

Review

Parthenocarpy, a pollination-independent fruit set mechanism to ensure yield stability

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Fruit development is essential for flowering plants' reproduction and a significant food source. Climate change threatens fruit yields due to its impact on pollination and fertilization processes, especially vulnerable to extreme temperatures, insufficient light, and pollinator decline. Parthenocarpy, the development of fruit without fertilization, offers a solution, ensuring yield stability in adverse conditions and enhancing fruit quality. Parthenocarpic fruits not only secure agricultural production but also exhibit improved texture, appearance, and shelf life, making them desirable for food processing and other applications. Recent research unveils the molecular mechanisms behind parthenocarpy, implicating transcription factors (TFs), noncoding RNAs, and phytohormones such as auxin, gibberellin (GA), and cytokinin (CK). Here we review recent findings, construct regulatory models, and identify areas for further research.

Flowering and fertilization success in a suboptimal environment

In flowering plants, the initiation of fruit development unfolds in a three-step process: ovary and stamina development, ovule fertilization, and fruit set. Successful fruit set hinges on flower fertility and pollinator visitation, which face mounting challenges due to climate change. Between 1951 and 2012, we have experienced an average global warming trend of 0.12°C per decade, and forecasts predict a global temperature rise of no less than 1.5°C by the end of the 21st century [1]. High temperatures have a drastic effect on pollen viability and pollen tube growth. On female sexual organs, high temperature interferes with ovule and ovary development (see Figure 1) [2–5]. Climate change also alters flowering times, misaligning their life cycles with those of pollinators [6,7]. The consequence is the decline of pollinator populations, exacerbated by the increased use of pesticides and the destruction of pollinator habitats [8–12].

To overcome the decline of crop pollination, producers have resorted to mechanical methods such as pollen dusting and hand pollination. However, these methods are costly [13]. Chemical treatments (e.g., hormone treatment) are also applied to improve fruit set and size or to modify the flower sex ratio [14–18]. In **monoecious** (see Glossary) species, the optimal female-to-male flower ratio is 1:1 [19], and a shortage of female flowers hampers fruit set in species such as melons [20]. In cucurbits, sex determination genes, such as *CmWIP1* and *ACS11*, are a promising means to optimize flower sex ratio [21,22]. Nectar production also plays a central role in attracting pollinators [23]. However, enhancing these flowering traits does not fully address the challenges of fertilization failure and pollination shortages. Improving pollen viability under adverse conditions is a potential solution [24]. An alternative approach is the parthenocarpy, a mechanism that leads to fruit development without flower fertilization [25]. Cultivating parthenocarpic plants has the potential to reduce reliance on pollinators and the need for chemical interventions [26,27]. The absence of seeds in parthenocarpy fruits can also be attractive to consumers and advantageous in food processing.

Highlights

The hormonal variation essential for fruit set differs regarding crop species.

Parthenocarpy is a key trait to reduce the climate dependency of fruit crops.

Two distinct molecular mechanisms lead to a gibberellin-induced fruit setting.

Transcription factors and miRNA interactions control parthenocarpy in several species.

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Parthenocarpic fruit setting occurs when the concentration of certain **phytohormones** exceeds a threshold [27]. As a result, hormone treatments have been widely used to induce fruit development. Chemical-free approaches are also possible through mutations in hormone-regulatory genes. Nonetheless, the variations in fruit set mechanisms between different species introduce a significant challenge when it comes to implementing parthenocarpy. To promote parthenocarpy in crop production systems, it is instrumental to understand the molecular mechanisms driving fruit set in different crop species. In this review, we synthesize recent research on fruit set, highlighting the role of the main phytohormones and key gene regulators. Focusing on successful case studies, we propose new research directions in the field of fruit set and parthenocarpy.

