Inheritance of parthenocarpy in tomato (\textit{Solanum lycopersicum}) and its association with two marker characters

P. Hazra* and A. K. Dutta1

Department of Vegetable crops, Bidhan Chandra Krishi Viswavidyalaya, Mohanpur, West Bengal -741252, India

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Parthenocarpy is the production of fruit without fertilization. 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. The investigations were carried out in Department of Vegetable crops, Bidhan Chandra Krishi Viswavidyalaya, West Bengal (2004-05 – 2007-08) to determine the inheritance pattern of parthenocarpy in ‘Oregon Pride’ tomato and to examine the linkage between parthenocarpy and two marker genes. Expression of parthenocarpy in ‘Oregon Pride’ was facultative and fruit with less than 20 seeds were classified as parthenocarpic in the short winter of Eastern India. Expression of parthenocarpy in the segregating population of all the 3 crosses indicated the involvement of the second gene designated as “ii”, an independent gene which influenced the \textit{pat-2} gene having major effect for the control of parthenocarpic. Inheritance of parthenocarpy, stem pigmentation (pigmented/non-pigmented stem), leaf character (cut/potato leaf) and their joint segregation could not detect genetic linkages between parthenocarpy (\textit{pat-2 pat-2 ii ii}) and two marker genes: stem pigmentation (\textit{aw+/aw}) and leaf character (\textit{c+/c}).

Key words : Tomato, \textit{Solanum lycopersicum}, parthenocarpy, facultative, inheritance, linkage

INTRODUCTION

Naturally occurring parthenocarpy might be useful in breeding tomatoes adapted to a wider range of environments normally unfavorable for fruit setting (Van Den Berkmortel, 1978; Hogenboom, 1978). Use of genetic parthenocarpy may solve the problem of low pollen viability and poor pollen release that often occurs under low light, and low and high temperatures of open field and greenhouse conditions. Parthenocarpy might be useful in developing heat tolerant varieties. Generally improved earliness and higher fruit set (Falavigna and Soressi, 1987) and improved fruit quality (Falavigna et al., 1978) make the parthenocarpic mutants of considerable practical interest in spite of several drawbacks like, difficulty of producing seeds, difficulty of simulating the correct environments that allows maximum expression of the parthenocarpic trait in facultative parthenocarpic lines and smaller fruit size in some cases. George et al. (1984) screened tomato lines carrying gene(s) for parthenocarpy and their subsequent selection. In tomato, three varieties with natural parthenocarpy have been widely studied because of their potential for practical application to produce seedless fruit (Gorguet et al., 2005): ‘Sorcssi’ or ‘Moutfavet 191’ (\textit{pat}), ‘Severianin’ (\textit{pat-2}) and ‘RP75/59’ (\textit{pat-3/pat-4}). In addition, two other sources of parthenocarpy in tomato, IVT-line 1 and 2 (Ziglstra, 1985) were found to give a higher and more stable level of parthenocarpy than ‘Sorcssi’ and ‘Severianin’. The IVT-line was developed from an inter-specific cross between \textit{Solanum habrochaites} S. Knapp & D. M. Spooner (\textit{Lycopersicon hirsutum} Dunal) and \textit{S. lycopersicun} L. (\textit{Lycopersicon esculentum} Mill.), followed by several generations of back crosses and at least one selfing (Ziglstra, 1985). The “\textit{sha}” mutant obtained by mutagenesis with ethyl methane sulfonate (EMS) is characterized by a high tendency to parthenocarpy and abnormalities which concurrently affect anther development (Bianchi and Soressi, 1969). The mutant phenotype was first ascribed to the action of two tightly linked genes, “\textit{sha}” for short

*Corresponding author Email: hazra.pranab05@gmail.com
anther and “pat” for parthenocarpic fruit (Sorensi and Salamini, 1975). The discovery of a spontaneous “sha-pat” mutation in 'Montfavet 191' (Pecant and Philouze, 1978) proved that the described phenotype was caused by a single recessive mutation with pleiotropic effects and the gene was finally designated “pat” (Philouze and Pecant, 1986).

The IVT line 1 was thought to be controlled by one single recessive gene (Ziglstra, 1985). Parthenocarpy in IVT line 2 originates from S. peruvianum L. (L. peruvianum L.) and was assumed to be polygenic (Ziglstra, 1985). According to Gorguet et al. (2008), parthenocarpy in IL5-1 developed through introgression from S. harbochaites is under the control of two QTLs, one on chromosome 4 (pat 4.1) and one on chromosome 5 (pat 5.1). Parthenocarpy in cv. Severianin was found by Philouze and Maissoneuve (1978) to be controlled by a single recessive gene, designated pat-2. However, according to Vardy et al. (1989), the gene, pat-2 gene has major effects on expression of parthenocarpy, and a second gene “mp” in the homozygous form influences expression of pat-2 in homozygous and heterozygous conformation and may be present in non-parthenocarpic phenotypes.

