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Physiological interventions in induction of parthenocarpy with fruits and vegetables: A Review

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Abstract

Seedless fruits have gained importance in the present era of the Horticulture Industry. One of the scientific reasons behind that seedlessness is parthenocarpy i.e. production of fruits without pollination and fertilization. The processes of positive and negative signaling that occur after pollination and fertilization are fundamentally dependent on plant growth hormones. These hormones are necessary for the growth and development of seeds and fruit. Exogenous application of different concentrated plant growth regulators, particularly auxin, cytokinins, and gibberellins, or combinations of these, prior to floral induction can also result in seedless fruit. It has been documented in a number of fruit and vegetable crops, including cucumber, tomato, brinjal, apple, and pears. A tight control between these two growth hormones can be seen in the early phases of fruit development, where auxin application promotes gibberellin biosynthesis and gibberellin application increases auxin content. Synthetic cytokinins are applied to pre-anthesis ovaries to activate cell division, which leads to the production of parthenocarpic fruit.

Keywords auxins, cytokinins, gibberellins, melatonin, phytohormones

Introduction

The term parthenocarpy denotes for the development of fruits without pollination and fertilization. When the fruit is entirely empty of seeds, contains only a very limited number of tiny seeds, or has aborted seeds, the fruit is said to be parthenocarpic. According to Pandolfini [1], consumers prefer seedless fruits both when they are consumed fresh (such as watermelons, grapes, citrus fruits, and bananas) and as processed one (such as frozen aubergine and tomato sauce). Parthenocarpy and stenospermocarpy (seeds abort after fertilization) are the ways to produce seedless fruits [2] and some external factors like temperature plays an important role in parthenocarpy production by interrupting the pollination and fertilization. The production of pollen, germination, and fertilization is adversely impacted by these environmental factors, which have a negative impact on the quantity and quality of fruit. Parthenocarpy is therefore regarded as the most effective method of producing fruits in environments that are unfavorable to pollination and fertilization. Additionally, in some crops such as egg plants, the lack of seeds can enhance fruit quality, while in dioecious plant species such as the Kiwi, fruit parthenocarpy may boost productivity because pollinator plants are no longer required.

With some supporting data from the literature, this review will focus on how hormones affect the production of parthenocarpic fruits and vegetables.

Growth phase in fruit development

Srivastava and Handa [3], have reported that the seeded fruits have four main growth phases. Floral development, pollination, fertilization, and fruit setting are the characteristics of phase I. Intense cell division characterizes phase II, during which the majority of fruit cells are formed. Cell expansion occurs in phase III, whereas fruit growth is reduced and ripening occurs in phase IV. Activation of cell division at the start of the second phase and cell expansion at the start of the third phase corresponds with two gibberellin accumulation peaks throughout fruit development. The authors claim that the accumulation of this plant growth hormone during phase III in parthenocarpic fruits is less pronounced than in fruits with seeds. Gibberellin increases in phase III occur during the peak fruit growth.

Importance of seedlessness

A few well-known benefits of seedless fruits have been highlighted as follows, 1. Fruits without seeds are often smaller than their seeded counterparts in size (eg: Grape, Mango). 2. Parthenocarpic fruits (induced by GA3) in apples were more elongated than seeded fruits. 3. In most grape varieties, seedless are sweeter than seeded fruits of the same variety. 4. Fruits usually have very smooth surfaces except guava which has warty surfaces. 5. Because of ethylene produced by seeds, seedless fruits generally mature later than their counterparts.

Causes for parthenocarpy

Lack of pollination, Pollination occurs but fertilization does not and Fertilization is followed by embryo (seed) abortion, these are all contribute to parthenocarpy.

Causes for absence of pollination

Lack of pollination is caused by male sterility, self-incompatibility, unfavorable environmental conditions, absence of pollinators and pollinizers, and some dioecious species.