Parthenocarpy, a pollination-independent fruit setting mechanism

Fruit set: the first step of fruit development

In angiosperms, the pollen grain contains two sperm cells, resulting from the division of the generative cell. Fertilization of the ovule follows a mechanism called 'double fertilization.' When the pollen tube reaches the embryo sac, a sperm cell fertilizes the egg cell, giving rise to the zygote, which develops into an embryo. The second sperm cell fertilizes the central cell of the embryo sac to form the triploid endosperm [28]. The contribution of parental genomes to embryo development is highly coordinated [29]. Recent research on *BABY BOOM1* (BBM1) indicates the transmission of pluripotency factors from the male genome [28]. These processes can last several hours. In *Cucumis* species, fertilization occurs approximately 30–36 h after pollination [30]. These synchronized events serve as a signal that triggers fruit set.

The occurrence of fruit set is characterized by a predominant state of cell division within the ovary. marked by the dynamic interplay of several phytohormones, including auxins [indole-3-acetic acid (IAA)], GAs, CKs, brassinosteroids (BRs), abscisic acid (ABA), and ethylene (ETH) [31-33]. These phytohormones, known as plant growth regulators (PGRs) (Box 1), orchestrate the growth and maturation of the fruit. The onset of fruit set is linked to a decrease in the concentrations of ABA and ETH within the ovary. In tissues surrounding the ovule, a transient oscillation of BR concentration and an increase of IAA, GA, and CK concentrations trigger ovary expansion through active cell division [32] (Figure 2A). The surge of IAA levels precedes the rise in GA levels and contributes to GA biosynthesis across ovary tissues. In Arabidopsis, it was highlighted that auxin is synthesized in ovules after fertilization, which triggers GA synthesis in silique [32,34,35]. However, in other species such as tomato or pear, the increase of both IAA and GA was measured in ovules [36,37]. Throughout the fruit set, all ovary tissues experience rapid growth, as described by Chevalier et al. in tomato, except the embryo and the endosperm [38]. Subsequent to the cell division phase, the pericarp undergoes continued growth via cell expansion, stimulated by IAA), GA, and BR [32]. In tomato, the increase in IAA concentration was shown to promote the accumulation of carbohydrates within the ovary [39]. The movement of carbohydrates, such as stachyose, raffinose, and sucrose, from sink tissues supplies energy and carbon resources to the actively dividing cells. In cucumber, the fruit set phase persists for 4 days, followed by the fruit development phase [40].

Parthenocarpic fruit set

In parthenocarpic plants, the involvement of phytohormones mirrors that of fertilization- and pollination-dependent fruit set, which includes fruit set following a successful fertilization or an unsuccessful one such as in stenospermocarpy or embryo abortion cases. However, a crucial distinction lies in the signal that initiates the hormonal variation necessary for fruit development. Unlike in fertilization-dependent fruit set, parthenocarpic plants do not require ovule fertilization for fruit set. The complex nature of parthenocarpy becomes apparent in the diversity of fruits it produces, ranging from seedless fruits to those with initiated but ultimately aborted seeds

Glossary

Anthesis: onset of flower opening. Carbohydrates: polysaccharides including sugars, starch, and cellulose. Endoreduplication: cell cycle that bypasses the mitosis step after DNA duplication, resulting in nuclear polyroloidy.

MicroRNAs (miRNAs): type of small noncoding RNA acting as regulators of gene expression.

Monoecious: sexual system where the same plant bears separate male and female flowers.

Phenylpropanoids: type of secondary metabolites derived from phenylalanine, synthesized by plants and involved in various functions, such as development and plant defense.

Phytohormones: hormones produced by plants regulating several processes, such as development, nutrition, and defense.

Recessive gene: a recessive gene is a type of gene that manifests its trait exclusively when an individual carries two copies of the recessive allele, one inherited from each parent.

Secondary metabolites: small

organic molecules produced by plants involved in survival functions, such as defense or development.





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Figure 1. Pollination and fruit setting threats under climate change and global warming. Schematic diagram of cucumber fruit set. Abbreviations: DAA, days ante-anthesis; DPA, days postanthesis.

[41,42]. This process can take two primary forms: obligatory, as exemplified by bananas, or facultative. In the latter, fertilization of flowers remains possible, and spontaneous fruit development only occurs in the absence of pollination [43]. Consequently, facultative parthenocarpy exhibits reduced dependence on climate conditions while remaining favorable to pollinators and holds promise for both indoor and outdoor agricultural production [44,45].