Philoze (1989) suggested that polygenic inheritance of parthenocarpy in the line 75/59. Linkage tests using 26 morphological marker genes, located pat-2 between “solanifolia”, “sf” (chromosome 3 site 111) and baby-lea syndrome, bsl (chromosome 3 L site 74) closed to “sf”. The location of a minor gene for parthenocarpy, mp, could not be detected (Vardy et al., 1989). Later the “pat” gene was mapped and found to be localized on the long arm of chromosome 3 (Beraldi et al., 2004). The expression of parthenocarpy in 'Severianin' is facultative with both seeded and seedless fruits produced on the same plant in certain environments. This facultative parthenocarpy character of 'Severianin' controlled by pat-2 has been introgressed to develop the parthenocarpic varieties 'Oregon Pride', 'Oregon Star' and 'Siletz' (Baggett et al., 1995; Baggett et al., 1997) and 'Oregon Pride' also showed facultative parthenocarpy character (Hazra and Dutta, 2010). Available information amply assumed polygenic inheritance of parthenocarpy and environmental influence in the expression of this character is expected. At the same time, no information is available on inheritance of parthenocarpy under predominantly tropical conditions. The project was undertaken to determine the expression and inheritance of parthenocarpy in 'Oregon Pride' tomato and to examine the linkage between parthenocarpy and two marker genes without emasculation of flowers, under field conditions involving seeded cultivars with diverse genetic backgrounds.

**MATERIALS AND METHODS**

The investigations were carried out under field conditions at Central Research Station, Bidhan Chandra Krishi Viswavidyalaya lying at 23°N latitude, 89°E longitude and at 9.75 m elevation above mean sea level during 2004-05 – 2007-08 period. The experimental site is in the Gangetic alluvial plains of West Bengal, India, with a sandy loam soil (organic carbon: 0.57%, available N, P, K: 256.6, 29.2 and 91.7 kg ha⁻¹, respectively) with 6.5 pH. The plant materials with prominent characters used were:

**Oregon Pride**

A facultative parthenocarpic variety developed through deriving pat-2 gene from 'Severianin' at the Department of Horticulture, Oregon State University, Agricultural and Life Sciences Building, Corvallis, OR, and received from the Indian Institute of Vegetable Research, Varanasi, Uttar Pradesh, India. Marker genes used in this study were aw+ (purple stem), c+ (cut leaf) and sp (determinate plant habit)

**BCT-115**

Dark green and high pigmented and normal seeded line containing dg gene, received from United States Department of Agriculture, Griffen, Georgia. Marker genes used were aw+, c+ and sp.

**CLN 2116 B**

A heat tolerant and normal seeded line selected in the Department of Vegetable Crops, Bidhan Chandra Krishi Viswavidyalaya, from material received from AVRDC, Taiwan. Marker genes used were aw (non-pigmented stem), c+ and sp+ (semi-determinate growth habit).

**BC ps**

A functional male sterile but normal seeded line due to ps gene was obtained from the Department of Vegetable Crops, Bidhan Chandra Krishi Viswavidyalaya. Marker genes used were aw, c (potato leaf) and sp+ (semi-determinate growth habit).

The parental, F₁'s, F₂'s and BC generations of 'Oregon Pride' × 'BCT-115', 'Oregon Pride' × 'CLN 2116 B' and 'Oregon Pride' × 'BC ps' developed during 2004-05 – 2006-07 period were employed to study the segregation of parthenocarpy. Genetic populations (50 each of P₁, P₂ and F₁; 80 F₂ and 60 each of BC₁ and BC₂ for 'Oregon Pride' × 'BCT-115'; 50 each of P₁, P₂ and F₁; 90 F₂; 65 BC₁ and 60 BC₂ for 'Oregon Pride' × 'CLN 2116 B' and 50 each of P₁, P₂ and F₁; 82 F₂; 72 BC₁ and 60 BC₂ for 'Oregon Pride' × 'BC ps') were field grown in Oct. 2007 to March 2008 (autumn-winter season) under the day temperature range of 22.5° to 31.9°C and night temperature range of 8.4° to 22.4°C, the average day/night being 27.6°C/15.1°C.

Since 'Oregon Pride' is basically a facultative parthenocarpic line, fruit with less than 20 seed were classified as parthenocarpic, while standard seeded cultivars produced no parthenocarpic fruit under these environmental conditions. Flowers of the line ‘BC ps’ manifesting functional male sterility were hand pollinated to set fruit. Ten matured fruit from the first three flower trusses from all the plants of the 6 genetic populations of the 3 crosses were sampled to determine seed/fruit. At the same time, stem pigmentation (pigmented/non-pigmented) and leaf character (cut leaf/potato leaf) of all plants of the populations were recorded.