Need for fruit without seeds

Due to the improvement in eating quality, seedlessness is a desirable attribute for customers and buyers. It is also preferred by processors so that less waste is generated and it increases novelty in fruit crops.

Types of parthenocarpy

(I). ***Nature or genetic parthenocarpy***

a) Obligatory parthenocarpy - Parthenocarpy due to prevention of pollination, Eg. Ivy gourd. b) Facultative parthenocarpy - Due to genetic sterility (continuous vegetative propagation), Eg. Tomato, Brinjal, Pine apple. c) Vegetative/Autonomic parthenocarpy - It does not require any external stimulus, Eg. Washington navel orange, Oriental persimmon, Cucumber, Banana.d) Stimulative parthenocarpy/ Aitionomic parthenocarpy – Pollination or other stimulus is required for fruit production, Eg. Black Corianth grapes, Blackberries, pear. e) Stenospermocarpy - Pollination fertilization occurs but the embryo gets aborted i.e. embryo abortion, eg. Thompson seedless grapes, Sindhu variety of Mango.

(II). ***Artificial parthenocarpy***

Different techniques, including the use of plant growth regulators, distant hybridization, mutation, the use of irradiated pollen, changes in the number of chromosomes, gene silencing, gene alterations, and genome editing, can be used to induce artificial parthenocarpy [4].

Parthenocarpic fruits tend to be produced with the application of different growth regulators at varied concentration is presented in Table 1.

Table 1. PGR induced parthenocarpy

Crop	PGR	Concentration	Reference
Muskmelon	CPPU	10mg/L and BA	Hayata et al., [5]
Kokrol	2, 4-D	50 ppm	Chowdhury et al., [6]
Pumpkin	GA3	150ppm	Sharif Hossain [7]
Watermelon	CPPU	0.5ml/lit	Kawamura et al., [8]
Pear	CPPU	-	Cong et al., [9]

Distant hybridization

In order to produce parthenocarpic fruits in a variety of crops, including citrus, banana, and watermelon, it is often necessary to alter the ploidy level by interspecific hybridization [10]. Three wild relatives of brinjal were crossed with seven cultivated accessions by Afful et al., [11] and the resulting hybrids of SA002- 02 x *Solanum torvum* and SMA003-03 x *Solanum torvum*, exhibit no seeds (parthenocarpic). The main contributing factor for this parthenocarpy was Allelic incompatibility at fertilization [12].

Use of irradiated pollen

The main benefit of employing X-ray irradiated bottle gourd pollen for parthenocarpy is the ability to produce diploid cultivars of seedless watermelon (*Citrullus lanatus*). The rate of fruit set when pistillate watermelon flowers were pollinated with bottle gourd pollen was 57.1% (with watermelon pollen it was 65.0%). Pollination with bottle gourd pollen resulted in the deformation (triangular or oblong shape) of all parthenocarpic fruits. The watermelon ovules were not reached by bottle-gourd pollen tubes. According to research [13], the parthenocarpy generated by bottle gourd pollination was stimulative parthenocarpy rather than false parthenocarpy (pseudogamy). Different gene modifications for parthenocarpic fruit production in different crops are listed in Table 2.

Table 2. Parthenocarpy by gene modifications

Gene	Function	Gene modification	Crop	Reference
DeH9-iaaM	Auxin biosynthesis	Expression of Ovule Specific Transgene	Tobacco, Raspberry. Tomato, Brinjal, Cucumber	Yin et al., [14], Mezzetti et al., [15], Pandolfini et al., [16], Rotino et al., [17],
SEP1/TM29	Cytokinin	Antisense or cosuppression; MADSbox	Tomato	Dwamena et al., [18]
SlDELLA	Gibberellin signaling	Antisense down regulation	Tomato	Marti et al., [19]
ARFs	Response of Auxin	RNAi Technolgy	Eggplant	Du et al., [20]
pTA29	Tapetum-specific promoter	Male sterility	Ponkan mandarin	Li et al., [21]

Physiological basis of parthenocarpy

Fruit development involves three sequential events i.e. fruit setting, cell division, and cell enlargement. After fruit setting a slow increase in fruit size has been seeded due to cell division and subsequently cell enlargement takes place. The number of small and tightly compressed divided cells determines the final size of the fruit. Cell expansion increases fruit size by 100 folds, and it makes the greatest contribution to the final fruit size. After pollination or the onsets of fruit development from the ovary to its maturity, which are regulated by phytohormones and closely coupled and synchronized [22]. How the plant hormones will control the growth of fruit and seeds are represented in Figure 1.