Parthenocarpic fruit setting can naturally occur in response to environmental stresses such as adverse temperatures or water stress [46–48]. In some species, interfering with pollination with methods such as anther ablation or pollen irradiation triggers parthenocarpy [27]. The carbohydrate content in the ovary, directly influenced by auxin concentration, positively correlates with the development of parthenocarpic fruits [48]. Certain metabolites, such as **phenylpropanoids**, have also been linked to either the promotion or reduction of parthenocarpy in various plant species, including tomato, tobacco, pear, and Arabidopsis [27]. Similar to the fertilization-dependent fruit set, flow cytometric analyses have revealed that the enlargement of nuclei and cells in the pericarp of parthenocarpic fruits prior to extensive cell expansion, the second phase of fruit development, and continues until ripening [49]. Although various factors can induce parthenocarpy, hormonal variations, whether upstream or downstream of fruit set, remain similar to fertilization-triggered fruit set.

Hormonal regulation of parthenocarpic fruit set

Parthenocarpic fruit set occurs when the concentration of specific phytohormones in the ovary crosses a threshold during flower development [50]. For instance, an increase in IAA

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Box 1. Roles of phytohormones in fruit set and their metabolism

IAA, under its active form, the indoleacetic acid, regulates cell division. The biosynthesis of IAA is catalyzed by YUCCA proteins or indole synthase. Auxin has an autoregulation system: a high level of IAA promotes *Aux/IAA* genes expression, which downregulates the auxin biosynthesis, whereas a low level of IAA downregulates *Aux/IAA* gene expression, suppressing the downregulation of IAA synthesis.

GA is mostly responsible for cell expansion. Five GA forms are considered as bioactive in angiosperms: GA₁, GA₃, GA₄, GA₇, and more recently DHGA₁₂. Their binding to *GID1*, a GA receptor, will activate the GA responsive pathways. GA 3β-hydroxylase and GA 20-oxidase (respectively, GA3ox and GA20ox) catalyze the biosynthesis of GA₁ and GA₄, which are then catabolized by GA 2-oxidase (GA2ox), whereas the biosynthesis of GA₃ and GA₇ is still unclear. GA are promoted by IAA response and repressed by DELLA proteins. GAs are responsible of DELLA protein degradation, enabling the activation of DELLA-repressed genes, initiating fruit growth.

ETH mainly impacts fruit maturation and abscission in climacteric fruits. Key enzymes in ethylene biosynthesis pathway, converting S-adenosylmethionine (SAM) to 1-aminocyclopropane-1-carboxylic acid (ACC) and ACC to ethylene, are, respectively, ACC synthase (ACS) and ACC oxidase (ACO). Ethylene receptors such as ETRs initiate ethylene signaling, which leads to the production of ethylene response factors (ERFs). Ethylene downregulation is induced under low levels of the hormone.

ABA is mainly described as regulating fruit maturation in nonclimacteric fruits and as a promoter of sugar accumulation. The main enzyme involved in its biosynthesis is the 9-cis-epoxycarotenoid dioxygenase (NCED), which catalyzes xanthoxin synthesis, a molecule then transported into the cytoplasm and metabolized in ABA. In *Arabidopsis thaliana*, the main catabolism pathway of ABA was characterized and the principal regulator identified is the cytochrome P450 monooxygenase, encoded by a member of the CYP707A family.

CKs are key promoters of cell division and differentiation. They are adenine derivatives, and their main active form in plants, trans-zeatins, are synthetized by three major enzymes: isopentyl transferase (IPT), cytochrome P450 CYP735A, and nucleoside 5'-monophosphate phosphoribohydrolase LONELY GUY (LOG). During flowering, another form, cis-zeatin riboside, is also described as important.

