Parthenocarpy: A potential trait to exploit in vegetable crops: A review

A.S. Dhatt* and Gagandeep Kaur

Department of Vegetable Science, Punjab Agricultural University, Ludhiana – 141 004, India.
Received: 16-04-2016 Accepted: 15-10-2016 DOI: 10.18805/ag.v37i4.6460

ABSTRACT
Parthenocarpy is the growth of ovary into seedless fruit in the absence of pollination and fertilization. It may occur naturally or can be induced artificially by exogenous application of hormones or their enhanced endogenous level. Parthenocarpy improves the yield, quality and processing attributes of vegetable crops like cucumber, eggplant and watermelon, where seed is a limiting factor during consumption. This trait proved highly useful to develop fruits under environmental conditions that are unfavorable for successful pollination and fertilization, particularly in greenhouse cultivation and especially in cross-pollinated crops. It is an established fact that phytohormones play an important role in fruit setting and their genetic manipulation can lead to seedlessness. Apical shoot is considered as source of inhibitors preventing fruit growth in the absence of stimulus like pollination or application of phytohormones. The exploitation of biotechnological tools can further enhance its utility for the benefit of mankind. Therefore, present review is focused on factors and potential of parthenocarpy in vegetable crops.

Key words: Parthenocarpy, Phytohormones, Pollination, Seedless fruit, Vegetables.

The biological function of the fruit is the protection of embryos and seeds during their development and the facilitation of seed dispersal after maturation. The onset of fruit development from the ovary, the so-called fruit set, occurs after fertilization of the ovules. Fertilization of the ovule generally triggers the ovary development into fruit (Nancy, 2015). The processes of seed and fruit development are intimately connected, synchronized and controlled by phytohormones (Pandolfi, 2009). Thus, the signaling processes are required for the development of the fertilization products necessary for the initiation of seed and fruit development (Raghavan, 2003). Various phytohormones, especially gibberellins, cytokinins and auxins, are involved in the signaling processes that follow pollination and fertilization and these are the main requirements for further growth and development of seeds and the fruit (Fos et al., 2001). Developing seeds are source of phytohormones and stimulate the fruit growth and development (Ozga et al., 2002). However, in some vegetables presence of seeds in fruit are undesirable due to hard or leathery texture, bitter taste and presence of toxic compounds, allergens and affect on the palatability (Dalal et al., 2006). Seedless fruits are desirable for improving the quality of fresh as well as of the processed fruit and it has been observed in cucumber, eggplant watermelon and tomato (Denna, 1973; Varoquaux et al., 2000; Yin et al., 2006). Therefore, replacing the seeds and seed cavities with edible fruit tissue is an attractive offer to the consumers and challenge to the researchers.

Hence, genetic tool of parthenocarpy can play important role in this direction, wherein, ovary developed into a fruit without fertilization. The separation of fruit growth from fertilization and seed development resulted into a seedless parthenocarpic fruit (Fos et al., 2000; Varoquaux et al., 2000). Parthenocarpy is genetically controlled and commercially exploited for production of seedless fruit (Sykes and Lewis, 1996; de Menezes et al., 2005; Goetz et al., 2006). Therefore, present review is focused on artificial and genetic causes of parthenocarpy and its utilization in vegetable crops.

Types of Parthenocarpy

Artificial parthenocarpy: It involves the stimulation for the growth of a fruit using both natural and artificial plant hormones. The induction of parthenocarpy is a common agricultural practice for some horticultural species (Schwabe and Mills, 1981). The exogenous use of irradiated pollen, natural or synthetic auxins and gibberellins increased IAA content during ovary development (Tsao, 1980). This resulted in elevated levels of endogenous phytohormones during parthenocarpic fruit set and development from sources other than seeds (Talon et al., 1992). Therefore, in Arabidopsis and a variety of agricultural species the parthenocarpy can be induced with exogenous application of auxins, cytokinins, or GAs (Smith and Kolotunow, 1999; Ramin, 2003; Serrani et al., 2007). Nitsch (1970) defined that a plant is parthenocarpic, if it exceeds a threshold in the concentration of growth regulators during a critical period at anthesis. In eggplant, the first increase takes place during
the first five days after anthesis, while a major peak of IAA appears at 20 days after anthesis in both pollinated and auxin treated flowers (Lee et al., 1997). The possible factors that induce parthenocarpic in vegetable crops are discussed as under:

