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Genetics and Breeding for Parthenocarpy in Tomato - A Review

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Abstract - Parthenocarpy is the production of fruit without fertilization. In tomato, parthenocarpy is considered as an attractive trait to solve the problems of fruit setting under unfavourable conditions. Substantially seedless tomatoes resulting from genetic parthenocarpy would be beneficial in the food preparation and process products industries because the seeds would not need to be removed prior to processing.

Keywords*: *Breeding, Genetics, Parthenocarpy, Tomato

I. INTRODUCTION

Parthenocarpy (*Parthenos*, virgin; *karpos*, fruit) is the natural or artificial induction of fruit development without pollination and fertilization. For various parthenocarpic plant varieties, an increased supply of phytohormones to the gynoecium from sources other than the developing seeds has been reported to be sufficient to induce fruit growth [1, 2 and 3]. This observation suggests that parthenocarpic gene/s might primarily affect the hormone production, transport, and/or metabolism leading to sensitivity or higher hormone levels in the ovary capable of promoting fruit growth even in the absence of pollination and fertilization [4].

Tomato (*Solanum lycopersicum*) is one of the most important vegetable crops of the world. Tomato fruits are consumed either fresh or processed. During winter cultivation in greenhouse the flowers are treated with auxinic phytohormones which cause parthenocarpic fruit development and production under environmental conditions (10-15°C short day and low light intensity) adverse for fruit set and growth [5]. However, either higher sensitivity to auxins or an excess of exogenous phytohormones causes malformations of the tomato fruit [6]. Consequently, breeding programs for fresh market tomatoes have usually screened tomato lines for an optimal response of the flowers to phytohormonal sprays.

II. THE THREE MAIN SOURCES OF PARTHENOCARPY IN TOMATO

Detailed reviews on the different types and sources of parthenocarpy in tomato were presented by [7] and [8]. Three sources have been widely studied because of their perspectives for practical application to produce seedless fruits: '*Soressi'* or '*Montfavet 191*', '*Severianin'* and '*RP75/59*'. [9] Considered these three sources as the only ones able to give parthenocarpic fruits after emasculation, with nearly the same properties as fruits obtained after pollination and fertilization.

THE *PAT-1* GENE

[10] Described the short anther (*sha*) mutant in tomato. This mutant has abnormal stamens and produces parthenocarpic fruits. This parthenocarpic phenotype was thought to be caused by two closely linked recessive genes, *sha*and *pat-1* (*parthenocarpic fruit-1*). However, [11] independently obtained a mutant with the same phenotype, designated '*Montfavet 191*'. These independent mutations were allelic [11 and 12] and the characters 'short anthers' and 'parthenocarpic fruits' could never be separated. It was concluded that the described phenotype was caused by a recessive mutation in a single gene, designated *pat-1*, with pleiotropic effects.

Studies have shown that the start of ovary growth in *pat-1* mutants occurs at the pre-anthesis floral stage compared to two days post anthesis in the wild type [13]. This results in a higher ovary weight and in higher numbers of pericarp cell layers in *pat-1* ovaries [14]. This *pat-1* mutant also shows irregular meiosis which results in a lower number of viable female gametes [13]. Apparently, aberrations in the ovule production play a role in seed set of *pat-1* fruits. However, fertilization in *pat-1* ovaries is strongly impaired, even in the ovules that appear normal, probably due to a defective pollen tube-placenta interaction [13]. Therefore, even in conditions favorable for seed production, *pat-1* genotypes give a very low seed set [12 and 13]. The *pat-1* mutant produces tomato fruits which are about two-thirds the normal size and weight [12, 15 and 16]. A reduction in fruit size combined with difficulties to obtain seeds has made the *pat-1* gene less attractive for breeding [12]. Recently, the *pat-1* gene has been mapped on the long arm of Chromosome 3 [17], opening the way towards cloning of the gene.

THE *PAT-2* GENE

Another source of parthenocarpy has been found in the tomato cultivar '*Severianin'*. [18 and 19] showed that a single recessive *pat-2* gene was responsible for parthenocarpy in '*Severianin'* while [20] hypothesized a model based on two recessive genes, one having a major effect (*pat-2*) and one a minor effect (*mp*). [12] Showed that the choice of the recurrent parent in which the *pat-2* gene is introduced is very important for plant vigor. In the genetic background of the tomato line *Apedice*, the plants are smaller and less vigorous, resulting in a reduction in yield, fruit set, and firmness of the fruits [12]. No differences in yield and vigor were found when *pat-2* was introduced into the genetic background of tomato lines '*Monalbo'* or '*Porphyre'*. Parthenocarpy may interact with growth habit. [21] Found that in a population segregating for growth habit and *pat-2*, the majority of the parthenocarpic plants had determinate growth. However, no genetic linkage was found between parthenocarpy and the locus controlling the determinate growth habit (*sp*). Probably, determinate growth allows better expression of parthenocarpy.

