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REVIEW

# Recent advances in genetics and molecular breeding of parthenocarpic cucumber (*Cucumis sativus* L.) under protected conditions

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**Abstract** Cucumber is an important member of Cucurbitaceae family which is grown and consumed globally. It is consumed in the form of salads or pickles and has abundant supply of minerals and vitamins. It has been a focus of extensive research due to its publically available genome sequences. Marker assisted breeding has been employed to generate improved varieties of cucumber with resistance to various diseases besides desirable horticultural traits. One such trait is the production of parthenocarpic fruits i.e. seedless fruits developed in the absence of pollination. Naturally, parthenocarpy occurs under unfavourable environmental conditions. However, it is possible to artificially induce parthenocarpy by applying plant growth regulators. At molecular level, parthenocarpy is a result of complex role-play of genes and hormones with tight regulation. Many researchers aim at developing parthenocarpic varieties by either transferring the trait into existing varieties with resistance to specific diseases or by knocking off genes controlling parthenocarpy. A comprehensive knowledge of background and genetics of parthenocarpy is required in both cases. This review includes an-inclusive study of the molecular basis of parthenocarpy. The genes and hormones involved and their functions, inheritance of parthenocarpy and markers associated with it have been given in detail.

**Keywords** *Cucumis sativus* L. · Inheritance · Molecular markers · Phyto-hormones · Regulation · Seedlessness

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## Introduction

Vegetables are an indispensable component of human diet. They can be consumed either raw or cooked or preserved in the form of pickles. Cucumber (*Cucumis sativus* L.) is one of the major horticultural crops which offer great economic benefits to the cultivators and nutritional benefits to the consumers. The world production of cucumber increased from 67.9 M tonnes in 2011 to 93.5 M tonnes in 2021 (www.fao.org/faostat/en/) with Asia alone accounting for 85.4% of the total production. It is a Cucurbit and is known to have its origin in foothill regions of the Himalayas in India, China and Burma (Sebastian et al. 2010). Modern day cucumber (*C. sativus* var. *sativus*) is known to originate from three wild and semi-wild varieties, *C. sativus* L. var. *sikkimensis*, *C. sativus* L. var. *hardwickii* and *C. sativus* L. var. *xishuangbannanesis*. The cultivated cucumber is

divided into four geographical groups based on their genomic analysis: India; Eurasia along with the West; Eastern Asia along with China; and Xishuangbanna from South-western China (Lv et al. 2012). The largest proportion of the genetic diversity belongs to the Indian group which also includes *C. sativus* L. var. *hardwickii.* The cucumber collection centers of the US, the Netherlands and China collectively comprise 3342 cucumber accessions (Lv et al. 2012). The widely available germplasm is beneficial to breeders for development of improved varieties of cucumbers having beneficial traits via marker assisted breeding. Production of seedless cucumbers also known as parthenocarpy is one such trait favoured by cultivators and consumers globally. In cucumber, parthenocarpy process has not been completely understood due to its complex mechanism under tight regulation by several environmental and genetic factors (Kaur et al. 2023). In-depth knowledge of hormones and genes regulating parthenocarpic fruit-set formation is essential for the development of parthenocarpic varieties either via conventional breeding or via genetic engineering approaches. The complete genomic sequences of cucumber are available at http://cucurbitgenomics.org/v2/ in public domain which prove beneficial for the study of genes. The updated database comprises five genome assemblies *Cucumis sativus* Chinese Long 9930 v3 (Li et al. 2019), *Cucumis sativus* Gy-14 v2 (Weng Lab, USDA-ARS Vegetable Crops Research Unit, Wisconsin), and *Cucumis sativus* B-10 v3 (Osipowski et al. 2020; Turek et al. 2023), *Cucumis sativus* var. hardwickii cv. PI 183967 v1 (Qi et al. 2013), and *Cucumis hystrix* v1 (Qin et al. 2021).

Parthenocarpy (Parthenos, virgin; karpos, fruit) is one of the most significant characters in cucumber which is the biological phenomenon of natural or artificial induction of fruit formation in the absence of pollination or any other kind of stimuli of the ovary (Gustafson 1939) (Fig. 1) and the plant is said to exhibit the trait of parthenocarpy when its fruits are either totally lacking seeds or have seeds of insignificant size (Pandolfini 2009). Cucumber is considered a favourable model plant to study the parthenocarpy as the trait is prevalent in its germplasm resources. Parthenocarpic cucumber fruits are bitterness free and juicier as compared to the seeded fruits and have the ability to upsurge the crop yields under unfavourable environmental circumstances such as its cultivation under protected conditions (Fabrice et al. 2000). The phenomenon of parthenocarpy in cucumber was first studied by Noll (1902) who coined the term 'Parthenocarpy'. During early researches, reports


**Fig. 1** **a** Fruit formation without pollination at each node in parthenocarpic plant. **b** Ovary abortion in the absence of pollination in non-parthenocarpic plant

for parthenocarpy were given by Ewert-Proskau (1909), Strong (1921, 1932), Wellington and Hawthorn (1928) and Hawthorn and Wellington (1930). It has been reported that in cucumber the facultative parthenocarpy varies quantitatively (Cao et al. 1997; El-Shawaf and Baker 1981a, b; Sun et al. 2006a, b). For the first time, De Ponti (1976) developed the parthenocarpic hybrid of cucumber by crossing parthenocarpic slicing cucumber line with gynoecious pickling cucumber line.