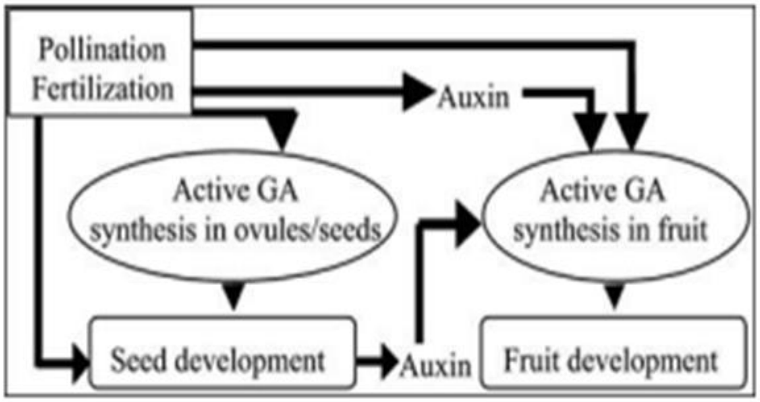

Figure 1. A proposed model for controlling the growth of fruit and seeds

A proposed model for the interaction between the plant hormones auxin, cytokinin and sugar accumulation during the parthenocarpic fruit development of cucumbers are shown in Figure 2. In comparison to non-parthenocarpic fruit, sugar biosynthesis was increased in parthenocarpic fruit. Auxin and cytokinin signaling were stimulated by the sugar buildup, which subsequently induced fruit initiation [23].

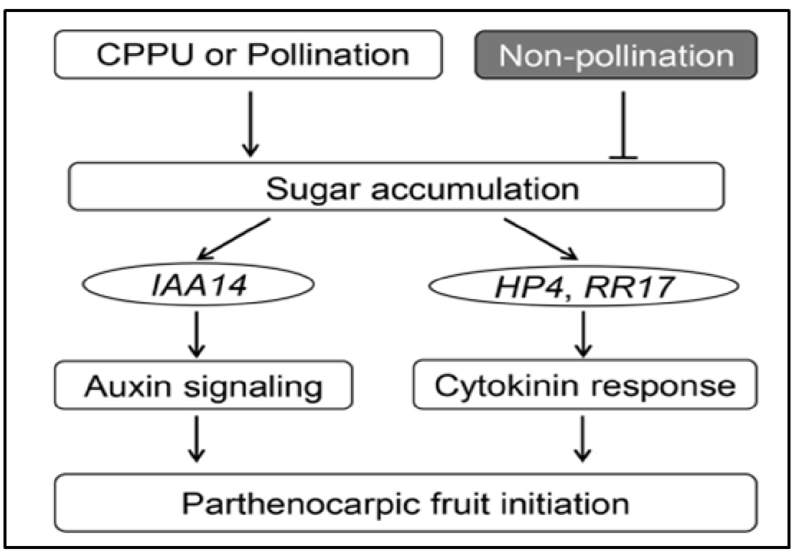

Figure 2. A model proposed for the control of fruit development in cucumber by Auxin and Cytokinin

Role of plant growth regulators in parthenocarpy production

Scientific evidence of the production of seeds-free fruits through the exogenous application of plant growth regulators has been provided by the authors listed below.

