Chapter 13
Parthenocarpy in Tomato

A.N. Lukyanenko[1]

13.1 Introduction

Tomato is a self-pollinated crop and normally produces seeded fruits when fertilization takes place. The current cultivars set fruits within a narrow range of temperatures of 15° to 21°C (night) and 30° to 35°C (day). Beyond these range of temperatures generally there is no fruit set because of the lack of production of sufficient amounts of fertile pollen and difficulties in pollination and fertilization. A low degree of flower fertilization and fruit set is observed in tomato plants grown in glasshouses with low light intensity and short days.

Synthetic growth regulators are often used to induce parthenocarpic fruit set by growers under adverse weather conditions and in greenhouses. Nevertheless, fruit defects are a problem when growth substances are used. Recently, excellent sources of genetic parthenocarpy with a great commercial value to improve tomato fruit set and yield in unfavorable environments have been reported.

13.2 Types of Parthenocarpy

Parthenocarpy may occur naturally or be induced artificially (Gustafson 1942). In case of induced parthenocarpy normal tomato fruits development takes place with the application of various growth regulators (Gustafson 1936; Nitsch 1952; Osborne and Went 1953).

Natural (genetic) parthenocarpy may be obligate or facultative. The former results from genetic sterility, arises without any external stimulation and requires a vegetative method of propagation (in banana, pineapple, etc.). Alternatively, in the latter either seeded or seedless fruits are produced in response to environmental stimuli. Facultative parthenocarpy is found in tomato and other species in which processes of pollination and fertilization depend on narrow environmental limits. The Severianin cultivar, which was bred in the USSR, is able to produce large fruits when all forms of fertilization are absent (Philouze and Maisonneuve 1978b).

[1]Plant Breeding Station, Krymsk-4, Krasnodar Region 353330, USSR

13.3 Sources

Parthenocarpy may be caused by genome ploidy, trisomy, aneuploidy and transloca-
tion heterozygotes. However, in diploid homozygous cultivars it may be due to the effect
of a particular gene. Parthenocarpy is often linked with male and female sterility. Avdeev
(1982) has observed that in the Astrakhan region lines with positional sterility produced
0.5–0.7 kg parthenocarpic fruits/plant and the cv Vrbchanske Nizke 1.5–2 kg fruits/plant.
The number of seeds per fruit was in the range of 1 to 16 as compared to 120–360
seeds/fruit for cv Volgogradskiy, which was commercially grown in that area. Obligate
parthenocarpy was found in male and female sterile aneuploid tomatoes (Lesley and
Lesley 1941). Johnson and Hall (1954) screened for naturally occurring parthenocar-
py at high temperatures (31°–37°C) and selected some seedless tomatoes. Style exser-
tion and loss of pollen viability were associated with parthenocarpy.

The cv Farthest North has been a parent of cultivars with parthenocarpic tenden-
cies. Parthenocarpic fruit set was observed at both high and low temperatures in cv
Sub Arctic Plenty, which had about 66% of Farthest North in its pedigree (Charles
and Harris 1972). Kubicki and Michalska (1978) found a useful degree of par-
thenocarpy among segregants of a cross between Early North and Beaverlodge 6703.
Farthest North is also in the parentage of the Oregon T5–4 parthenocarpic tomato
line, which may have about 30% seedless fruit (Baggett and Frazier 1978). These lines
could also have received parthenocarpic tendencies from a line developed in Hawaii
by W.A. Frazier from an interspecific cross *L. esculentum* × *L. hirsutum* and from
the cv Immune Prior Beta which set fruits at a low temperature. Similar breeding
lines as well as an accession of *L. pimpinellifolium* occurred in the pedigree of
Oregon 11, and Gold Nugget, which usually produced 50%–70% seedless fruits
in Western Oregon (Baggett and Frazier 1982; Baggett and Kean 1985).

A short-anther mutant (stock 2524) which produced parthenocarpic fruits was
found by Soressi (1970) following ethylmethane sulfonate seed treatment. Inde-
pendently, Pecaut and Philouze (1978) discovered a spontaneous mutant in a F_3 (later
designated Montfavet 191) from a cross between the cultivar Santa Cruz Samano
(from Brazil) and a breeding line from Montfavet, France. The Montfavet 191 par-
thenocarpic fruits mature 6–10 days earlier than similar cultivar types. Its flowers have
short anthers which are more or less free, sometimes with extruse dehiscence and a
good content of fertile pollen. However, seed yield of this parthenocarpic line was nil
after open pollination and nil or very low after artificial pollination with self pollen or
pollen from the cultivar Ape dice. Both lines, 2524 and Montfavet 191, are highly
female-sterile, which limits their usefulness in breeding.