Parthenocarpy could be affected by abiotic, physiological, and genomic factors. Abiotic factors such as low temperature and short day length are known to enhance parthenocarpy (Rudich et al. 1977). Such environmental factors along with their interaction with genotype also effect the degree of parthenocarpy (Sun et al. 2006a), which makes selection of parthenocarpic progenies difficult during breeding programs. Certain hormones tend to regulate parthenocarpy. For example, the endogenous levels of indole-3-acetic acid (IAA) in parthenocarpic ovaries and fruits were higher in comparison to their pollinated counterparts (Boonkorkaew et al. 2008; Kim et al. 1992a, b). Various studies have demonstrated the role of exogenously applied growth-promoting chemicals which include auxins and auxin transport inhibitors, gibberellins, cytokinins, and brassinosteroid in inducing parthenocarpy (Cantliffe 1972; Fu et al. 2008; Kim et al. 1994; Quebedeaux and Beyer1972). Thus, fruit setting could be induced by applying compatible foreign pollen to the stigma in cucurbits (Yasuda 1935) because pollens have the above mentioned phytohormones (Gustafson 1937, 1942). Moreover, parthenocarpy can be stimulated in cucumbers by introduction of the *DefH9-iaaM* auxin-synthesizing gene (Yin et al. 2006).

The parthenocarpic varieties are also not suitable for outdoor cultivation as they develop fruits with seeds which render them unmarketable. Parthenocarpy was used for both protected and open-field production after Peterson (1960) developed a gynoecious cucumber line (MSU 713-5) and Peterson and Andher (1960) discovered a method for maintenance of such lines by inducing staminate flowers via gibberellic acid application. In case of greenhouse hybrids, the fruits set at initial five nodes are not vital as such fruits are removed. But in case of open cultivation, it is important that fruit setting at the initial nodes starts as early as possible. This provides early harvest opportunity, which is especially important for early yield (Kushnereva 2008). Thus, in order to develop parthenocarpic cucumber hybrids which are suitable for outdoor conditions, it is essential that the parental genotypes are selected such that their parthenocarpic potential is less reliant on environment.

## Role of *phyto*-hormones in parthenocarpy

The formation of parthenocarpic fruits is thought to be initiated by gibberellic acid (GA) biosynthesis pathway (Fos et al. 2000). Furthermore, because auxin can be applied exogenously to promote parthenocarpy, auxins are essential for the formation of parthenocarpic fruits. Normally, auxin helps in maintaining the concentration of enzyme gibberellic acid oxidase which in turn regulates synthesis of GA (Fig. 2). However precise interactions between gibberellins and auxins might differ depending upon the plant type and tissue (Nitsch 1972). However, the role of endogenous levels of GAs in development of seedless fruit might not necessarily be required during the entire period of fruit development as high levels of GAs produced from 3 to 4 weeks after anthesis might not be required in later stages. Contrarily, low levels of gibberellins from 1 to 4 weeks after anthesis might result in inhibition of fruit development (Kataoka et al. 2004).

The first hormone known to cause parthenocarpy in plants was auxin. Cucurbitaceae crops, including watermelon, cucumber, and zucchini, undergo parthenocarpy when exposed to analogs of auxin (Wong 1938, 1939). Cucumbers have been successfully induced to exhibit parthenocarpy by Qian et al. (2018) using naphthaleneacetic acid (NAA), an exogenous plant growth regulator, one day prior to and on the day of flowering. There have been reports of a number of auxin biosynthetic routes involved in induction of parthenocarpy, including IAOx (indole-3-acetaldoxime), IAM (indole-3-acetamide), and Trp-IPyA (tryptophan-indole-3-pyruvic acid). In case of Trp-IPyA pathway, which is the most widely studied pathway, *TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS* (*TAA1*) genes convert tryptophan into indole-pyruvic acid which undergoes decarboxylation to form indole acetic acid in an irreversible reaction catalysed by *YUCCA* genes (Homayouni and Strader 2020).