BRs, in fruit development, act in cell elongation, cell division, and fruit ripening. The most active BR identified is called brassinolide. BR biosynthesis begins with campesterol which undergoes a C-6 oxidation and a C-22 oxidation. Its biosynthesis is also catalyzed by a cytochrome P450 (CYP90B1 and CYP85A1/2).

concentration can supplant the need for pollination, initiating fruit set in various species [51]. Many studies described the induction of parthenocarpic fruits by application of PGR. These fruit set inducers are typically applied directly to the flowers, often at specific developmental stages that vary according to the treatment and the species. Commonly employed PGRs for inducing parthenocarpy include urea-derivative cytokinins, N-(2-chloro-4-pyridyl)-N'-phenylurea (CPPU), and GA₃. Several other hormone treatments have also been reported (refer to Table 1). ABA- and ETH-based treatments are not considered fruit set inducers, aligning with their antagonistic roles in fruit set [52]. In this regard, ETH-related treatments primarily involve ETH inhibitors. The effectiveness of these treatments may differ on the basis of species. For example, NAA does not trigger parthenocarpy in apples, and the effectiveness of various bioactive GAs in inducing parthenocarpy varies across species [53]. For instance, in cucumber and pear, the application of GA_{4+7} induces parthenocarpy, whereas GA₃ does not [54,55]. Considering the diverse potential of PGR-induced fruit set, the requisite hormonal dynamics for initiating fruit development can be either a decrease in ETH or ABA levels or an increase in BR, IAA, GA, or CK levels (Figure 2A). However, the GA increase, initiated by IAA and CK, is required for fruit development and occurs downstream of variations in ABA and ETH levels, suggesting a regulatory interplay with these two hormones [14,32,51].

Two hormonal mechanisms for inducing parthenocarpic fruit set have been proposed in the literature (Figure 2B). The first entails the induction of GA_4 and GA_7 biosynthesis, driven by IAA (highlighted in yellow in Figure 2B). For instance, in tomatoes, the rise in IAA levels in the ovary prompts the expression of *GA 20-oxidases* (*GA200x*), *GA200x1* or *GA200x2*, leading to the biosynthesis of GA₄ and GA₇ [56]. The second mechanism involves the inhibition of GA catabolism in conjunction with an induction of GA₃ biosynthesis (highlighted in red in Figure 2B). Across various









Figure 2. Hormonal and molecular mechanisms involved in fruit setting. (A) Phytohomone dynamics during fruit set initiation. At 1,5 DPA, in pollinated or parthenocarpic flowers, fruit set is initiated by a decrease of ETH and ABA levels or an increase in BR. At 3 DPA, the increase of IAA and CK levels triggers the biosynthesis of GA, leading to fruit development. In the nonfertilized and nonparthenocarpic flower, after anthesis, ABA and ETH levels remain high and inhibit the increase of IAA, CK, and GA levels, leading to flower abortion. Abbreviations: DAA, days ante-anthesis; DPA, days postanthesis. (B) Simplified model of fruit development. Two mechanisms of parthenocarpic fruit set have been proposed. The first mechanism, highlighted in yellow, involves the induction of GA biosynthesis driven by IAA. The second mechanism, highlighted in red, involves the inhibition of GA catabolism. Genes reported to induce parthenocarpy are framed in red. Genes involved in parthenocarpy under cold condition are indicated by a blue snowflake. Abbreviations: ACO, 1-aminocyclopropane-1-carboxylate oxidase; ACS, 1-aminocyclopropane-1-carboxylic acid synthase; AGL6, AGAMOUS-LIKE 6; ARF5/7/8/19, auxin/response factors; AUX/IAA9, auxin/indole-3-acetic acid 9; CDK, cyclin-dependent kinase; CYP, cytochrome P450;

(Figure legend continued at the bottom of the next page.)



Hormone related	Treatment	Species	Refs
Auxin	Naphthaleneacetic acid (NAA) 2,4,5-Tri-chlorophenoxy propionic acid (2,4,5-TP) Chlorophenoxy-acetic acid (4-CPA) 2,4-Dichlorophenoxy-acetic acid (2,4-D) Indole-3-acetic acid (IAA)	Cucumis sativus, Elaeis guineensis, Elaeis oleifera, Elaeis guineensis Solanum lycopersicum Solanum lycopersicum, Elaeis guineensis, Elaeis oleifera, Pyrus spp. Arabidopsis thaliana	[54,64,85,94–99]
Brassinosteroids	24-Epibrassinolide (EBR)	Cucumis sativus	[54]
Cytokinin	N-(2-chloro-4-pyridyl)-N'-phenylurea (CPPU) 6-Benzylaminopurine (BA, benzyladenine)	Citrullus lanatus, Cucumis melo, Ficus carica L., Cucumis sativus, Pyrus spp., Solanum lycopersicum Arabidopsis thaliana	[57,58,94,99–103]
Ethylene	1-Methylcyclo-propene (1-MCP) (ethylene inhibitor)	Solanum lycopersicum	[56]
Gibberellin	GA ₃	Malus domestica, Annona spp., Ficus carica L., Vitis vinifera, Solanum lycopersicum	[41,63,64,94,95,104–106]
	GA _{4+7,} GA ₄	Cucumis sativus, Pyrus spp.	