Line 75/79, which has strong parthenocarpic expression, was developed by R.
Reimann-Philipp from a multiple cross Atom × Bubjekosoko and Heinemanns
Jubilaum × Priora. In favorable environmental conditions female fertility in RP 75/79
is quite normal and its pollen has normal fertilizing power. Parthenocarpic fruits have
a normal appearance (Philouze and Maisonneuve 1978a).

Cultivar Severianin was bred by N. Soloviova at the Gribovskaya Vegetable
Breeding Station near Moscow, which is an excellent source of facultative parthenocarpy.
This cultivar developed from an interspecific cross between *L. esculentum* and
L. hirsutum has the remarkable ability to produce seedless fruits of about the same
size (80–110 g), with completely filled locules (Philouze and Maisonneuve 1978c; Lin

et al. 1984). As a result of hybridization between *L. esculentum* and *L. pennellii* highly parthenocarpic lines (P-26, P-31, etc.) were developed (Stoeva et al. 1985). Recently, a new source of parthenocarpy — Line RG was obtained from a cross between *L. esculentum* and *L. cheesmanii* var. *minor* (Mikhailov and Georgiev 1987). Two new lines, IVT 1 and IVT 2, with more complete parthenocarpy and greater stability, have been developed. IVT 1 has been developed from a cross involving *L. esculentum* and *L. hirsutum*, and IVT 2 from a cross of *L. esculentum* and *L. peruvianum* (Zijlstra 1985).

A spontaneous mutant designated *sds* (seed development suppressor) was found in Bulgaria. This mutant forms normal fruit without seeds or only with a little quantity of very small seeds. Its fruits are superior in quality to those of *pat-2* lines, but the mutant has a number of undesirable pleiotropic effects: very low fertility and a reduced germination rate (K. Georgiev et al. 1984).

Potential sources of parthenocarpy are listed in Table 13.1.

Table 13.1. Potentially useful sources of parthenocarpy in tomato

Cultivar/ Breeding lines	Country of origin	Genetic control	References
PI 190256	New Caledonia	Unknown	Johnson and Hall (1954)
Stock 2524	Italy	*pat*	Soressi (1970)
Oregon Cherry	USA	Unknown	Baggett and Frazier (1978)
Oregon 11	USA	Unknown	Baggett and Frazier (1978)
Montfavet 191	France	*pat*	Pecaut and Philouze (1978)
Severianin	USSR	*pat-2*	Philouze and Maisonneuve (1978c)
PSET 1	USA	*pat-2*	J.W. Scott and George (1983)
Mutant	Bulgaria	*sds*	K. Georgiev et al. (1984)
Carobeta	Bulgaria	One recessive gene	K. Georgiev and Mikhailov (1985)
P-26, P-31 etc.	Bulgaria	Unknown[a]	Stoeva et al. (1985)
IVT 1	Netherlands	One recessive gene	Zijlstra (1985)
RP 75/59	West Germany	*pat-3* and *pat-4*	Nuez et al. (1986)
Sub Arctic Plenty	Canada	*pat-5*	Nuez et al. (1986)
Oregon T5–4	USA	Two recessive genes	Kean and Baggett (1986)

[a] Recessively inherited.

13.4 Expression

Comparative studies of different germplasm sources for parthenocarpy made by the French researchers Philouze et al. (1980) have shown various levels of expression: Low-degree — environment-dependent parthenocarpy in cvs Atom and Bubjekosoko (Germany), Sub Arctic Plenty (Canadian cultivar), Oregon Cherry (USA)

and Pobeda (USSR); consistent tendency for parthenocarpy in Lycopea (German selection), Early North (Canada), Oregon T5–4 (USA) and the Polish cultivar Parteno; excellent expression of parthenocarpy in RP 75/59 (West German selection) and in the Russian cultivar Severianin.

About 50 cultivars from different countries with reported parthenocarpy were studied by Nesterenko and Ignatova (1987) in winter glasshouses and plastic houses. They found strong expression of parthenocarpy in the cvs RP 75/79 (West Germany), Oregon T5–4 (USA), A-33 and Rod 271 (Poland), Severianin, Pridnestrovskii, Pridneprovskii korotkostolbchatyi and Breeding line 443 (all from USSR). Generally, low night temperatures, low light intensity and high humidity were favorable for expression of parthenocarpy of tomato cultivars grown in plastic houses in the year 1985 (Table 13.2). Furthermore, high temperatures (Johnson and Hall 1954), as well as low temperatures plus short days and high humidity (Baksh et al. 1978) favor parthenocarpy in tomato.