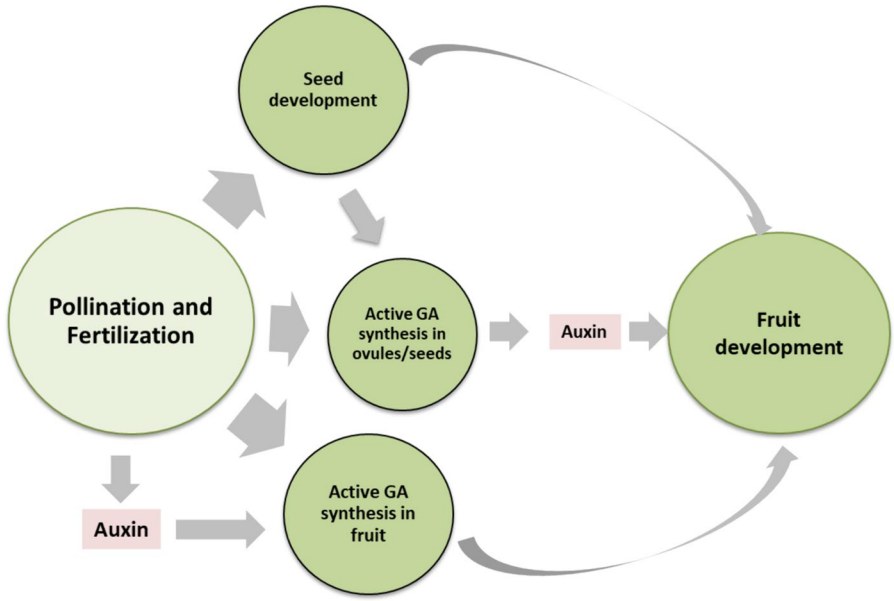


**Fig. 2** Mechanism of parthenocarpy in cucumber

Another essential plant hormone that regulates plant parthenocarpy after auxins is GA (Davison 1960). The ability of various gibberellins to produce parthenocarpy varies throughout species. For example, Qian et al. (2018) found that although $GA_3$ does not successfully promote parthenocarpy in cucumbers, it robustly stimulates the production of seedless fruit in tomatoes. However, gibberellin $GA_{4+7}$ treatment resulted in parthenocarpic cucumbers. There was no discernible weight difference between $GA_{4+7}$-treated and pollinated cucumbers. According to Qian et al. (2018), $GA_{4+7}$-treated cucumbers exhibited less firm flesh and higher amounts of total flavonoids and proteins during storage in contrast to pollinated cucumbers.

Another essential plant hormone that encourages parthenocarpy in plants is cytokinin. Cell division is stimulated by spraying N-(2-chloro-4-pyridyl)-N′-phenylurea (CPPU), an exogenous cytokinin growth regulator. CPPU was initially used by Hayata et al. (1995) to treat watermelon ovaries that were not pollinated, which led to the development of seedless fruit. Furthermore, the form, soluble solids content, and rind thickness of the watermelon fruit were unaffected by a 200 $g/m^3$ CPPU concentration, indicating its direct application in production (Hayata et al. 1995; Maroto et al. 2005). When compared to pollinated watermelons, watermelons treated with CPPU might have a little lower sugar content; however, this could be due to varietal differences (Huitrón et al. 2007, Lopez-Galarza et al. 2004). In the production of Cucurbitaceae crops, such as cucumber (Qian et al. 2018), melon (Hayata et al. 2000; Liu et al. 2023), pumpkin (Ogawa and Takisawa 2022), and watermelon (Maroto et al. 2005), CPPU is frequently used to stimulate or augment parthenocarpy. This treatment positively impacts fruit setting, promotes fruit enlargement, and increases production overall. According to Sakakibara (2005), the primary roles of cytokinins are to suppress leaf senescence, promote plant germination and bud differentiation, and regulate meristem cell proliferation. Adenosine phosphate-isopentenyl transferase (IPT) catalyzes the initial stage of the production of cytokines. Nucleotide precursors are transformed into the active form by the LONELY GUY (LOG) enzyme (El-Showk et al. 2013). Cytokinin oxidases (CKXs) mediate the breakdown of cytokinins (Köllmer et al. 2014).

The exogenous application of phyto-hormones greatly influences parthenocarpic fruits in various crops. The hormones include auxins {NAA 2,4-dichlorophenoxyacetic acid (2,4-D)}, cytokinins {CPPU, 6-benzylaminopurine (BAP)}, GAs, brassinosteroids, ethylene and melatonin (De Jong et al. 2009; Kumar et al. 2014; Sharif et al. 2022). 2,4-D is a synthetic auxin which had been proven to induce parthenocarpy in tomato and pear (Cong et al. 2019; Serrani et al. 2007). Similarly, NAA effectively

induced parthenocarpy in cucumber (Qian et al. 2018) and strawberry (Kang et al. 2013). Application of zeatin (cytokinin) to the unpollinated ovaries resulted in parthenocarpic fruits in case of tomato with a fruit setting percentage of 80% (Ding et al. 2013). Exogenous application of CPPU in pear cultivar resulted in parthenocarpy by accumulating IAA and reducing abscisic acid levels (Cong et al. 2020). GA positively regulates various fruit-related traits (Garmendia et al. 2019). Treating cucumber with combination of different GAs ($GA_{4+7}$) successfully induced parthenocarpy (Qian et al. 2018). Brassinosteroids belong to group of steroid hormones playing a critical role in plant growth. However, fewer reports are available for brassinosteroids induced parthenocarpy as compared to other hormones. An analog of brassinosteroids i.e. 24-epibrassinolide was able to induce parthenocarpy in cucumber (Fu et al. 2008).

## Environmental factors affecting parthenocarpy

Parthenocarpy is induced by a number of environmental conditions, including temperature, photoperiod, light intensity, and nutrient availability (Gou et al. 2022; Rylski 1974; Smith and Cochran 1935; Sun et al. 2016). According to genetic studies, most of a crop's natural parthenocarpic qualities are quantitative traits that are influenced by both environmental and genetic variables (Beraldi et al. 2004; Fos et al. 2000; Leitzow et al. 2016; Wu et al. 2016). A healthy supply of nutrients is essential for fruit growth and is particularly important for parthenocarpic fruit development (Gou et al. 2022). It has been documented that parthenocarpy can be induced by low temperatures in Cucurbitaceae crops, such as cucumber, melon, and zucchini (De Ponti 1976; Hao et al. 2009; Rylski 1974).