Auxin

The dwarf tomato cultivar MicroTom was utilized as a model in investigations on the hormonal regulation of fruit set and growth due to its diminutive size and rapid reproductive cycle (Serrani et al., [24]). In addition, auxins and GAs appear to control fruit growth by regulating cell expansion and division. The effect of different growth regulators on tomato ovary is represented in Figures 3, 4, and 5.

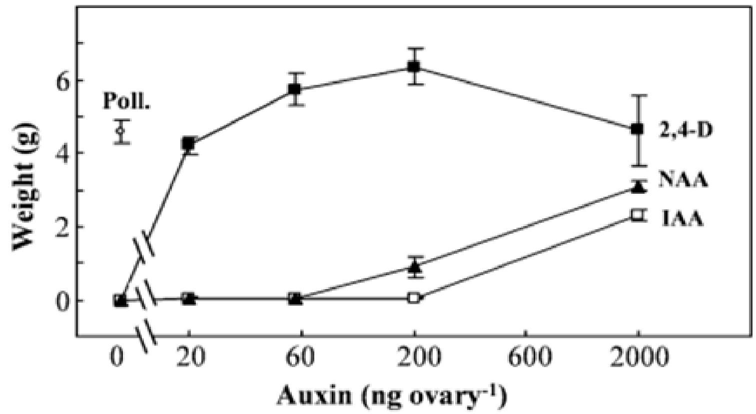

Figure 3. Unpollinated tomato ovary dose response to 2,4-D, NAA, and IAA treatment.
The fruits were harvested at 20 days following the hormone treatment (Source: Serrani et al., 2007 [24])