Studies on nine inbred families of Severianin grown in the field and greenhouse during 2 years exhibited that the expression of parthenocarpy is facultative; seedless fruits were produced in environments unfavorable for pollination and fertilization, such as high day and night temperatures (Lin et al. 1984). Lin et al. (1984) found no significant differences in the percentages of parthenocarpic fruits among nine Severianin families derived from nine single plants when grown in the summer of 1978. However, when the same nine selections were grown in a glasshouse during the winter of 1978–1979, the expression of parthenocarpy among families varied significantly.

In Severianin, more parthenocarpic fruits were produced when temperatures were unusually high, but factors other than temperatures appear to be involved too. Although high temperatures could affect the viability of male or female gametes, under high night temperatures (26°C), hand-pollinated Severianin fruit contrived to produce as many seeds as the heat-tolerant line CL 11d. This demonstrates that Severianin is able to produce normal male and female gametes under high night temperatures. How-

Table 13.2. Setting of parthenocarpic fruit in different parthenocarpic lines (after Nesterenko and Ignatova 1987)

Cultivar/Line	Glasshouse				Plastic house			Mean
	Spring mean	Autumn 1984	1985	Mean	1984	1985	Mean	
Pionerskii-check	0	0	0	0	0	0	0	0
Severianin	72[a]	50	38	44	48	86	67	61
RP 75/59	94	70	46	58	66	100	83	78
B Line 443	96	35	15	25	58	84	71	64
A-33	65	56	65	60	27	82	54	60
Oregon T5–4	–	90	88	89	86	100	93	91
Rod 271	–	30	21	25	51	100	75	50

[a]Percentage.

ever, under favorable night temperatures (16°C) Severianin produced seeded fruits. Both CL 11d and Severianin produced more viable pollens, too (93% and 83%, respectively) than the heat-sensitive cvs Heinz 1350 and Ohio MR 13. The data indicate that a high night temperature did not result in female or male sterility in Severianin (George et al. 1982).

Parthenocarpy from Severianin is generally better expressed in large-fruited, multilocular types than in small-fruited types with few locules (Philouze 1981).

Expression of parthenocarpy in Montfavet 191 was stable irrespective of time of the year both in the field and the greenhouse, although stamen length varied with environmental conditions (Philouze and Pecaut 1986). Only the line Oregon T5–4 set parthenocarpic fruits when temperatures were below 18°C (Baggett and Frazier 1978). In spring and autumn greenhouse experiments conducted by Scott and Kedar (1986) with parthenocarpic genotypes Severianin, PSET 1 and RP 75/59, the parthenocarpic expression was greater for PSET 1, while Severianin showed very low parthenocarpy and had the largest seed number per fruit.

Moreover, in many experiments Severianin set fruits after emasculation of flowers, without their pollination. The setting percentage after this treatment ranged from 67 to 73 and after self-pollination by hand from 69 to 81 (Philouze and Maisonneuve 1978c). Lin et al. (1983) have treated Severianin and the non-parthenocarpic variety Chico III with different pollination methods, on July 17, a favorable date for the expression of parthenocarpy, and on September 25, favorable for seed formation. Emasculated flowers of Severianin on both dates set seedless fruits, whereas Chico III set no fruits.

Seedlessness in West German material was dependent on low temperature and ripe fruits were seedless when buds were exposed to low night temperatures (5°C, day 25°C) about 65 days before harvest (Preil 1973). J.W. Scott and George (1984) reported that RP 75/59 had greater total parthenocarpic fruit set in their experiments with different pollination treatments than Severianin and PSET 1. Vibration of the flowers completely inhibited parthenocarpic fruit set for all genotypes except PSET 1, which had 15.7% parthenocarpic fruits. However, good parthenocarpic expression is regarded as possibly detrimental to seed production.

13.5 Genetics

Nowadays the genetics of parthenocarpy is fairly well understood (Table 13.1). Parthenocarpy in the EMS-induced short-anther mutant (sha) is controlled by a single recessive gene, pat (Soressi and Salamini 1975). The pat is linked with sha with a crossover value of 0.12%. Separate control of the two characteristics in the mutant (Stock 2524) was confirmed by Mapelli et al. (1978).