Short day conditions in cucumbers increase auxin activity, which in turn promotes parthenocarpy (Rudich et al. 1977). Cucumber ovary auxin level rises in response to low night-time temperatures, causing parthenocarpy. On the other hand, high temperatures prevent the beginning of parthenocarpy in cucumber ovaries by inhibiting the manufacture of auxin and gibberellin (Matlob and Kelly 1975). Rudich et al. (1977) reported that under high temperature conditions, parthenocarpic fruit development was greatly reduced in non-parthenocarpic Gy irrespective of day length. However, parthenocarpic line produced significant number of fruits under high temperature with long-day or short-day conditions. Cucumber parthenocarpy was shown to be more common when ovaries were found to have twice as much auxin at 15 °C as at 25 °C (Kim et al. 1992a, b). Meng et al. (2023) examined the impact of hormones on the low-temperature parthenocarpic fruit's development and discovered a small number of differentially expressed genes (230–460 DEGs) among the ovaries prior to anthesis According to endogenous hormone determination, the IAA and ACC accumulation throughout fruit development displayed an inverted curve: IAA accumulated continuously whereas ACC synthesis was suppressed during parthenocarpy at low temperatures.

## Inheritance of parthenocarpy

The genetic basis of cucumber has been narrowed to 3–8% polymorphism among cultivated varieties and 10–25% among botanical cultivars (Behera et al. 2011). India has a huge genetic diversification as well as variability in case of fruit traits that have not been completely utilized for improving the crop's genetic makeup. The development of gynoecious cucumbers possessing parthenocarpy has emerged a significant hurdle for breeders because these are used as parent in $F_1$ hybrid development (Dhall et al. 2023). Although, the genetics of parthenocarpy have been a focus of research in previously published literature, the studies differ from each other due to the variations on genetic background, experimental designs as well as environmental factors. Table 1 exhibits the summary of the studies on the inheritance of parthenocarpy in cucumber. In cucumber, the genetic study of parthenocarpy started in 1930 and Pike and Peterson were the first to report inheritance of parthenocarpy in 1968. They reported that parthenocarpy was conditioned by a gene *P* which showed incomplete dominance. When occurring as homozygous, this gene formed parthenocarpic fruits at early nodes (usually at 5th node); while in heterozygous condition, it produced late fruits with parthenocarpy and also fewer in number than homozygous genotypes. Similar reports on the inheritance of parthenocarpy via incomplete dominant gene were given by Kim et al. (1992a); Juldasheva (1973) and Jat et al. (2017) (Table 1).

**Table 1** Inheritance of parthenocarpic trait in cucumber

| Gene(s)/QTL(s) | Cross | References |
|---|---|---|
| Single incomplete dominant gene *P* | PPC-2 (Gynoecious Parthenocarpic) × Pusa Uday (Monoecious Non-Parthenocarpic) | Jat et al. (2017) |
| | – | Juldasheva (1973) |
| | Pandex (Parthenocarpic) × Khira (Non-Parthenocarpic) | Kim et al. (1992a) |
| | Spotvrije (Monoecious Parthenocrpic) × MSU713-205 (Gynoecious Non Parthenocarpic) | Pike and Peterson (1969) |
| Single recessive gene | European (Parthenocarpic) × American (Non Parthenocarpic) varieties | Wellington and Hawthorn (1928) |
| | English Forcing (Parthenocarpic) × Arlington White Spine (Non Parthenocarpic) | Hawthorn and Wellington (1930) |
| | – | Meshcherov and Juldasheva (1974) |
| Incomplete recessive multiple genes | Anshan (Parthenocarpic) × Mnogoplodnyj (Non Parthenocarpic) | Kvasnikov et al. (1970) |
| Three independent major genes with equal additive effect | 72436, 72426, 72430, 72201, 72190, 72186, 72433, 72175 (Gynoecious Parthenocarpic) × 72421a & b (Gynoecious Non Parthenocarpic) | De Ponti and Garretsen (1976) |
| QTLs controlled by two major genes and additional minor genes | 6401(Gynoecious Parthenocarpic × 6429 & 6426 (Gynoecious Non-Parthenocarpic) | Yan et al. (2008) |
| The two major additive-dominant-epistatic genes and additive-dominant minor genes | Jiangning (Nanjing) (Monoecious Parthenocarpic) × Changli (Hebei) (Monoecious Non Parthenocarpic) | Yan et al. (2010) |
| | 6457 (Monoecious Parthenocarpic) & 6401 (Gynoecious Parthenocarpic) × 6429 (Non Parthenocarpic) | Yan et al. (2012a) |
| Polygenes | Inbred 6457 (High Parthenocarpic) × Inbred 6426 (Low Parthenocarpic) | Zhihong et al. (2020) |