Table 1. Hormone treatments used to induce parthenocarpy and species related

species, a reduction in ETH or ABA levels or an increase in CK levels inhibits the expression of a *GA 2-oxidase* (*GA2ox*), *GA2ox4*, and induces downstream *GA20ox3* expression, thereby facilitating GA₃ biosynthesis [52,57]. More recent research by Cong *et al.* has proposed a GA-independent mechanism for fruit set in pears induced by cytokinins [58]. However, their study primarily measured GA₃ concentration and *GA20ox* expression, leaving open the possibility of downregulation of *GA2ox* expression and the induction of GA₄ and GA₇ levels [58]. An alternative hypothesis is that the active GA forms involved in fruit set may vary between species.

Molecular mechanisms controlling fruit set

Hormone-related genes

The genetic dissection of parthenocarpy in several species has revealed both monogenic and polygenic inheritance. In tomatoes, parthenocarpy is regulated by several **recessive genes** (*pat* genes), whereas in peppers and cucumbers, it is controlled by single genes [48]. The genetic foundation of parthenocarpy has been unraveled through a combination of physiology, genetics, and omics analyses. Among the genes recognized for their pivotal role in parthenocarpy, a significant proportion are implicated in phytohormone metabolism or signaling. Genes that have already been shown to be directly responsible for parthenocarpy induction when mutated or under modified expression are listed in Table 2. Notably, genes linked to auxin metabolism are the most prominent players in parthenocarpy regulation [51]. Evidence suggests that an increase in spontaneous fruit setting is associated with an increased expression of *YUCCA10* and a pyridine nucleotide-disulfide oxidoreductase (PNO) coding gene, both involved in auxin biosynthesis [59,60]. Spontaneous fruit set was obtained through the downregulation of IAA receptor genes such as an auxin transporter gene *AUX1* or *Transcriptor Inhibitor Response 1 (TIR1)* [60,61], as well as genes connected to auxin signaling, such as auxin response factors (ARF), including

EIN, ethylene-insensitive; ERF, ethylene response factor; ETR1/2, ethylene receptors; GA200x, gibberellin 20-oxidases; GA20x, gibberellin 2-oxidases; GA20x, gibberellin 2-oxidases; GA30x, gibberellin 3-oxidases; GID1, gibberellin insensitive dwarf 1; IaaM, tryptophan-2-monooxygenase; NCED, 9-cis-epoxycarotenoid dioxygenase; pad-1, parental advice-1; PF1, parthenocarpic fruit 1.