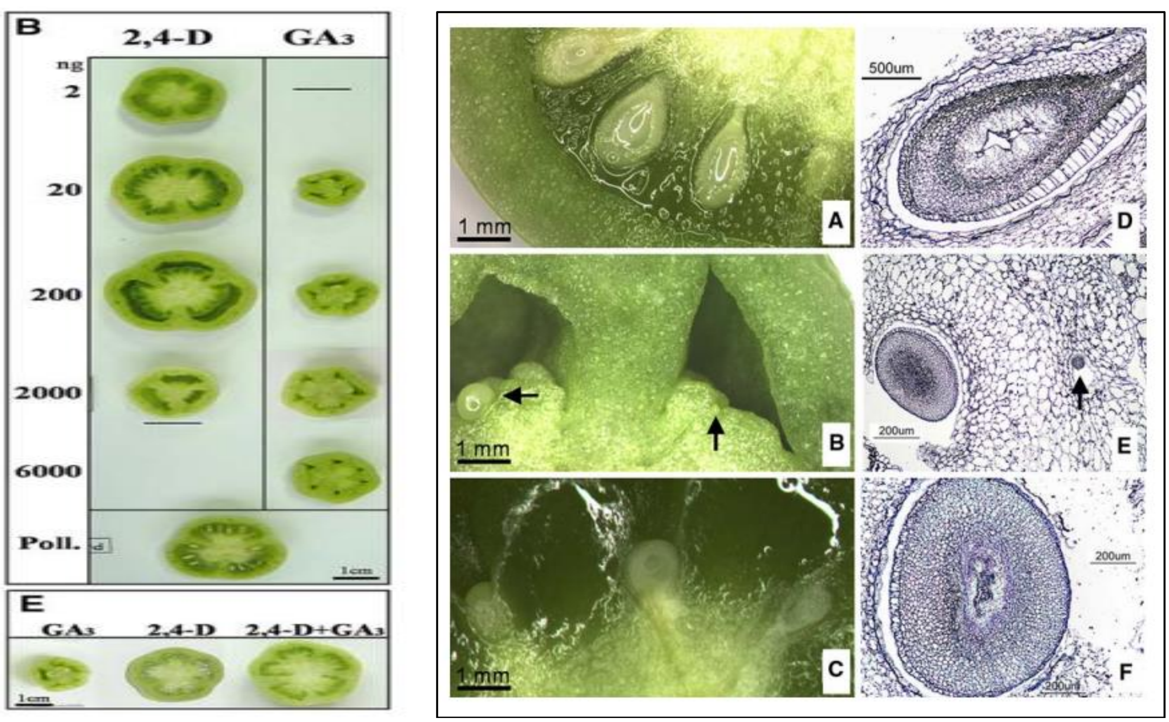

Figure 4. GA$_3$, and fruits generated by 2,4-D have varying hormone levels. (A, D)- Pollinated fruit seeds, (B, E)- Ovules that are poorly developing and degenerating in GA$_3$-induced fruits, and (C, F)- Pseudoembryos in 2,4-D-induced fruits. A cross section (D, E, and F) was made from a tissue that had been fixed in paraffin embedded tissues. Fruits were collected 20 days following hormone application or pollination. The ovule position in the GA$_3$-treated ovaries is indicated in B with arrows (Source: Serrani et al., [24]).

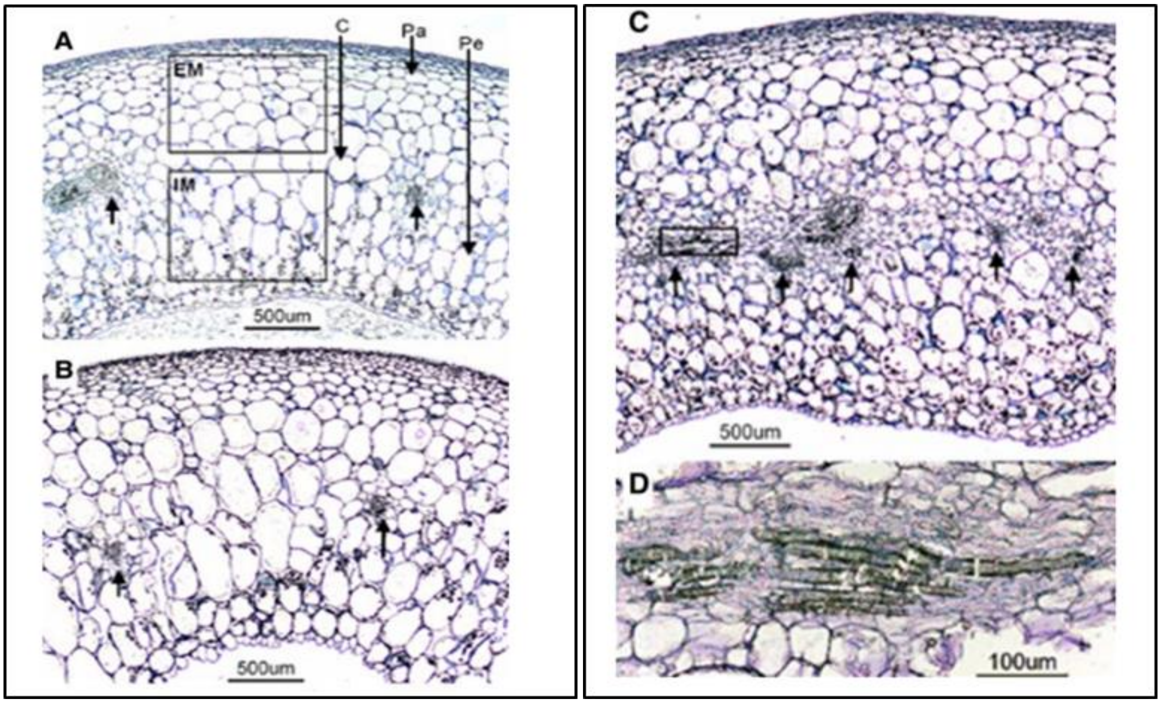

Figure 5. Pollination, GA3, 2,4-D, and its effects on the pericarp histology. (A). Transverse pericarp portions of 20-day-old fruits shown in representative images pollinated (B). Fruit produced by 2000 ng per ovary- GA3 that has parthenocarpy. (C, D). Parthenocarpic fruit produced by 200 ng/ovary. The enlarger from C depicts representative tracheid bundles formed in 2,4-D-induced fruits-D. (Source: Serrani et al., 2007 [24]).