However, According to Hawthorn and Wellington (1930) and Meshcherov and Juldasheva (1974), there is single recessive gene that controls parthenocarpy. Kvasnikov et al. (1970) used a European type of processing cucumber to propose that multiple genes showing incomplete recessiveness were responsible for controlling parthenocarpy. De Ponti and Garretsen (1976) studied the inheritance of parthenocarpy in the pickling cucumber by crossing eight pure gynoecious lines having different degrees of parthenocarpy (43–90% fruit set) with two plants (72421a, 72421b) from non-parthenocarpic gynoecious (NPG) line in incomplete diallel fashion and also developed six generations ($P_1$, $P_2$, $B_{11}$, $B_{12}$, $F_1$, $F_2$) of above crosses to study the presence of non-allelic gene interaction (epistasis) by using six generation mean analysis. They reported that the inheritance of parthenocarpy could be explained by three independent, isomeric major genes with additive action, together with additive × dominant (j) interaction. Independent studies by Castle (1921) and Wright (1968) report that all alleles controlling parthenocarpy are unlinked and exhibit equal additive effects, and that both parthenocarpic and non-parthenocarpic parental lines are homozygous for alternative alleles at all loci affecting the parthenocarpy. Since then, numerous studies have been carried out in regard to parthenocarpy in cucumber.

Numerous researches have suggested that parthenocarpy inheritance is congruent with qualities that are quantitative in nature, utilizing a variety of analytical techniques. The techniques include variance component analysis (Sun et al. 2006a; Yan et al. 2008), generation means analysis (Cao et al. 1997; Sun et al. 2006b), diallel analysis, and North Carolina Design II (El-Shawaf and Baker 1981a, b). Other genes are also involved in controlling the parthenocarpic behaviour

resulting in parthenocarpic fruit set with a range of 0.33–0.62 with narrow-sense heritability as well as 5–13 effective factors (Sun et al. 2006a). The earliest case of parthenocarpy was observed in greenhouse slicers, followed by greenhouse Beit Alpha type and pickling type for production in high tunnels and fields respectively. The trait of parthenocarpy could be transferred from a donor to genotypes via few backcrosses (Sun et al. 2006c). They also suggested that 10 QTLs distributed across four genomic regions and 8 linked AFLP markers were responsible for controlling parthenocarpy in cucumber. Yan et al. (2008) reported parthenocarpy as quantitative trait under the control of two major genes and additional minor genes and suggested that, for the breeding of high parthenocarpic gynoecious cucumber, both parents used for crossing should have high parthenocarpy. While in another study by Yan et al. (2010, 2012a) on the inheritance of parthenocarpy in same backgrounds in cucumber using the mixed major and polygene model for inheritance of quantitative traits suggested that two additive-dominant-epistatic major genes and additive-dominant minor genes controlled parthenocarpy in gynoecious cucumber while in monoecious cucumber additive-dominant-epistatic polygenes were responsible instead of additive-dominant polygenes along with additive-dominant-epistatic major genes. Kumar et al. (2016) reported the predominant role of non-additive gene action governing the parthenocarpy in monoecious and gynoecious cucumber crosses. Devi et al. (2022) developed six generations by crossing parthenocarpic line PPC-6 with non-parthenocarpic genotype (Pusa Uday) and observed that a single incomplete dominant gene controlled parthenocarpy in the PPC-6 and QTL-seq analysis identified two major genomic regions, one each on chromosomes 3 and 6 spanning over a region of 2.7 Mb and 7.8 Mb, respectively. Gou et al. (2022) used 31 parthenocarpic cucumber lines for Genome-wide association study (GWAS) and observed the incompletely dominant control of parthenocarpy in cucumber and detected 5324 SNPs associated with parthenocarpy, from which six parthenocarpic loci, including two novel loci (*Pfs1.1* and *Pfs4.1*) were identified.

## Gene expression studies for parthenocarpy

Important details regarding the levels of gene expression connected to different plant metabolic processes can be found in the transcriptome of plants. The study of expression profiles of the genes becomes important in understanding the complete picture behind parthenocarpy. The endogenous levels of IAA modify the expression of parthenocarpy. The first report on the effect of endogenous level of auxins modifying the parthenocarpy in cucumber was given by Kim et al. (1992b). They stated that accumulation of IAA in the ovary was closely related with parthenocarpy and revealed that IAA is the major hormone which regulates parthenocarpy in cucumber and also stated that exogenous applied hormones promoted IAA accumulation in ovary. The actual elucidation of mechanism of regulating parthenocarpy remains uncertain. But Li et al. (2017) provided some evidences on the mechanism of parthenocarpy and revealed that the mechanism might be supported by a 'parallel switch' which consists of hormone dependent as well as hormone independent pathways. In case of pathway independent of hormones, process of fruit set is stimulated by certain regulatory proteins which are hormone insensitive known as the NP (Natural Parthenocarpy)-specialized proteins in 'EC1' (environmentally stable parthenocarpic cucumber cultivar). However, when sufficient amount of hormones are present, the young fruits which are formed through both pathways continue to grow till maturity. In hormone independent pathway, hormone sensitive fruits are developed which ultimately leads to fruit abortion. However, in case of hormone dependent pathway, the fruits became unresponsive to hormones and remains in a resting state because of increased expression of proteins which inhibits abortion. However, in such case, the fate of dormant fruits remains unknown. The genes involved in regulation of parthenocarpy include those involved in phytohormone, biosynthesis, signalling and transduction (Sharif et al. 2018). The known auxin transporter gene families include *PIN-FORMED* (*PIN*), *AUX1/LAX*, and the *B subfamily of ATP-binding cassette* (*ABCB*) transporters, of which *PIN* genes constitute the major auxin efflux transporters (Hu et al. 2021). The auxin signalling gene families which regulate parthenocarpy include auxin*/IAA* (*AUX/IAA*), transport inhibitor response 1/auxin signalling f-box proteins (*TIR1/AFB*), and

auxin-responsive factor (*ARF*) families (Luo et al. 2018). The auxin signalling genes (*AUX 22A-like-1, AUX22B-like-2,* and *AUX 28-like*) were expressed higher in parthenocarpic cucumber as compared to non-parthenocarpic cucumber (Su et al. 2021). Other auxin signalling genes (*TIR1* and *AFB2* genes) have also been reported in cucumber by Xu et al. (2017). They investigated the heterologous overexpression of *CsTIR1* and *CsAFB2* in tomato resulting in an early fruit set.