Table 2. Key regulators of parthenocarpic fruit setting

Gene name	Gene ID or accession	Species	Function	Expression variation inducing parthenocarpy	Refs
SIARF5	HM19248.1	Solanum lycopersicum	Auxin response factor	Downregulation	[63,64]
SIARF7	Solyc07g042260	Solanum lycopersicum	Auxin response factor	Downregulation	[107]
SIARF8A	Solyc03g031970	Solanum lycopersicum	Auxin response factor	Downregulation/deletion of IAA9-interacting PB1 domain	[65,108]
SIARF8B	Solyc02g037530	Solanum lycopersicum	Auxin response factor	Downregulation/deletion of IAA9-interacting PB1 domain	[65,108]
CsTIR1	Csa7M393970.1 Csa3M597350.1	Cucumis sativus	F-box protein, auxin receptor	Downregulation	[61,109]
SIIAA9	Solyc04g076850	Solanum lycopersicum	Auxin-responsive AUX/IAA family protein	Downregulation	[66,110]
PIN4	Solyc03g120450	Solanum lycopersicum, Solanum melongena L	Aminotransferase – auxin transport	Downregulation	[111]
Pad-1		Solanum lycopersicum, Solanum melongena L	Parental advice-1 Aminotransferase – auxin regulation	Downregulation	[112]
GA20ox1	At4g25420 orthologue	Solanum lycopersicum Cucurbita pepo	GA biosynthesis	Overexpression	[69]
GA20ox2	AT5G51810	Pyrus bretschneideri Rehd	GA ₄ biosynthesis	Overexpression	[37]
GA2ox1		Solanum lycopersicum	GA catabolism	Downregulation	[113]
FveRGA1	AT2g01570 orthologue	Fragaria x ananassa	GRAS family TF family protein	Downregulation	[114]
DELLA	Solyc11g011260	Solanum lycopersicum	Repressor of GA signaling	Downregulation	[70,71]
ETR1	At1g66340 orthologue	Cucumis melo Solanum lycopersicum	Ethylene receptor	Downregulation	[56]
SINCED1	Solyc07g056570.1.1	Solanum lycopersicum	9-Cis-epoxycarotenoid dioxygenase - ABA biosynthesis	Overexpression	[74]
CYP78A9	At3g61880	Arabidopsis thaliana	P450 monooxygenase	Overexpression	[115]
PbCYP78A6	LOC103964254	Pyrus bretschneideri	CYP78A family enzymes (related to cell proliferation)	Overexpression	[106]
AGL6–pat-k	VIT_07s0031g01140 (AtAGL66 homologue) Solyc01g093960	Vitis vinifera Solanum lycopersicum	AGAMOUS-LIKE 6 gh3 box - putative pollen maturation and function genes	Downregulation	[76,77]
WOP1	At2g40970 orthologue (atMYBC1 orthologue)	Citrullus lanatus	WithOutPapa 1 - TF	Downregulation	[81]
SIHB15/PF1	SolyC03g120910	Solanum lycopersicum	TF - repressor of auxin signaling and inducer of ethylene	Downregulation	[36]
egDREB1	<i>VIT_07s0031g00190</i> orthologue	Solanum lycopersicum	Drought-responsive element-binding protein	Overexpression	[116]
SIHWS	Solyc01g095370	Solanum lycopersicum	F-box protein	Downregulation	[117]
SITPL1	Solyc07g008040	Solanum lycopersicum	Topless-like protein1 – transcriptional corepressor	Downregulation	[118]

ARF8A/8B, *ARF18*, and *ARF5* [62–65], and Aux/IAA responsive genes such as *IAA9* [66] (Table 2). In parthenocarpic fruit set, a downregulation of *GH3* gene, such as *GH3.1*, was also observed [67]. Genes involved in auxin transport or regulation, such as *PIN-formed genes* [*PINsand parental advice1 (pad-1)*] were also proposed as key genes controlling parthenocarpy [68] (Table 2).

Several genes related to GA metabolism and signaling have been suggested as candidates for inducing parthenocarpy. One such candidate is *Gibberellin-Insensitive Dwarf1* (*GID1*), a gene encoding a GA receptor [59]. In tomatoes, parthenocarpy was achieved in a small proportion