Cytokinin

When synthetic cytokinin was applied to pre-anthesis ovaries, it stimulates cell division, which led to the production of parthenocarpic fruit (Phase II) [25]. Consequently, cytokinin serves as a beneficial regulator for fruit development. Regardless of accessions with significantly greater length, diameter, and weight than seeded fruits, using forchlorfenuron and CPPU at a concentration of 100 ppm, Hassan and Miyajima [26] developed an efficient method for cultivating seedless fruits in pointed gourds.

Gibberellic acid

The application of GA3 results in the growth of parthenocarpic apples as compared to NAA, and other treatments like 1-n-naphthylphthalamic acid (NPA), Hand pollinated, open pollinated and negative control. However the fruits treated with GA3 were less acidic than hand-pollinated controls but maintained an equal level of firmness, starch, and sugar (Figure 6). The transcriptome study revealed that the RNA expression profiles of fruits treated with GA3 and those that were hand-pollinated were very similar. In contrast to the pH changes, the observed shape changes in GA3-treated ovaries were connected with early expression differences in potential cell division, cytokinin degradation, and cell wall modification genes. However, the acidity gene Ma1 may have been the root cause of the pH changes. Overall GA3 promotes the growth of parthenocarpic apple fruits with morphological abnormalities that are connected to alterations in the expression of numerous candidate genes [27].

Increased bioactive gibberellin deactivation by GA 2-oxidases (GA2oxs) could also contribute to the rise in gibberellin concentration following pollination. According to Shinozaki et al., [28] parthenocarpic tomato fruit production was caused by the negative GA signaling regulators GA2ox and DELLA's genes being silenced. The cytokinin biosynthetic gene IPT (isopentenyl transferase), which seems to regulate cytokinin expression, has also been linked to the development of parthenocarpic tomatoes [25]. According to Chai et al., [29] the exogenous application of cytokinin to grapes increases the expression of GA biosynthetic genes, which leads to parthenocarpic fruit set that is mediated by GA.

Figure 6. Hormone-treated and control fruit morphology. (a-g). Fruits on the tree, 14 days following treatment (DAT), (a). The GA3 treatment, (b). NAA treatment, (c). GA3 treated with NAA, (d). 1-n-naphthylphthalamic acid (NPA) treated, (e). Negative control, (f). Control via hand pollination, (g). Control for open pollination. (h-n). Fruits that were longitudinally sectioned at 18 DAT, (h). GA3 treatment, (i). NAA treatment, (j). GA3 treated with NAA, (k). NPA-treated, (l). Negative regulation, (m). Control that was hand-pollinated, (n). Control for open pollination. (o-r). Fruit morphology at harvest after hand pollination and GA3 treatment (132 DAT), (o). Fruit treated with GA3 in longitudinal section, (p). Medial cross-section of fruit treated with GA3 reveals the absence of seeds, (q). a fruit that was hand-pollinated, cut longitudinally, (r). A medial cross-section of a hand-pollinated fruit reveals that three of the fruit's five locules contain seeds. White arrows and a dashed line serve as a partial indication of the ovary wall/hypanthium borders. Typical locules are denoted by black arrows. (Adopted from Galimba et al., [27]).