According to Philouze and Pecaut (1986), parthenocarpy and short anthers were due to the pleiotropic effects of a single locus. This view is shared by Stevens and Rick (1986), who believe that the spontaneous induction of both mutants suggests that a single gene determines both pleiotropically. The parthenocarpic mutant Montfavet 191 proved allelic to Soressi's mutant designated Stock 2524 (Pecaut and Philouze 1978). Crosses between Severianin and Montfavet 191 demonstrated that pat and pat-2 were non allelic (Philouze and Meisonneuve 1978b). No linkage has been noticed between pat-2 and

any of the 13 marker genes tested (Philouze 1981, 1983a): *ms-32* (chromosome 1), *ms 35* (chromosome 2) *bls* (chromosome 3), *c* and *sp* (chr. 6), *bs-2* (chromosome 7), *bu, dl* and *al* (chromosome 8), *u* (chromosome 10), *j-2, hl* and *a* (chromosome 11). The gene *pat-2* is independent of the disease resistance genes *Mi* (chromosome 6), *Tm-2²* (chromosome 9), *I* and *I 2* (chromosome 11) and *Ve* (chromosome 12). It was independent also of such fruit characteristics as the number of locules and firmness.

Crosses made between Severianin (*pat-2*) and lateral suppressor (*ls/ls*) lines to obtain *ls/ls pat 2/pat 2* recombinants with the hope that *pat 2* is able to overcome the very low fertility characteristic of the *ls* gene have revealed that as far as fruit-setting ability is concerned the *ls* gene is epistatic to *pat-2* and prevents the expression of the latter. No fruits of normal size developed on any of the 300 F_2 *ls/ls* plants grown in the open field or in a heated glasshouse (Philouze 1983b).

Lin et al. (1984) suggested that in their material *pat-2* was associated with the determinate growth habit and/or earliness throw pleiotropic effects and not genetic linkages. The *pat-2* and *sp* genes in their experiments did not segregate independently, which suggests a possible genetic linkage between the two genes. However, no linkage of *pat-2* was detected with *c* gene, which is one map unit from *sp* on chromosome 6, indicating that genetic linkage of *pat-2* and *sp* is not likely.

However, Lin et al. (1984) have found no linkage between *pat-2* and five other marker genes (*aw, c, ps, u* and *y*) and have revealed no cytoplasmic inheritance. Recently, Vardy et al. (1989a) suggested that two recessive genes are involved in the expression of parthenocarpy in Severianin under low temperature conditions. The expression of gene *pat-2* was influenced by a second gene, *mp*, when *mp* was homozygous. Parthenocarpy in the German line RP 75/59 is controlled by recessive genes not allelic to either *pat* or *pat-2* (Philouze and Maisonneuve 1978b) and there are at least three of them responsible for parthenocarpy in this line (Philouze and Maisonneuve 1978c; Vardy et al. 1989b).

Nuez et al. (1986) reported that RP 75/59 carries two recessive genes for parthenocarpy (*pat-3* and *pat-4*) and Sub Arctic Plenty carries one (*pat-5*). They have developed a model in which parthenocarpy exhibits in the presence of three recessive alleles from RP 75/59. Putative genotype, suggested for the RP 75/59, is *pat-3/pat-3, pat 4/pat-4* (Cuartero et al. 1987); two alleles from RP 75/59 in combination with one from Sub-Arctic Plenty or Severianin; two alleles from Sub-Arctic Plenty combined with one from Severianin; or the two recessive alleles of Severianin.

Recently Philouze (1989) advocated that the parthenocarpy of 75/59 is controlled by at least three recessive genes.

The parthenocarpy in Carobeta is controlled by a single recessive gene, which is not linked with *ps-2* gene (Georgiev and Mikhailov 1985). Zijlstra (1985) has considered the parthenocarpy in the Wageningen lines IVT-1 and IVT-2 to be partially dominant. However, it was found later that parthenocarpy in line IVT 1 was determined by a single recessive gene and in line IVT 2 by a gene with intermediate inheritance.

Parthenocarpy in Oregon T5–4 is controlled by the recessive alleles of two complementary gene pairs, and these loci also interact in a complementary manner with the gene *pat-2* in Severianin (Kean and Baggett 1986).

13.6 Physiology

A comprehensive review on the induced parthenocarpy was addressed by George et al. (1984).