Environmental factors: Adverse environmental conditions inhibit fruit set and growth of several vegetable crops. High or low temperature, humidity, low light intensity, heavy rain and strong wind are all factors, which negatively influence several steps of the reproductive process, such as formation, dispersal and germination of pollen, fertilization and seed maturation, consequently, fruit production is impaired (Krug, 1997). On the other hand, these environmental factors are known to induce parthenocarpy also. Among these factors, the most important is temperature stress, which induces parthenocarpic fruit growth in tomato plants due to flower abortion (Sato et al., 2001) and in pepino due to inability to produce viable pollen (Ruiz et al., 1996). The maximum expression of parthenocarpic in tomato was related with high temperature stress above the optimal 24-25°C (Hazra et al., 2010). Under high temperature stress most of the tomato flowers were aborted, but 4% remained on the plant and developed into fruit without the seed due to failure in production and release viable pollen (Sato et al., 2000). Sato et al (2001) added that under high temperature, most of the tomato flowers (53%) developed into parthenocarpic fruit and remainder (43%) stayed on the plant as undeveloped flowers with a transition phase to parthenocarpic fruit. The development of flowers to parthenocarpic fruit may be correlated with carbohydrate availability or the presence of seeded fruit on the vine. Photosynthetic rate declined in tomato at high temperature, so carbohydrate availability declined too and may cause parthenocarpic fruit development (Sato et al., 2000). Carbohydrate content affects the expression of flower abortion genes through hexokinases, which have roles in sugar metabolism and signal transduction to other genes (Jang and Sheen, 1997). In peppers, induction of parthenocarpy was also observed due to climatic stress like low irradiance (Jaafar et al., 1994), severe water stress and high irradiance (Jaafar et al., 1994) or high temperatures (Rylski and Spigelman, 1982).

Phytohormonal level: Plant growth regulators except ethylene and abscisic acid induced the fruit development; however, gibberellins, auxins and cytokinins induced parthenocarpy (Ozga and Reinecke, 2003). Exogenous auxin application to flowers for induction of parthenocarpy was first reported by Gustafson (1936), while, the effects of various growth regulators on its initiation was studied later in a wide variety of horticultural crops, such as watermelon (Pak, 1993), cucumber (Kim et al., 1994), sweet pepper (Heuvelink and Korner, 2001) kakrol (Chowdhury et al., 2007) and teasle gourd (Mohammad et al., 2008). The exogenous application of auxin triggers the expression of auxin-biosynthetic genes in ovaries and ovules to induce parthenocarpic fruit (Carmi et al., 2003, Mezzetti et al., 2004). When the auxin-biosynthetic iaaM gene expressed in ovaries and ovules under the control of the placenta- and ovule-specific DefH9 promoter, parthenocarpic fruit in tobacco, eggplant, tomato, strawberry and raspberry was induced (Pandolfini et al., 2002). Auxin is the major inducer of fruit set that acts in part by inducing gibberellin biosynthesis (Fig. 1). Interestingly, gibberellin does not significantly contribute to the final fruit size, but seems to play an important role in preventing flower and fruit abscission (Tiwari et al., 2012). Therefore, gibberellin along with auxin seems to be playing an important role in parthenocarpy. As the ovaries of parthenocarpic tomato had three times more gibberellins than non-parthenocarpic hybrids of tomato (Hassan et al., 1987). The involvement of GAs in early tomato fruit development was supported by multiple evidence including exogenous treatments, hormone levels and gene expression in wild-type and parthenocarpic mutant lines (Alabadi and Carbonell, 1998; Bohner et al., 1988; Fos et al., 2000, 2001; Rebers et al., 1999). Therefore, coordinated action of auxin and gibberellin is required for normal fruit development in tomato (Bunger-Kibler and Bangerth, 1983), blueberry (Cano-Medrano and Darnell, 1997), watermelon (Sedgley et al., 1977), pea (Vercher and Carbonell, 1991) citrus (Guardiola et al., 1993) and Arabidopsis (Smith and Koltunow, 1999). The pollen produce gibberellins, while the exogenous application of gib-berellins augments the auxin level in the ovary of an unpollinated flower to trigger the fruit setting in absence of fertilization. The developing em-bryo renews the rate of cell division in the contiguous fruit tissue. As considered that developing seeds support cell expansion within the fruit by the production of auxin. Gibberelin that triggers fruit setting in the course of ovary auxin increase is supported by its increased transcription at the time of fruit set and by its expression in the mitotic cell layers of the placenta (Testa, 2002). The GA response is under the negative control of a family of DELLA nuclear factors, namely RGA, GAI, RGL1, RGL2 and RGL3 (Wen and Chang, 2002). Auxin up-regulates gibberellins biosynthesis and stimulates GA-dependent degradation of DELLA proteins (Fu and Harberd, 2003), as silencing of DELLA also induces facultative parthenocarpic in tomato fruits (Marti et al., 2007). Furthermore, the fruit growth was inhibited by inhibitors of GA biosynthesis and it is reversed by GAs application (Santes and Garcia-Martinez, 1995).