The genes involved in GA synthesis also regulate parthenocarpy. In case of pear, *GA20ox* (gibberellic acid oxidase) was found be highly expressed in pollinated fruits (Wang et al. 2020). Similarly in tomato, fruit set was accompanied with the increased expressed of GA biosynthesis genes (*SlGA20ox1, SlGA20ox2, and SlGA20ox3*) along with decreased expression of GA deactivation gene *SlGA2ox1* (Okabe et al. 2019). In case of cucumber, the genes *CsGA3ox3, CsGA3ox4, CsGA2ox1, CsGA2ox2, CsGA2ox3*, and *CsGA2ox5* were feebly expressed in the parthenocarpic genotypes which indicated their negative role in inducing parthenocarpy (Mandal et al. 2022). In addition to these, gibberellin signalling genes *DELLA* and *GID1* (*GA INSENSITIVE DWARF1*) also regulate parthenocarpy. It was observed that the *DELLA* and *GID1*arenegative and positive regulators of gibberellic acid biosynthesis, respectively (Hedden 2020). In addition to genes regulating auxin and gibberellin synthesis, cytokinin genes also regulate parthenocarpic fruit development. The cytokinin biosynthesis genes (*CYP735A1, CYP735A2,* and *LOG1)* were highly expressed in parthenocarpic cultivar of cucumber in contrast to cytokinin dehydrogenase genes (*CKX1* and *CKX3*) which were down-regulated (Su et al. 2021). Similarly, Mandal et al. (2022) reported the elevated expression of the cytokinin biosynthesis genes (*CsIPT, CsIPT1, CsIPT3, CsLOG1, CsLOG2, CsCYP735A1*, and *CsCYP735A2*), and decreased expression of *CsCKX1, CsCKX2*, and *CsCKX3* in parthenocarpic cucumbers. The cytokinin signalling genes (*CsRR3/4a, CsRR3/4b, CsRR8/9a*, and *CsRR8/9c*) negatively regulate parthenocarpy in cucumber as they expressed strongly in non-parthenocarpic genotype (Su et al. 2021). Negative regulation of parthenocarpy by *CsRR3/4a, CsRR3/4b*, *CsRR8/9a*, and *CsRR8/9c* and positive regulation by *CsRR8/9b, CsRR8/9d, CsRR8/9e,* and *CsRR16/17* in cucumber has also been reported (Mandal et al. 2023). In case of tomato, increased expression of cytokinin biosynthesis genes *SlIPT1, SlIPT2, SlCYP735A1, SlCYP735A2*, and *SlLOG2* was observed in ovaries after anthesis (Matsuo et al. 2012).

## Genetic engineering for parthenocarpy

The field of biotechnology has provided us with varied opportunities with easy technologies for obtaining parthenocarpic varieties as compared to conventional breeding approaches (Rotino et al.1997; Varoquaux et al. 2000). The developments of seeds and fruits are inter-connected and are regulated by plant hormones (Gillaspy et al. 1993). These processes are important to achieve parthenocarpic fruits and to guarantee expression of parthenocarpy without affecting the growth of vegetative parts of the plant. The gene of interest contains certain regulatory region(s) that exhibits highly valuable genetic information for controlling their expression. Thus, an abundance or decline in the expression of such phytohormone regulating genes might result in either development of parthenocarpic fruit with altered morphology or an inefficient fruit setting (Falavigna and Rotino 2006). Hence, the approach to generate transgenics via silencing a particular gene through RNA interference (RNAi) and antisense RNA technology is dominant tool to achieve parthenocarpy in fruits. The gene regulation for parthenocarpy in cucumber reported by various researchers is mentioned in the Table 2. Yin et al. (2006) introduced chimeric *DefH9-iaaM* construct in cucumber genome to generate parthenocarpic cucumber fruits. The construct had *DefH9* promoter and *iaam* coding sequence which produces parthenocarpic fruits by synthesis of auxins without pollination and the non-parthenocarpic or seeded fruits are obtained after pollination. The parthenocarpy achieved though was facultative (Rotino et al. 1997). To date, the use of *DefH9-iaaM* chimeric gene for parthenocarpic fruit development has been reported in tobacco (Rotino et al. 1997), eggplant (Rotino et al. 1997), tomato (Ficcadenti et al. 1995; Pandolfini 2009), strawberry and raspberry (Mezzetti et al. 2000).