It is recognized that naturally occurring parthenocarpic lines have a greater amount of growth-promoting substances in the ovary and as a result the failure of pollination or lack of seed formation will not prevent the development of fruit. Gustafson (1939) was the first to find that the auxin content in the ovaries of parthenocarpic orange, lemon and grape cultivars was much higher than in seeded ones. This led him to a conclusion that the auxin content in the ovaries at the time of blossoming was high enough to induced ovary growth even though there was no fertilization.

Mapelli et al. (1978) compared the endogenous auxin and gibberellin levels in Ventura and its parthenocarpic *sha-pat* isogenic lines and found that at anthesis the auxin concentration was about three times higher in the ovary of the parthenocarpic line than in Ventura. The auxin concentration reached a maximum 2 days after anthesis in the seedless fruits and 6 days later in the seeded fruits. The gibberellin activity was four times higher in the seedless fruits during the first 8 days of their growth. As a result, ovaries developing on a parthenocarpic line increased in weight faster during the first week following anthesis than ovaries on an isogenic non-parthenocarpic cultivar. The maximum growth rate was reached 11 days after anthesis in the parthenocarpic line. Seeded fruits attained their higher growth rate between the 15th and 20th day after anthesis. Four days after anthesis the weight of normal ovaries began to increase, but parthenocarpic ones were already five times heavier. However, the parthenocarpic tomato fruit was only two-thirds of the final weight of normal fruit (Mapelli 1981).

Hall et al. (1986) have observed that the ovaries of the parthenocarpic genotypes (PSET 1, Severianin, RP 75/59 and Stock-2524, with different genes for parthenocarpy) in newly opened flowers excised and placed on nutrient media increased in diameter and weight to a much greater extent than the ovaries of the non-parthenocarpic genotypes during a 6-day period at 25°C. In other comparisons, they found that the parthenocarpic genotypes had larger ovaries than the non-parthenocarpic genotypes after 2, 4, 6, 12, 18 and 24 days. The ovaries of buds excised 1 and 3 days before anthesis and at anthesis from Severianin and PSET 1 were larger after 6 days than those excised from non-parthenocarpic cvs Walter and Flora-Dade.

It was suggested that ovaries of Severianin contain the minimal amount of hormone needed for fruit set therefore a small amount of exogenous hormone results in maximum fruit set and development (Chareonboonsit and Splittstoesser 1984).

Auxin increased the number of fruits per cluster in PSET-1, but auxin or hand-pollination had no effect on the correlation of seed number or weight with fruit weight in all the parthenocarpic genotypes studied (Severianin, PSET 1 and RP 75/79), whose fruits developed independently of seed formation. Non-parthenocarpic cultivars are dependent on the seed number to increase fruit weight (Chareonboonsit et al. 1985).

Application of the auxin hydroxymethyl-2-chloro-4 phenoxyacetic acid reduced fruit development period in Severianin and RP 75/59, although there was a greater reduction in the F_1 genotypes heterozygous for parthenocarpy genes (Corella et al. 1986). The cytokinin levels in the ovary of the parthenocarpic mutant *sha-pat* was 20 times lower than that in the normal line during the first week after anthesis. The low levels of cytokinin did not decrease during growth and ripening of partheno-

carpic fruit (Mapelli 1981). According to studies (Varga and Bruinsma 1974; Mizahi et al. 1975), cytokinin is transported to the fruit (the sink activity of the seeds is responsible for this process) and it is not involved in the prevention of ripening. On the contrary, the high cytokinin levels found in normal seeded fruit decreased after the mature green stage (40 days after anthesis), suggesting that cytokinins can delay fruit ripening above a threshold level (Mapelli 1981).

Tarakanov et al. (1978) have established the relationships between parthenocarpy and incompatibility in Severianin. However, Mapelli et al. (1979) found that parthenocarpy was not due to sterility or auto-incompatibility as hand-selfing could induce seeds. Expression of parthenocarpy is related to the rapid growth of the ovaries at anthesis, induced by the different concentration of growth-promoting substances found there (Mapelli 1981). It is believed that the rapid enlargement of the ovary prevents fertilization and cause parthenocarpic fruit set (Mapelli et al. 1979).