of fruits by overexpressing GA20ox1, a GA biosynthesis gene upregulated during the early fruit set [62,69] (Table 2). Parthenocarpic fruit set was also achieved through loss-of-function mutations in DELLA protein, involved in the repression of GA signaling [70,71] (Table 2). Concerning CK, only a limited number of genes have been identified as inducers of parthenocarpy. CK genes associated with parthenocarpy included CK biosynthetic and signal transduction genes as the cytochrome P450 monooxygenase CYP735A gene (CYP735A) and Cytokinin Response 1 (CRE1), encoding for a cytokinin hydroxylase, which catalyzes the biosynthesis of trans-zeatin and a histidine kinase playing the role of cytokinin receptor, respectively [60,72]. By contrast, downregulation of several ETH biosynthesis or signaling genes was identified in parthenocarpic fruits. These include biosynthesis genes (e.g., ACO1) [62], receptor genes [e.g., Ethylene Receptor 1 (ETR1) and ETR2] [62,73], signaling genes [e.g., Ethylene-Insensitive1 (EIN1) and EIN3] [72], and genes associated with ETH response [e.g., Ethylene Response Factor 11 (ERF11) and ERF17 [62]. In addition, parthenocarpic tomatoes were produced by silencing ETR1 expression [56]. Similarly to ETH, silencing ABA biosynthesis-related genes such as 9-cis-epoxycarotenoid dioxygenase 1 (NCED1) [74] was shown to lead to parthenocarpy in tomato [59] (Table 2). These different hormone regulation mechanisms are synthetized in Figure 2B. The role of BR in fruit set has been discussed in a cucumber study [60]. Transcriptomic comparisons between nonparthenocarpic and parthenocarpic cucumbers revealed that over 30% of deregulated genes related to hormones were associated with BR. However, considering the significant role attributed to BR in fruit set, further studies are required.

Transcription factors, the potential key regulators

Throughout the fruit set process, a robust interplay exists between hormones and various TFs. For instance, GA regulates the expression of TFs from the GAMYB family through DELLA proteins, essential TFs for fruit set in tomato [75] (Figure 2B). Within the early stages of fruit set, several TFs from the ethylene-responsive factors (ERF) family experience deregulation. Besides, certain genes associated with parthenocarpy, such as the *parthenocarpic fruit (pat)* genes, encode TFs. For instance, *pat-2* encodes a TF from the zinc finger homeodomain (ZHD) family, whereas *pat-k* encodes an AGAMOUS-like TF of the MADS-box family, SIAGL6 [76–78]. In tomato, *SIAGL6* loss-of-function mutation abolishes its inhibitory effect on tomato *KLUH* (*SIKLUH*) expression, a cell proliferation regulator that induces parthenocarpy induction also encompass the HD-Zip family, represented by *SIHB15A* [36], the MYB family, with *WithOut Papa* 1 (*WOP1*) being an orthologue of *AtMYBC1*, as well as NAC, ERF/AP2, WRKY, and bHLH families [62,81]. These TFs can also be subject to regulation through their interactions with noncoding sequences.

Epigenetic mechanisms and noncoding RNA

The role of epigenetic mechanisms in orchestrating developmental processes and tissue differentiation has been widely described [82]. Key epigenetic regulators encompass DNA methylation/ demethylation, chromatin remodeling, histone modifications, and noncoding RNAs. These epigenetic regulators function independently or in a concerted manner, forming a wide regulatory network. Methyltransferase 1 (MET1), a primary maintenance methyltransferase, is responsible for reproducing DNA methylation during DNA replication [83]. Yang *et al.* reported that knockout (KO) mutants of *SIMET1* in tomato exhibited leaf and inflorescence development defects along with a parthenocarpic fruit setting [84]. The role of DNA methylation in fruit development and setting was also demonstrated in oil palm, where the methylation near the Karma transposon yields normal fruit development [85]. In contrast, hypomethylation induces homeotic transformation and parthenocarpic fruit setting [86]. Histone modifications are another epigenetic mechanism

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influencing fruit setting. In tomato, H3K9ac and H3K4me3 histone modification marks were shown to be associated with the genetic reprogramming underlying the fruit setting process. Mutants with KO in the *SET-Domain Group 27* (*SISDG27*) gene, which encodes a potential histone methyltransferase, result in the development of parthenocarpic fruit setting [87].

Noncoding RNAs (ncRNAs) are emerging as prominent regulators of plant development, including their involvement in fruit set. For instance, **microRNAs (miRNAs)** that target TFs involved in fruit setting and hormone interactions have been identified as potential inducers of parthenocarpy. In tomato, *miR159* regulates *GAMYB* expression, and the resulting downregulation of *GAMYB* in ovaries triggers a pollination-independent fruit set [75]. Similarly, the knockdown of *SIHB15A*, also known as *PF1*, by miR166 leads to a continuum of aberrant ovules correlating with parthenocarpic fruit set under cold stress. In line with this observation, plants carrying an miRNA166-resistant allele of *SIHB15A* exhibited regular ovule development and failed to undergo parthenocarpic fruit setting [36].