Apart from *DefH9-iaaM,* other genes have also been targeted for inducing parthenocarpy in different crops. The techniques could be used to achieve

**Table 2** Gene regulation of parthenocarpy in cucumber

| Gene | Function | Modification | Reference |
|---|---|---|---|
| *DefH9-iaam* | Auxin Synthesis | Ovule specific transgene expression | Yin et al. (2006) |
| Hormone | Mode of action | | References |
| IAA | Accumulation in ovary | | Kim et al. (1992b) |
| Hormone independent and dependent parthenocarpy | Fruit set regulated via hormone-insensitive protein: When sufficient amount of hormones are present, young fruits which are developed via both the pathways could mature continuously | | Li et al. (2017) |

high yielding parthenocapic cucumber genotypes. The down-regulation or loss-of-function mutation of *SlIAA9,* an Aux/IAA transcription factor which negatively regulates auxin response, induced parthenocarpy in tomato (Kim et al. 2019; Klap et al 2016; Saito et al. 2011; Wang et al. 2005). Auxin biosynthesis genes *SlTAR1*, *ToFZY2*, and *ToFZY3* were found to be up-regulated in genome edited parthenocarpic tomato *SlAGL6*mutants (Gupta et al. 2021). The RNAi-mediated silencing of the *SlDELLA* increased the GA biosynthesis genes' expression, thereby resulting in parthenocarpy (Marti et al. 2007). Down-regulation of *SlTPL1* led to facultative parthenocarpy in tomato (He et al. 2021). In tomato, RNAi mediated gene suppression of *Aucsia* resulted in auxin-related phenotypes which included parthenocarpy (Molesini et al. 2009). The *PARENTAL ADVICE-1* (*PAD-1*) is known to coordinate the reverse reaction of Trp-IPyA in the IAA biosynthesis pathway and its loss-of-function mutation tend to increase IAA accumulation in un-pollinated ovaries, thereby producing parthenocarpic fruits in case of eggplant (Matsuo et al. 2020).

Although, various studies of gene silencing/loss-of-function mutation have been successfully utilized to induce parthenocarpy, some genes can be over-expressed to yield the same results. The transient expression of *CYP735A* resulted in parthenocarpy in non-parthenocarpic cucumber (Cui 2013). Carmi et al. (2003) utilized ovary-specific expression of the *Agrobacterium rhizogenes*-derived gene *rolB* for inducing parthenocarpy in tomato.

## Molecular breeding for parthenocarpy

In the initial studies it was exhibited that parthenocarpy in cucumber had been regulated by single or dual incomplete or recessive genes. But, recent studies suggested that the trait was controlled by several QTLs. The first molecular marker (ISSR) linked to parthenocarpy was developed by Chen et al. (2008). They found marker N92 showed polymorphism for non-parthenocarpic and parthenocarpic cucumber lines and estimated that there is genetic distance of 18.9 cM between this primer and cucumber parthenocarpy trait. Report for first QTL-linked marker associated with the parthenocarpy in cucumber was given by Sun et al. (2006c). They developed eight fluorescent amplified length polymorphism (AFLP) markers that are linked to parthenocarpy through QTL mapping and identified 10 QTLs related to parthenocarpy which were distributed over four genomic regions in cucumber. Selection for phenotypic bulks (high and low parthenocarpic) in small population of $F_{2:3}$ (126) likely lead to the early generation fixation of alleles conditioning parthenocarpy. In addition, as the bulks used for BSA were derived by selfing instead of random mating in $F_3$ generations, the assortment of all alleles for parthenocarpy into individual $F_4$ plants would not be expected unless the ancestral $F_2$ plant possessed all favourable alleles. Another development of AFLP markers associated with parthenocarpy in cucumber is defined by Yan et al. (2012b) and they reported AGG/$CAA_{325}$ marker linked to non-parthenocarpy locus at distance of 9.7 cM. The name of the marker is based on 325 bp specific fragments that were amplified with the help of primer E41/M47 and no bands were observed in the parthenocarpic genotypes pool. Several attempts were also made to develop markers linked to parthenocarpy in pickling or processing types of cucumber. Wu et al. (2016) identified 7 QTLs linked with parthenocarpy including *Parth2.1* as major QTL along with two candidate genes. Wu et al. (2016) discovered four related markers (SSR16226, Indel-T-32, Indel T-34, and Indel-T-39) to parthenocarpy