Hassan et al. (1987) have found that gibberellin content of the ovaries was nearly three times higher in Severianin than in UC 82, VF 145B 7879 or non-parthenocarpic hybrids, confirming the importance of high gibberellic acid content in ovaries for parthenocarpic fruit set. The role of endogenous gibberellins (GA) in seed and fruit development was studied by Groot et al. (1987) with the use of Ga-deficient *ga-1* dwarf mutant of cv Moneymaker. They came to a conclusion that GA is indispensable for the development of fertile flowers and for seed germination, but only stimulates in later stages of fruit and seed development.

It is now generally accepted that for parthenocarpic fruit set and development the plants, under some conditions, produce enough growth hormone so that with or without pollination they are able to prevent an abscission layer from being formed in the pedicel. Under favorable nutritive conditions and with a minimum of competition they are further able to transport the necessary materials to the fruit to bring about enlargement of the cells in the ovary. This produces mature fruits without seeds (George et al. 1984).

13.7 Quality of the Parthenocarpic Fruits

Parthenocarpic fruits produced under unfavorable conditions often have various malformations, such as puffiness. The size of parthenocarpic fruits is frequently reduced (Mapelli et al. 1978) although that in the Severianin cultivar was almost the same. Severianin is able to produce large fruits (90–120 g) without any form of pollination and fertilization. Parthenocarpic fruits of this cultivar appear normal with complete locule filled even in the absence of any seed (Philouze and Maisonneuve 1978c). According to Avdeev (1982), seedless fruits exceed seeded fruits in dry matter content up to 1%. The content of soluble solids of *pat/pat* fruits was, on an average, 1° Brix higher than in normal fruits (Falavigna et al. 1978).

Acidity may be lower in parthenocarpic fruits, which could have an adverse effect on flavor (Stevens et al. 1977). The genetically parthenocarpic fruits had a higher content of dry matter and sugars and a lower content of cellulose than the non-parthenocarpic fruits. However, the induced parthenocarpic fruits had a lower content of all these substances than the non-parthenocarpic fruits (Khong et al. 1987). On the other hand, contents of acids and dry matter were lower in the parthenocarpic forms of Ape'dice,

carpic fruit (Mapelli 1981). According to studies (Varga and Bruinsma 1974; Mizahi et al. 1975), cytokinin is transported to the fruit (the sink activity of the seeds is responsible for this process) and it is not involved in the prevention of ripening. On the contrary, the high cytokinin levels found in normal seeded fruit decreased after the mature green stage (40 days after anthesis), suggesting that cytokinins can delay fruit ripening above a threshold level (Mapelli 1981).

Tarakanov et al. (1978) have established the relationships between parthenocarpy and incompatibility in Severianin. However, Mapelli et al. (1979) found that parthenocarpy was not due to sterility or auto-incompatibility as hand-selfing could induce seeds. Expression of parthenocarpy is related to the rapid growth of the ovaries at anthesis, induced by the different concentration of growth-promoting substances found there (Mapelli 1981). It is believed that the rapid enlargement of the ovary prevents fertilization and cause parthenocarpic fruit set (Mapelli et al. 1979).

Hassan et al. (1987) have found that gibberellin content of the ovaries was nearly three times higher in Severianin than in UC 82, VF 145B 7879 or non-parthenocarpic hybrids, confirming the importance of high gibberellic acid content in ovaries for parthenocarpic fruit set. The role of endogenous gibberellins (GA) in seed and fruit development was studied by Groot et al. (1987) with the use of Ga-deficient *ga-1* dwarf mutant of cv Moneymaker. They came to a conclusion that GA is indispensable for the development of fertile flowers and for seed germination, but only stimulates in later stages of fruit and seed development.

It is now generally accepted that for parthenocarpic fruit set and development the plants, under some conditions, produce enough growth hormone so that with or without pollination they are able to prevent an abscission layer from being formed in the pedicel. Under favorable nutritive conditions and with a minimum of competition they are further able to transport the necessary materials to the fruit to bring about enlargement of the cells in the ovary. This produces mature fruits without seeds (George et al. 1984).

13.7 Quality of the Parthenocarpic Fruits

Parthenocarpic fruits produced under unfavorable conditions often have various malformations, such as puffiness. The size of parthenocarpic fruits is frequently reduced (Mapelli et al. 1978) although that in the Severianin cultivar was almost the same. Severianin is able to produce large fruits (90–120 g) without any form of pollination and fertilization. Parthenocarpic fruits of this cultivar appear normal with complete locule filled even in the absence of any seed (Philouze and Maisonneuve 1978c). According to Avdeev (1982), seedless fruits exceed seeded fruits in dry matter content up to 1%. The content of soluble solids of *pat/pat* fruits was, on an average, 1° Brix higher than in normal fruits (Falavigna et al. 1978).