Even, apical shoot acts as a source of inhibitors, which prevents the fruit growth in the absence of a stimulus like pollination or application of gibberellic acid in pea (Rodrigo and Garcia-Martinez, 1998). Plant decapitation stimulated parthenocarpic growth, even in derooted plants, and this effect was counteracted by the application of indole acetic acid (IAA) or abscisic acid (ABA) in agar blocks to
Table 1: Parthenocarpic fruit development in some vegetable crops by using biotechnological tools

<table>
<thead>
<tr>
<th>Gene</th>
<th>Biotechnological tool</th>
<th>Role of gene in plant</th>
<th>Vegetable crop</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>DefH9-iaaM</td>
<td>Transgenics</td>
<td>Auxin synthesis</td>
<td>Tomato, eggplant, cucumber, raspberry</td>
<td>Acciarri et al. (2002), Yin et al. (2006), Mezzetti et al. (2004), Yin et al. (2006)</td>
</tr>
<tr>
<td>rolB</td>
<td>Transgenics</td>
<td>Auxin signaling</td>
<td>tomato</td>
<td>Nancy D (2015)</td>
</tr>
<tr>
<td>CHS</td>
<td>Gene silencing</td>
<td>Auxin transport</td>
<td>tomato</td>
<td>Schijlen et al. 2007</td>
</tr>
<tr>
<td>ARFs</td>
<td>RNA interference</td>
<td>Auxin response</td>
<td>eggplant</td>
<td>Liming et al. (2015)</td>
</tr>
<tr>
<td>AUCSIA</td>
<td>Gene silencing</td>
<td>Auxin response</td>
<td>tomato</td>
<td>Molesini et al. (2009)</td>
</tr>
<tr>
<td>DELLA</td>
<td>Gene silencing</td>
<td>Gibberellin response</td>
<td>tomato</td>
<td>Marti et al. (2007)</td>
</tr>
</tbody>
</table>

Fig 1: Role of phytohormes in parthenocarpic fruit development (Arrows indicate the positive regulation and lines ending in a bar indicate negative regulation).

the severed stump (Rodrigo and Garcia-Martinez, 1998). The decapitation diverts the GAs from mature leaves to the unpollinated ovary, which stimulates the parthenocarpic growth of ovary (Garcia-Martinez et al., 1991). Further, Serrani et al. (2010) also proved that application of auxin transport inhibitor (NPA; N-1-naphthylphthalamic acid) to unpollinated ovaries of tomato induced parthenocarpic fruit set, this was caused by enhanced indole-3-acetic acid (IAA) content and its effect also negated by inhibitor of gibberellins biosynthesis (Paclobutrazol).