**Table 3** QTLs associated with parthenocarpic trait in cucumber

| Cross | Mapping population | QTL(s)/gene(s) | Remarks/findings/ Position | Type of molecular markers | References |
|---|---|---|---|---|---|
| 2A (parthenocarpic, gynoecious) × Gy8 (non-parthenocarpic, gynoecious) | $F_3$ | 10 QTLs related to parthenocarpy spread across four genomic regions | *parth1.1-2A, parth1.2-2A, parth4.1-2A, parth1.3-Gy8, parth1.4-Gy8, parth4.2-Gy8, parth5.1-Gy8, parth1.5-Gy8, parth5.2-Gy8, parth 5.3-Gy8* | SSR | Sun et al. (2006c) |
| EP-6 (parthenocarpic) × ZR-2 (non-parthenocarpic) | $F_2$ | Primer N92 used for phenotyping of parthenocarpy | Marker located at genetic distance of 18.9 cM from parthenocarpy trait | ISSR | Chen et al. (2008) |
| 6457 (parthenocarpic, monoecious) × 6429 (non-parthenocarpic, monoecious) | $F_2$ | Marker AGG/CAA325 detected in non-parthenocarpic DNA pool | The genetic distance between marker AGG/CAA325to and non-parthenocarpy locus was 9.7 cM | AFLP | Yan et al. (2012b) |
| EC1 (parthenocarpic, gynoecious) × 8419 s-1 (non-parthenocarpic, monoecious) | $F_{2:3}$ | 7 QTLs | QTLs were mapped to all chromosomes except 4 and 7. Of these a major-effect QTL, *Parth2.1*, was located on chromosome 2 (flanking markersSSR00684-SSR22083) | SSR Indel markers | Wu et al. (2016) |
| 2A (parthenocarpic, gynoecious) × Gy8 (non-parthenocarpic, gynoecious) | $F_3$ | 7 linked QTLs | Located *parth2.1* on chromosome 2, *parth4.1* on chromosome 4, *parth5.1* on chromosome 5, *parth6.1, 6.2 and 6.3* on chromosome 6, and *parth7.1* on chromosome 7 | SSR | Lietzow et al. (2016) |
| 6467 (strong parthenocarpic) × 6426 (weak parthenocarpic) | $F_{2:8}$ | 4 QTLs | 4 QTLs were identified on chromosomes 1(4.38–11.00 Mb), 3 (2.24–10.66 Mb) and 6 (15.67–17.93 Mb; 26.33–27.49 Mb) | SSR | Niu et al. (2020) |
| DDX (strong parthenocarpic) × ZK (low parthenocarpic) | $F_2$ | 1 major effect QTL | Major effect QTL *par2.1* located on chromosome 2 accounted for 26.6% of the total phenotypic variation | SSR | Yan et al. (2022) |

in addition to reporting a major-effect QTL *Parth2.1* and six minor-effect QTLs that contribute to the phenotypic variance of parthenocarpy in cucumbers. Minor effect QTL were designated as *Parth1* at 101.0 cM on chromosome 1, *Parth3.1* at 93.8 cM on chromosome 3, *Parth5* at 58.0 cM on chromosome 5, *Parth7* at 23.4 cM on chromosome 7, *Parth2.2* at 50.3 cM on chromosome 2 and *Parth3.1* at 57.5 cM on chromosome 3. The marker closely associated with *Parth2.1* could be used for efficient marker assisted selection of parthenocarpy in cucumber. Lietzow et al. (2016) detected 7 QTLs related to parthenocarpic fruit set assigned as *parth2.1* (on chromosome 2), *parth4.1* (on chromosome 4), *parth5.1* (on chromosome 5), *parth6.1, parth6.2, parth6.3* (on chromosome 6) and *parth7.1* (on chromosome 7). The QTLs *parth5.1, parth6.1*, *parth6.2* and *parth7.1* contributed equally in expressing parthenocarpy at commercially appropriate harvest stage while, *parth7.1* was responsible for early parthenocarpy fruit set. This study is crucial in understanding parthenocarpy in cucumber for breeders as well as for researchers. Teams led by Wu et al. (2016) and Lietzow et al. (2016) detected 12 QTLs in two sources, although only 2 QTLs (*parth2.1* and *parth7.1*) were found to be co-localized between them. This inconsistency in results reflects the problems in phenotyping parthenocarpy with accuracy, a trait which is hard to distinguish from yield. He et al. (2016) identified 9 genes including *Csa2M349050.1*, *Csa2M350390.1*, *Csa2M351550.1*, *Csa2M354670.1*, *Csa2M354750.1*, *Csa2M355020.1*, *Csa2M353460.1*, C*sa2M354910.1,* and *Csa2M354980.1* which were expected to be potential genes involved in parthenocarpy of cucumber. All the genes except one were responsible for biosynthesis, regulation, and/or signal transduction for phytohormones and were expected to be involved in cell division. Zhihong et al. (2020) discovered 4 QTLs on chromosomes 1, 3 and 6, as well as one minor-effect QTL on chromosome 3 which occurred consistently throughout years. Gou et al. (2022) established that several QTLs and genes governed the parthenocarpy, which was inherited in an incompletely dominant way. The summarised information on development of QTLs for parthenocarpy in cucumber is provided in Table 3.

Thus validated identified molecular markers ease the incorporation of parthenocarpy in varied cucumber background that are accompanied by other desirable genes which might take longer time and more tedious ways if done through conventional breeding techniques.

## Conclusion

Parthenocarpy is a phenomenon that results in the formation of seedless fruits without pollination. Such fruits are preferred over seeded ones by consumers. Thus, it becomes important for breeders to generate seedless varieties of cucumber with high resilience. The publically available genome sequences of cucumber accessions make it easier for breeders for generating improved varieties of cucumber. The QTLs and molecular markers associated with parthenocarpy further ease the processes. The major-effect QTLs *parth2.1* and *parth6.1* have been identified on chromosomes 2 and 6. Various genes have been identified which are directly involved in regulation of parthenocarpy. These genes form part of biosynthesis, signalling and perception of plant hormones such as auxins, cytokinins and gibberellins. These genes could be targeted via genetic engineering approaches for production of parthenocarpic fruits in cucumber.

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**Declarations**

**Competing interests** The authors declare no competing interests.

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