Acidity may be lower in parthenocarpic fruits, which could have an adverse effect on flavor (Stevens et al. 1977). The genetically parthenocarpic fruits had a higher content of dry matter and sugars and a lower content of cellulose than the non-parthenocarpic fruits. However, the induced parthenocarpic fruits had a lower content of all these substances than the non-parthenocarpic fruits (Khong et al. 1987). On the other hand, contents of acids and dry matter were lower in the parthenocarpic forms of Ape'dice,

Monalbo and Porphyre than in original cultivars, while contents of carotene and lyco-
pene were higher (Philouze et al. 1987).

13.8 Methods of Screening for Parthenocarpy

Lin et al. (1984) have found that in segregating populations, selection for partheno-
carpy by cutting fruit has been effective under heat stress. However, this method may
be less effective under conditions favorable for pollination and seed development.
Cutting the anthers and style requires less time than emasculation but both these
treatments can reduce fruit set, which could be a problem when such flowers are
competing with normal flowers, especially during favorable pollination weather
periods (George et al. 1984). Alberola and Tarrega (1984) compared four different
indices to measure parthenocarpy of eight parthenocarpic cultivars grown in the field
over a 12-month period and found that the ratio of number of harvested fruit to
number of emasculated flowers most accurately reflected varietal differences in
degree of parthenocarpy. Parthenocarpy (%) was not clearly affected by following
emasculation technique: two days before anthesis with or without removal of sepals
(Scott and Kedar 1986).

The best method for establishing whether a particular plant was capable of agro-
nomically valuable parthenocarpy was the comparison of the sizes of seedless fruits
gathered in cold weather from each plant, with the sizes of seedless fruits obtained
from the same plant under good climatic conditions (Cuartero et al. 1987). Nesterenko
and Ignatova (1987) have compared two methods of parthenocarpy assessment:
(1) emasculation of flowers without subsequent pollination and (2) estimation of
fruit seediness by cutting fruits developed from free pollination. Both the methods
should be used to get reliable data. Nevertheless, to accelerate the selection of par-
thenocarpic plants in segregating generations the use of only flower emasculation is
preferable. Recently, Hall et al. (1986) have found that the in vitro growth of par-
thenocarpic ovaries was more rapid than non-parthenocarpic ovaries (Table 13.3).
This was similar to the response of ovaries on whole plant, reported by Mapelli et al.
(1978). The results were consistent for three different genetic sources of parthenocar-
py. The development of the ovaries of parthenocarpic flowers in vitro was evident at
least 3 days before anthesis.

Differences in ovary size and especially weight for buds and especially open
flowers after 6 days on nutrient medium at 25°C of parthenocarpic genotypes
(Severianin and PSET 1) were two to four times larger than of non parthenocarpic
genotypes (Table 13.3). In other experiments (comparisons), the parthenocarpic
genotypes had larger ovaries than the non-parthenocarpic genotypes after 2, 4, 6, 12,
18 and 24 days.

From these results they have suggested that it may be possible to screen genetic
population by the in vitro technique, using early forming flowers. Plants found to be
parthenocarpic could be crossed or selfed during the same season. Recently Young
et al. (1990) also suggested in vitro method for screening for the presence of par-
thenocarpic gene in tomato.

Table 13.3. Ovary size for open flowers, large buds, and small buds of 2 parthenocarpic and 2 non-parthenocarpic tomato genotypes at 0 and after 6 days on nutrient medium (After Hall et al. 1986)

Genotype	Open flower Day		Difference	Large bud Day		Difference	Small bud Day		Difference
	0	6	(6 to 9)	0	6	(6 to 0)	0	6	(6 to 0)
				Ovary diameter (mm)[a]					
PSET 1	3.0	6.1	3.1	3.1	5.2	2.1	2.7	4.8	2.1
Severianin	4.0	7.0	3.0	3.9	6.8	3.9	3.2	6.0	2.8
Walter	3.7	5.0	1.3	3.5	4.9	1.4	3.3	4.5	1.2
Flora-Dade	3.1	4.2	1.1	3.1	4.0	0.9	2.7	3.8	1.1
				Ovary weight (mg)[a]					
PSET 1	8.4	90.4	82.0	7.9	60.5	52.6	4.2	41.8	37.6
Severianin	18.7	117.2	98.5	14.8	92.1	77.3	8.7	65.8	57.1
Walter	17.7	41.5	23.8	14.4	37.1	22.7	12.3	28.1	15.8
Flora Dade	11.2	30.3	19.1	9.6	26.3	16.7	5.8	22.1	16.3

[a] The genotype – time interaction was significant.