Natural or Genetic parthenocarpy: Genetic parthenocarpy is called obligatory, when expression of the parthenocarpic trait is not influenced by external factors and is facultative, if occurs only under adverse conditions for pollination and fertilization. Elevated level of endogenous hormones in the ovary in the absence of pollination and fertilization causes the natural parthenocarpy (Nitsch, 1970; Gillaspy et al., 1993). It has been reported in various crops like grape (Wong, 1941), tomato (Groot et al., 1987), mandarins (Talon et al., 1992), banana (Gustafson, 1939), opuntia (Weiss et al., 1993), pepino (Prohens et al., 1998), eggplant (Yoshida et al., 1998), cucumber (Yan et al., 2010) and capsicum (Tiwari et al., 2011). Genetic parthenocarpy can solve the problem of low pollen viability and poor pollen release, which often occurs under low light, low or high temperatures under open and greenhouse conditions.

Genetics of parthenocarpy: Parthenocarpy is heritable, but does not fit in a simple genetic model. As in tomato it is controlled by several single-gene recessives (Fos et al., 2001; Gorguet et al., 2005), in Capsicum annum L. by a single recessive gene (Tiwari et al., 2011), while in pepino (Solanum muricatum) by a single dominant gene (Prohens et al., 1998). However, parthenocarpic trait of cucumber is controlled by two major additive-dominant-epistatic genes and additive-dominant polygenes, in either monoecious or gynoecious forms (Yan et al., 2010). Molecular and physiological basis of parthenocarpy have showed involvement of genes controlling auxins and gibberellins.
biosynthesis, self-incompatibility, histones and alcohol dehydrogenase activity (Fos et al., 2001; Gorguet et al., 2005; Testa et al., 2002).

In tomato, pat gene responsible for parthenocarpy is single recessive mutation with pleiotropic effects. The pat gene enhance the growth rate of ovary during the first 10 days of anthesis, which correlates with a precocious onset of cell divisions in the pericarp and higher auxin, gibberellin and DNA contents in the ovaries (Mapelli et al., 1978). In addition to parthenocarpy, the pat gene causes aberrations that affect male floral organs. The androecium of pat flowers is short, irregular and apparently unfused anthers that leave the stigma exerted and preferentially external dehiscence (Philouze and Pecaut, 1986). The pat syndrome describes that parthenocarpy caused by a secondary effect of a gene controlling at early stages organ identity and development (Mazzucato et al., 1998). Three alleles i.e. pat-2 and pat-3/pat-4 have altered hormonal balances in the ovary of parthenocarpic tomato plants as compared with that of wild type and these alleles are considered natural source of facultative parthenocarpy (Fos et al., 2001). Genetics of parthenocarpy in two different lines of tomato i.e. IL5-1 and IVT-line-1, both carrying Solanum habrochaites chromosome segments, confirmed that parthenocarpy in tomato is controlled by two QTLs (Gorguet et al., 2008). In IL5-1, one QTL is on chromosome 4 (pat4.1) and other on chromosome 5 (pat5.1), whereas, in IVT-line-1, one on chromosome 4 (pat4.2) and one on chromosome 9 (pat9.1). It is likely that pat4.1 from IL5-1 and pat4.2 from IVT-line-1 located near the centromere of chromosome 4 are allelic. Micro synteny between tomato and Arabidopsis in this genetic region also identified that ARF8 as a potential candidate gene for these two QTLs. ARF8 is known to act as an inhibitor for further carpel development in Arabidopsis in absence of pollination/fertilization. Expression of an aberrant form of the Arabidopsis ARF8 gene in tomato has also caused parthenocarpy (Gorguet et al., 2008).

