes associated with parthenocarpy (Nothmann *et al.*, 1975) [29].

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3. **Environmental Factors**: Environmental factors play an important role in regulating parthenocarpic fruit development. Climatic conditions, particularly temperature, light intensity, and water availability, can significantly influence fruit initiation and growth. Elevated temperatures during the flowering stage may stimulate auxin production, thereby promoting parthenocarpy. Similarly, sufficient water availability is essential for normal fruit development, whereas water deficit may adversely affect fruit growth and restrict parthenocarpic fruit formation (Dalal *et al.*, 2006) [30].
4. **Pollination and Fertilization**: Parthenocarpic fruit development involves complex interactions with reproductive processes, particularly pollination and fertilization, which differ among plant species (Gorguet, 2008) [31].

Utility of parthenocarpy in vegetable crops improvement

1. **Tomato (*Solanum lycopersicum* L.):** Polyploidization, particularly the development of triploid cultivars, represents a potential approach for inducing parthenocarpy in tomato. These genotypes are often associated with elevated dry matter and total soluble solids (TSS) contents (Fayaz *et al.*, 2021) [32]. Furthermore, seedless fruits generally exhibit desirable quality attributes, including improved flavour, increased sugar accumulation, higher dry matter content (up to 1%), reduced acidity and cellulose content, and enhanced TSS. Despite these compositional differences, fruit morphology and locular jelly content remain comparable to those of seeded tomatoes (Ganvit *et al.*, 2024) [33].
2. **Eggplant (*Solanum melongena* L.):** In eggplant, parthenocarpic fruit development can be stimulated by β-naphthoxyacetic acid treatment, yielding seedless fruits with characteristics comparable to pollinated fruits in terms of size and external appearance (Makrogianni *et al.*, 2018) [34]. Moreover, conventional hybridization with high-performing lines possessing desirable fruit quality attributes has facilitated the incorporation of parthenocarpy into improved cultivars (Patel *et al.*, 2022; Ganvit *et al.*, 2024) [10, 33].
3. **Sweet pepper (*Capsicum annum* L.):** The induction of parthenocarpy in 'Shishito' sweet pepper was accomplished by treating the ovaries with 2,4-D (20 ppm) after eliminating the stamens and stigmas from the flowers (Kondo *et al.*, 2021) [3].
4. **Muskmelon (*Cucumis melo* L.):** Parthenocarpic fruit production in muskmelon can be effectively promoted through different approaches. Gamma irradiation of pollen at 550 Gy has been reported to achieve complete parthenocarpic fruit formation, while CPPU treatment at 10 ppm during anthesis has also resulted in a 100% fruit-set response (Bagheri *et al.* 2021; Fayaz *et al.* 2021) [32].
5. **Cucumber (*Cucumis sativus* L.):** Exogenous application of GA_3 (100 ppm) during the pre-flowering stage has been identified as an effective approach for inducing parthenocarpic fruit development (Chaudhari *et al.*, 2024) [11]. In addition, the F_2 hybrid PPC-2 × *Pusa* Uday exhibited promising parthenocarpic potential, producing a considerable number of fruits under both early- and late-season growing conditions (Jat *et al.*, 2017) [35].

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