Melatonin

According to Liu et al., [30] the 'Starkrimson' pear (P. communis L.) benefited from the exogenous application of MT because it encouraged the expansion and division of the mesocarp cells in a way that was comparable to hand pollination. Here, the normal seeded fruits were produced by hand pollination, but the fruit without seeds was produced by MT-treated ovaries (Figure 7). However, the exogenous melatonin-treated fruit seeds were immature and failed to develop later on in the fruit-setting stage. Researchers examined variations in related hormones in the ovaries to learn more about how MT produced parthenocarpy. 'The MT ovaries had a bigger area of mesocarp cells than the CK ovaries, but the MT and HP ovaries did not differ significantly in size, and the MT ovaries had a significantly smaller number of ovular cell layers than the hand pollination. Therefore, MT can encourage cell growth and division but not typical ovular development (Figure 8). They found that the gibberellins GA3 and GA4 were considerably more abundant in the ovaries after exposure to MT. Therefore, the association between gibberellic acid and melatonin was investigated using paclobutrazol (PAC), an inhibitor of GA-biosynthesis. Furthermore, neither parthenocarpy nor the concentration of gibberellic acid was increased by spraying MT following treatment with PAC. A transcriptome analysis revealed that MT can greatly upregulate PbGA20ox and dramatically downregulate PbGA2ox genes which are induced by MT treatment in GA biosynthesis pathway. Additionally, MT controls parthenocarpy through the GA synthesis pathway and exogenous melatonin is involved in the metabolism of plant hormones. GA20ox and GA2ox genes are principally regulated to raise Gibberellic acid content and promote fruit set. Melatonin promotes GA production, which causes cell division and the development of the mesocarp, which yields fruit, to be stimulated (Liu et al., [30]).

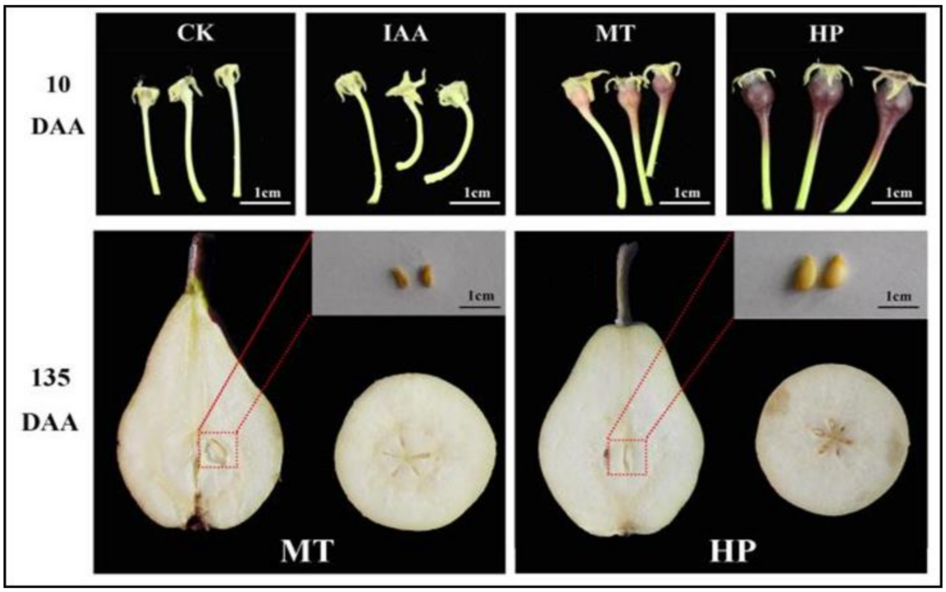

Figure 7. Compared to other treatments, the effects of melatonin on fruit morphology and seed development. Control-cytokinin; treated with indole-3-acetic acid-IAA; treated with melatonin-MT; hand pollinated-HP. (Source: Liu et al., [30])