13.9 Use of Parthenocarpy in Tomato Breeding

Poor fruit set of tomato plants under certain field and glasshouse conditions is a common problem. Work on the adverse effects of environments on fruit set has been reviewed by George et al. (1984). Unfavorable environmental factors for tomato fruit set include mainly low and high temperatures and low and poor light intensity.

The poor fruit set at high and at low temperatures is due to poor anther dehiscence and pollination. Thus genetic parthenocarpy is considered as a feasible approach to develop cultivars which would set fruits under such conditions (Van den Berkmortel 1978; Hogenboom 1978; Philouze and Maisonneuve 1978c).

Lin et al. (1982) found that *pat-2* gene contributed to heat-tolerant fruit setting, particularly in crosses with heat-sensitive cultivars. In controlled temperature studies, Severianin exhibited excellent fruit-setting heat tolerance, as did C 11d, a heat-tolerant line from AVRDC, Taiwan. These cultivars set about 70% more fruits than Ohio MR 13, a heat-sensitive greenhouse cultivar, when grown at a constant temperature of 26°C during day and night. Most of the fruits set at a high temperature in the field (day 30°–38°, night 20°–25°C) in segregating populations with Severianin as a parent were parthenocarpic. From these experiments George et al. (1982) concluded that the parthenocarpic gene *pat-2* has contributed to some of the heat-tolerant fruit-setting ability. The selection of lines with a strong tendency of parthenocarpy and other genes for heat tolerance may lead to the development of tomato cultivars with abilities to set fruits under wide environmental regimes. The C11d × Severianin progenies had an excess of plants with early fruit set under high temperatures (George et al. 1982). There are indications that some cultivars capable of setting fruits under low night temperatures are also able to set fruits at relatively high night temperatures. Severianin

produced significantly higher early yield and percentage of fruit set under cold weather conditions (night temperatures below 12°C) than the four non-parthenocarpic cultivars in the experiments of Hassan et al. (1987). Nowadays Severianin is the best and most widely used source of parthenocarpy in many countries.

Philouze (1984) has introduced the gene *pat-2* from the cultivar Severianin into the lines Apé dice, Monalbo and Porphyre by backcrossing. It was found that *pat-2* was responsible for a low vigor level in Apé dice, but not in Monalbo, and for reduction of average fruit weight in Monalbo, but not in Porfyre. Two new parthenocarpic cvs UC-PK and MH-PK have been developed which are suitable for industrial processing and have firm fruits of which more than 50% are seedless (Georgiev et al. 1984).

Parthenocarpic fruits were found to be generally smaller and more deformed than the normal fruits from the same plant. Attempts to eliminate these defects by combining genes for parthenocarpy and male sterility (to prevent self-pollination) resulted in the creation of several totally seedless cultivars and F_1 hybrids. In Spain Severianin and RP 75/59 are being used in backcross breeding programs to develop new parthenocarpic cultivars and hybrids which can produce fruits of acceptable size, shape and color in an unheated greenhouse in winter without treatment with growth regulators. Some lines are used to establish new parthenocarpic hybrid cultivars or to introduce parthenocarpy into the parental lines of existing hybrid cultivars resistant to tobacco mosaic (Nuez et al. 1985).

In Bulgaria the cv Carobeta (*sp sp BB*) was developed from the cross of *L. esculentum* and *L. pimpinellifolium* f. *galapagos* Rick. Under unfavorable conditions the cultivar manifests a tendency to form seedless or partially seedless fruits (Georgiev and Mikhailov 1985). Parthenocarpy of P-26 and P-31 lines was transferred into a *ps-2* sterile background (Stoeva et al. 1985). Gene *pat* is only of limited interest in breeding (Philouze and Pecaut 1986), owing to severe female sterility.

Thus, among the different sources for parthenocarpy, Severianin is particularly interesting and easy to use in breeding programs, owing to its monogenic nature and ease of maintenance, as natural selfing takes place under favorable environmental conditions.

Early and total yield of tomato genotypes with *pat* genes, especially under adverse weather conditions, increased considerably. Parthenocarpy may be a key component in future tomato breeding for enhanced fruit quality (grade, color, chemical composition of fruit) and yield stability.