Concluding remarks and future perspectives

As climatic conditions deteriorate, fruit set becomes a limiting factor in fruit production. Growing plants that are less reliant on pollination may be an attractive means to improve fruiting under adverse conditions. Parthenocarpic fruit set can be genetically engineered or induced through hormone treatments. Given the advancements in gene editing, it is now feasible to swiftly engineer parthenocarpic crops by specifically targeting candidate genes associated with parthenocarpy. Recent research has underscored the capacity of TFs, such as SIAGL6 and SIHB15A, in controlling fruit set. However, targeting such genes in distantly related species may not lead to parthenocarpy. Although the molecular mechanisms governing fruit set vary among species, a shared essential component is the hormonal crosstalk involving IAA, GA, CK, ETH, ABA, and BR for the induction of fruit set. The absence of ABA and ETH prevents the initiation of ovary senescence, whereas the increase in IAA, GA, and CK triggers ovary swelling, initiating the transition toward fruit development. Selecting candidate genes regulating hormones for gene editing will likely increase the chance of leading to parthenocarpy.

Recently, the existence of a hormone-independent mechanism for parthenocarpic fruit setting in cucumber has been proposed [88]. This hypothesis remains uncertain, given that numerous hormone-related genes were found to be deregulated in the variant supposedly displaying hormone independence. Besides hormones, **secondary metabolites** such as flavonoids were found deregulated during parthenocarpic fruit setting [89], and the alteration of flavonoid biosynthesis through knockdown of chalcone synthase or overexpression of stilbene synthase has led to parthenocarpic fruit set [90,91]. Still, chalcone synthase has been suggested to regulate auxin response in tomato [91]. Therefore, targeting genes involved in secondary metabolite biosynthesis or plant treatment with secondary metabolites could be a new means of fruit set induction.

Nevertheless, substantial genetic barriers persist (see Outstanding questions). Notably, there is no known genetic source of parthenocarpy in several key fruit crops, including peaches, melons, and legumes. The multifaceted nature of parthenocarpy, which may involve the coordinated action of multiple genes, has likely complicated the identification of relevant alleles. Efforts to characterize major regulators of parthenocarpic fruit setting in various fruit and vegetable species will likely help to understand the implicated molecular mechanism. To pinpoint genes expressed upstream of the fruit set initiation, investigations should focus on early floral stages. In the case of parthenocarpy, Zhang *et al.* even suggested that the flowers' fate is determined before **anthesis** [92]. Identifying genetic markers for early fertilization and fruit set events would enable a better

Outstanding questions

What enables the program switch in ovules inducing fruit set without pollination stimuli?

Do ovary tissues contribute equally to ovary development?

How were the variations in molecular pathway controlling parthenocarpy raised during plant evolution and selected?

How can we reach an optimized marketable fruit yield coming from parthenocarpic plants?

Can fruit set be achieved independently of phytohormones?



characterization of this process. Moreover, tissue-specific transcriptome analyses, such as those using laser capture microdissection, could unveil spatial specificity in gene expression patterns and discern whether the signal for fruit set originates from one or multiple ovary organs [36].

A better understanding of the parthenocarpy process will open exciting avenues for the targeted improvement of fruit set. Recent studies have reported higher yields in parthenocarpic plants compared with their nonparthenocarpic counterparts [36]. Additionally, various parthenocarpic plants have demonstrated increased fruit production even under challenging environmental conditions, such as high salinity [93] or low temperatures [36]. As a result, parthenocarpy holds the potential to mitigate the issues arising from inadequate pollination while ensuring a stable and enhanced crop yield. When considering the two types of parthenocarpy, obligatory and facultative, the latter is preferable because it allows the cultivation of pollinator-friendly crops [45]. Facultative parthenocarpy is particularly advantageous because it is compatible with pollination, thus maintaining the fertility of flowers. Consequently, crops exhibiting facultative parthenocarpy are well suited for both indoor and outdoor cultivation systems.

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Declaration of interests

No interests are declared.

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