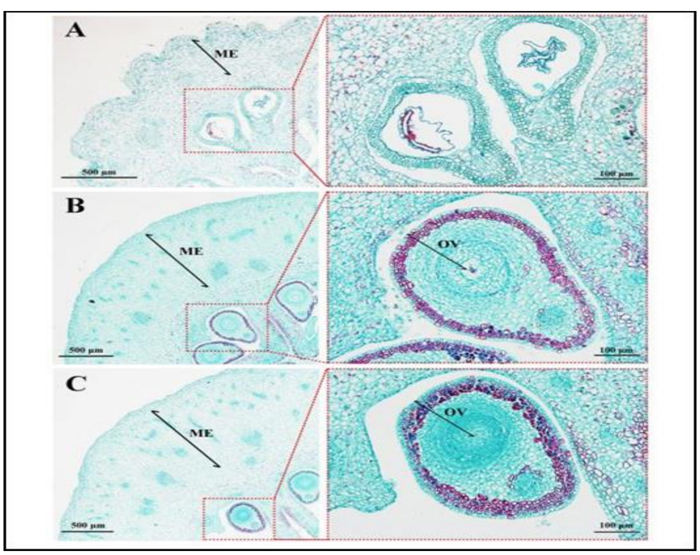

Figure 8. Five days after anthesis (DAA), observations on the histological composition of the 'Starkrimson' pericarps. (A) Control-CK (B) Melatonin treatment-MT; and (C) Hand pollination - HP. Ovule-OV; Mesocarp-ME. (Source: Liu et al., [30]).

Recent technologies in parthenocarpic production

Using cultivars of both parthenocarpic and non-parthenocarpic cucumber, the first RNA sequencing study for parthenocarpic fruit development in zucchini (*Cucurbita pepo* L.) was conducted. This study demonstrated the activating effects of auxins and GAs against the inhibitory effects of ethylene, and the author identified several candidate genes that may serve as markers for parthenocarpic selection in the ongoing breeding programs for zucchini [31] and they concluded that phytohormones play a significant role in fruit set. So, several studies have proven that parthenocarpy production of fruits and vegetables is possible through many scientific ways. Here, some of the public and private sector parthenocarpic varieties and hybrids are presented in Table 3 and 4.

Table 3. Public sector parthenocarpic varieties in India

Institute	Crop	Varieties Developed
IARI, New Delhi	Cucumber	DPaC-6, 4 DPaC- 9 and 5 DPaC-10, Pusa seedless cucumber-6
	Watermelon	Pusa Bedana
GBPUAT, Pantnagar	Cucumber	Pant Parthenocarpic Cucumber 2, Pant Parthenocarpic Cucumber 3
IVRI, Varanasi	Pointed gourd	IIVRPG- 105
KAU, Kerala	Cucumber	KPCH-1
	Watermelon	Shonima (Red) and Swarna (Yellow)
IIHR, Bengaluru	Watermelon	Arka Madhura
PAU	Cucumber	Punjab Kheera Hybrid -11

Table 4. Private sector parthenocarpic cucumber hybrids

SN.	Name of the hybrid	Source
1.	Asma	Tropic seeds Pvt Ltd.
2.	Aviva	Tropic seeds Pvt Ltd.
3.	Claudia	Tropic seeds Pvt Ltd.
4.	Hilton	Nickerson zwaan (Netherland)
5.	Isatis	Nunhemps India Pvt Ltd.
6.	Kian	Nunhemps India Pvt Ltd.
7.	NS-492	Namdhari seeds India Pvt Ltd.
8.	NS-498	Namdhari seeds India Pvt Ltd.
9.	NS-499	Namdhari seeds India Pvt Ltd.
10.	Pusa Parthenocarpic Cucumber-6	Agrinnovate India Ltd.
11.	PY-1026	East West seeds India Pvt Ltd.

Conclusion

Through the above mentioned scientific analyses, it was revealed that parthenocarpic fruit development could be achieved by employing an advanced technical tool and exogenous application of plant growth regulators, even in environments that were adverse to fruit set and growth. The molecular characterization of fruit growth and ripening as well as the enhancement of fruit quality in terms of shelf life and nutritional value require an in-depth understanding of the hormonal regulation of fruit development.

Future thrust and prospects

Exploitation of biotechnological tools can enhance the efficiency and identification of parthenocarpic genes across crops for the benefit of mankind. Parthenocarpic production is beneficial when they are stable without any segregation in further generations. This fundamental understanding of the development process is crucial because it will give the precise knowledge required to eventually create designer vegetables and fruits with improved quality and longer shelf lives.

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