Genetic causes of parthenocarpy in eggplant was first reported in 1998 by Yoshida and co-workers in a cross between European parthenocarpic cultivar Talina and a Japanese non-parthenocarpic cultivar EPL1. Their segregation tests in F1 and BC1F1 populations confirmed that it is controlled by a single major gene. Later on, a cross between an European parthenocarpic cultivar Mileda and a Japanese non-parthenocarpic line ASL-1 also confirmed the presence of single dominant gene in eggplant (Kuno and Yabe, 2005). Using this information intraspecific linkage map in eggplant was developed (Barchi et al., 2010).

Most of the markers developed by Doganlar et al (2002) and Barchi et al (2010) were RFLP (restriction-fragment-length polymorphism) and AFLP (amplified-fragment-length polymorphism) markers, respectively. Therefore, it is difficult to apply those markers to detailed genetic studies on other populations of different intraspecific crosses, because of the low numbers of polymorphisms. This problem is solved by the development of simple sequence repeat (SSR) markers for S. melongena species (Nunome et al., 2009) and completes the detailed integrated linkage map. Quantitative trait locus (QTL) analysis of eggplant by using co-dominant simple sequence repeat and single nucleotide polymorphism markers revealed that two QTLs on chromosomes 3 and 8, which are controlling parthenocarpy 3.1 (Cop3.1) and Cop8.1, respectively (Miyatake et al., 2012).

Biotechnological interventions for parthenocarpy: Phytohormones especially, Auxins and GAs play important roles in parthenocarpic fruit development (Ozaga and Reincke, 2003; Serrani et al., 2008; Dorcey et al., 2009). Increased levels of these hormones in the ovary or ovule substitutes pollination for fruit development, which has been exploited using biotechnological tools (Table 1.) (Varoquaux et al., 2000; Carmi et al., 2003; Goetz et al., 2006). The different methods that increases auxin level in ovary gave promising results in induction of parthenocarpy (Gorguet et al., 2005). As seedless fruits can be obtained by expressing the auxin synthetising gene iaaM of Pseudomonas syringae pv. Savastanoi under the control of the ovule/placenta specific promoter from the DefH9 gene of Antirrhinum majus (Rotino et al., 1997; Pandolfini et al., 2002). The promoter found active in ovules and placenta and in the tissues derived from there, consequently auxin synthesised during the whole growth of the fruit (Acciarri et al., 2002). This gene has been used to confer parthenocarpy in several horticultural crops including tomato, eggplant, cucumber, raspberry (Rotino et al., 1997; Pandolfini et al., 2002; Mezzetti et al., 2004; Yin et al., 2006). The genetically modified parthenocarpic tomatoes and eggplants with DefH9-iaaM gene have showed more productivity under environmental conditions unfavourable for pollination (Ficcadenti et al., 1999; Acciarri et al., 2002). The parthenocarpic fruits have same shape and equal or bigger size as compared with seeded fruits (Acciarri et al., 2002; Pandolfini et al., 2002). The DefH9-iaaM fruits did not contain seeds, when grown under adverse conditions for pollination and showed much reduced number of seeds under optimal environmental conditions (Acciarri et al., 2002; Rotino et al., 2005). The quality of DefH9-iaaM tomato fruits was equivalent to that of seeded fruits except higher beta-carotene in the parthenocarpic fruit (Rotino et al., 2005). Hence, increased level of beta-carotene is a valuable trait of DefH9-iaaM seedless tomato from nutritional angle.

Ovary-specific expression of the A. rhizogenes derived gene rolB manifests several auxin related functions. Tomato plants produced parthenocarpic fruits, if transformed with a chimeric construct containing the rolB gene fused to the ovary and young fruit specific promoter TPRP-F1(Table
1). Fruit size and morphology of the seed-less fruits were comparable to those of seeded fruits of the parental line. (Carmi et al., 2003). Seedless fruits have also been obtained by down regulating Chalcone synthase (Chs), the first gene in the flavonoid biosynthetic pathway (Schijlen et al., 2007). Interestingly, loss of CHS activity in A. thaliana caused an increase in polar auxin transport. It is possible that in Chs silenced tomato parthenocarpy resulted from an altered distribution of auxin caused by the reduced level of flavonoids. Aucsia genes encode a family of plant peptides that control fruit initiation and affect other auxin-related biological processes in tomato. Aucsia-silenced tomato plants exhibited parthenocarpic fruit development, leaf fusions, and reflexed leaves. In addition, Aucsia-silenced plants showed an increased sensitivity to 1-naphthylphthalamic acid, an inhibitor of polar auxin transport (Molesini et al., 2009).