The main advantage of exploiting parthenocarpy from *Severianinis* the potential that the deleterious pleiotropic effects of *pat-2* can be overcome by a suitable genetic background.

Studies have shown that the expression of parthenocarpy in 'Oregon Pride' was facultative in nature with seedless fruit, and fruit with 1-20 seed/fruit produced on the same plant up to the third flower truss. This was expected because the line 'Severianin', from which the pat-2 gene had been derived, to develop 'Oregon Pride' was also facultative in parthenocarpic expression [22].

THE *PAT-3* AND *PAT-4* GENES

The tomato line *RP75/59* was found in the progeny from a cross between 'Atom' x 'Bubjekosoko'. A high level of parthenocarpy was observed without obvious effects on fruit size and appearance. However, in this new source of parthenocarpy an association was observed between seed set and size of fruits within the same truss or plant: When both seeded and seedless fruits are present on the same plant, the seeded fruits grow bigger than the seedless fruits. Genetic studies on *RP75/59* showed that two to five genes control this trait [19 and 20]. The differences in the number of genes involved in parthenocarpy are probably due to the very difficult assessment of the trait. *RP75/59* is facultative parthenocarpic, therefore, to obtain seedless fruits, the plants have to be grown in conditions adverse to pollination and/or fertilization, or the flowers have to be emasculated. Nowadays, a genetic model with the two genes *pat-3* and *pat-4* in *RP75/59* is commonly accepted. [9] Showed that *pat-2* and *pat-3/pat-4* are not allelic. The polygenic inheritance of the RP75/59 parthenocarpy source and the different fruit sizes of seeded and seedless fruits on the same truss make the use of *pat-3/pat-4* genes less attractive for breeding.

TABLE 1. Potentially useful sources of parthenocarpy in tomato

Cultivar/ breeding line	Country of Origin	Genetic Control	Reference
PI190256	New Caledonia	Unknown	[23]
Sub-arctic Plenty	Canada	Unknown	[24]
Oregon T5-4	USA	Unknown	[25]
Oregon Cherry	USA	Unknown	[25]
Oregon 11	USA	Unknown	[25]
Stock 2524	Italy	pat	[26]
Montafavet 191	France	pat	[11]
Severianin	Russia	pat-2	[18]
RP75/59	West Germany	Unknown1	[18]
PSET-12	USA	pat-2	[27]

TABLE 2. Genetics of Parthenocarpy in tomato

Genotype	Gene action	Reference
IVT -line1	Quantitative trait	[27]
IL5-1	Quantitative trait	[27]
IVT line 2	Polygenic	[28]
Severianin	Single recessive gene(pat-2)	[18]
RP 75/59	Polygenic (pat-3/pat-4)	[9]
Montfavet-191	Single recessive gene (pat)	[11]

III. LIMITATIONS

Two main problems have so far strongly limited the development of parthenocarpic vegetables.

- Stability and uniformity of parthenocarpic production are difficult to obtain in vegetable crops. Several sources of parthenocarpy are known in tomato. However they are often associated with unfavourable characteristics or are poorly expressed in indeterminately growing plants. In addition, when seeded and seedless fruits develop on the same tomato cluster, seeded fruits are generally larger. A logical approach to overcome this problem would be to combine several parthenocarpy genes to obtain a higher level of parthenocarpy, but pyramiding genes is impossible without molecular assisted selection.

- Parthenocarpy hampers the production of commercial seeds. The development of tomato lines with a high parthenocarpy level is problematic for commercial seed production. With a high level of parthenocarpy, the swelling of the ovary, characteristic of fruit setting, often starts before anthesis. Therefore, at anthesis the ovary cannot be pollinated anymore and the production of seeds becomes impossible.

IV. FUTURE THRUST

- Combining several parthenocarpy genes to obtain a higher level of parthenocarpy through gene pyramiding.

- Combining parthenocarpy with male sterility. A combination of parthenocarpy with pollen sterility has the advantage of preventing the presence of seeded fruits and therefore would lead to a more uniform production of seedless fruits. However the seed production would become impossible. A way to solve this problem is by the use of functional sterility, which is characterized by a normal development of viable pollen, but natural pollination is strongly restricted due to some deviation from the normal morphology and function of the flower. One of the best functional male sterility genes in tomato is positional sterility 2 (ps-2), which is characterized by non-dehiscent anther bags. The combination of parthenocarpy with positional sterility-2 would prevent the development of seeded fruits and the production of seeds would still be possible by manual anther opening. Breeding for parthenocarpy in a functionally sterile background would focus on the parthenocarpic potential of the plants and not on a selection against seed set as it has been done so far.

V. CONCLUSION

In conclusion, the interest of consumers, farmers and seed companies in seedless fruit and the technical progress of genetic engineering of seedlessness lead us to believe that, in the near future, seedlessness could be an improvement introduced into a wider range of fruits and vegetables. Parthenocarpy is an efficient tool to obtain stable yields under adverse conditions and to obtain quality fruits for processing industry.

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