ARFs influence the expression of auxin-responsive genes by interacting with auxin/indole acetic acid (Aux/IAA) proteins (Kumar et al., 2011) and regulate the fruit development (Guilfoyle and Hagen, 2001; Kumar et al., 2011). A typical ARF protein contains a conserved N-terminal DNA-binding domain (DBD), a non-conserved middle region (MR), and a conserved C-terminal dimerization domain (CTD) (Guilfoyle and Hagen, 2001). The DBD of an ARF binds specifically to TGTCTC auxin response elements (AuxREs) in promoter regions to regulate the expression of auxin-responsive genes (Ulmasov et al., 1997). The MR located between the DBD and CTD determines, whether the ARF functions as a transcriptional activator or as a repressor (Tiwari et al., 2003). RNA interference of SmARF8 induced parthenocarpy in unfertilized flowers of eggplant, suggesting that SmARF8 negatively regulates fruit initiation (Liming et al., 2015).

**Exploitation of parthenocarpy in vegetable crops:** Parthenocarpy is an economically valuable trait in number of horticultural crops. Consumers often prefer seedless fruit for aesthetic and quality reasons, because many such fruit have more attractive appearance, added convenience in terms of preparation, consumption and processing. Parthenocarpic cucumber does not require pollination, even though, it is a cross-pollinated crop. Combination of parthenocarpic and gynoecism gave added advantage of yield and palatability of cucumber (Denna, 1973). In eggplant, parthenocarpic improves fruit quality and reduces the labour needed for its out-of-season cultivation. Since the commercial ripeness of eggplant fruits precedes its physiological maturity, the presence of seeds considerably depreciates the value of fruits for both fresh and processed market. The negative effects associated with the presence of seeds have a faster and more intense browning of the fruit flesh upon cutting, increased saponin and solasonin compounds causing bitter taste and hard flesh. The absence of seeds increased the shelf life of the fruits for better conservation (Aubert et al., 1989). This effect was also observed in watermelon, where seeds are the origin of fruit deterioration (Varoquaux et al., 2000). Further, in tomato seedless fruits are tastier than the seeded variety. The parthenocarpic tomato does not require removal of seed during processing. Seedless tomatoes have 1% more dry matter, more sugars, less acidity, less cellulose and more soluble solids than seeded cultivars (Lukyanenko, 1991). An important advantage of parthenocarpic plants is that they set and develop fruits under environmental conditions that are unfavorable for successful pollination and fertilization, particularly green house cultivation (Yin et al., 2006; Gorguet et al., 2008).

**CONCLUSION**

Parthenocarpy is an important trait for improving the yield, quality and processing traits of vegetable crops. This trait proved highly useful in green house cultivation, particularly cross-pollinated vegetable crops. This is established fact that phytohormones play important role in fruit setting, however, their genetic manipulation can lead in development of seedlessness. Further, exploitation of biotechnological tools can enhance the efficiency and identification of parthenocarpic genes across the crops for the benefit of mankind.

**REFERENCES**


Bunger-Kibler S and Bangerth F (1983) Relationship between cellnumber, cell-size and fruit size of seeded fruits of tomato (Lycopersicon esculentum Mill), and those induced parthenocarpically by the application of plant-growth regulators. Plant Growth Regul 1:143-54.


Wong C Y (1941) Chemically induced parthenocarpy in certain horticultural plants, with special reference to the watermelon. *Bot Gaz* **103**: 64-86.