The possibility of genetic linkage between stem pigmentation (aw+) and non-pigmentation (aw) with parthenocarpy was studied from the F₂ and back cross populations of the crosses 'Oregon Pride' × 'CLN 2116 B' and 'Oregon Pride' × 'BC ps' because 'CLN 2116 B' and 'BC ps' have a non-pigmented stem (aw) while 'Oregon Pride' has a pigmented stem (aw+) and the possibility of
Table 1 Inheritance of parthenocarpy in three ‘Oregon Pride’ crosses

<table>
<thead>
<tr>
<th>Population</th>
<th>Number of plants</th>
<th>Without parthenocarpic fruit</th>
<th>With parthenocarpic fruit</th>
<th>$\chi^2$</th>
<th>$F_2$ (15:1)</th>
<th>$BC-P_1$ (3:1)</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oregon Pride</td>
<td>50</td>
<td>0</td>
<td>50</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BCT-115</td>
<td>50</td>
<td>50</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F₁</td>
<td>50</td>
<td>50</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F₂</td>
<td>80</td>
<td>76</td>
<td>4</td>
<td>0.20</td>
<td>0.74</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BC-Oregon Pride</td>
<td>60</td>
<td>52</td>
<td>8</td>
<td>3.26</td>
<td>0.08</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BC-BCT 115</td>
<td>60</td>
<td>60</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CLN 2116 B</td>
<td>50</td>
<td>50</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F₁</td>
<td>50</td>
<td>50</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F₂</td>
<td>90</td>
<td>85</td>
<td>5</td>
<td>0.16</td>
<td>0.77</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BC-Oregon Pride</td>
<td>65</td>
<td>58</td>
<td>7</td>
<td>5.06</td>
<td>0.03</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BC-CLN 2116B</td>
<td>60</td>
<td>59</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BC ps</td>
<td>50</td>
<td>50</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F₁</td>
<td>50</td>
<td>50</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F₂</td>
<td>82</td>
<td>75</td>
<td>7</td>
<td>0.8</td>
<td>0.81</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BC-Oregon Pride</td>
<td>72</td>
<td>64</td>
<td>8</td>
<td>5.55</td>
<td>0.011</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BC-BC ps</td>
<td>60</td>
<td>58</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The corresponding probability value $p$ is used to interpret the $\chi^2$ value and $p$ values of 0.05 to 1.0 allow the null hypothesis to be accepted.

Segregation patterns for the parthenocarpic and two morphological marker traits were determined by chi-square ($\chi^2$) analysis. $\chi^2 = \Sigma (O-E)^2/E$, where $O$ = observed frequencies and $E$ = expected frequencies. The values of the $\chi^2$ were tested against table value (at 5% or 1% level) of $\chi^2$ at $n-1$ degrees of freedom where $n$ is the number of classes.

RESULTS

Inheritance of parthenocarpy

In the $\chi^2$ analysis, the “$p$”, the corresponding probability value is also used to interpret the $\chi^2$ value and $p$ values of 0.05 to 1.0 indicate that observed deviation will be obtained by chance alone 5% or more of the time, allowing the null hypothesis to be accepted.

Data from the genetic population of ‘Oregon Pride’ × ‘BCT-115’ (Table 1) supported the hypothesis that the inheritance of parthenocarpic in ‘Oregon Pride’ was controlled by two independent recessive genes. Among progenies of ‘Oregon Pride’ × ‘BCT-115’, only $F_2$ and BC-Oregon Pride exhibited segregation for parthenocarpic fruit. Chi-square values for the $F_2$ and BC-Oregon Pride population were 0.20 and 3.26 (Table 1), respectively, which supported the hypothesis of 15:1 and 3:1 segregation of non-parthenocarpic : parthenocarpic segregation for independent digenic control of recessive genes. In the $\chi^2$ value of 0.20, the “$p$” value for $F_2$ segregation was 0.74 which indicated that if the same experiment is repeated many times, 74% of the trials would be expected to exhibit chance deviation as great as, or greater than, that seen in the initial trial. However, in BC-Oregon Pride population, significant deficiency of parthenocarpic segregates was found.

Segregation data of $F_2$ and BC-Oregon Pride populations of the other two crosses Oregon Pride × CLN 2116 B and Oregon Pride × BC ps (Table 1) supported the hypothesis that inheritance of parthenocarpic in ‘Oregon Pride’ was controlled by two recessive genes. The $\chi^2$ values fit the test of digenic hypothesis with high probability. Expression of parthenocarpic in the segregating populations of all the 3 crosses indicated involvement of the second gene designated as “$ii$”, an independent gene which influenced pat-2 gene having major effect for the control of parthenocarpic.

The BC-Oregon Pride populations of both the crosses did not fully agree with the digenic hypothesis for inheritance of parthenocarpic where deficiency of parthenocarpic segregates was found. One segregate in the BC-CLN 2116 B population and two segregates in the BC-BC ps population produced parthenocarpic fruit out of the expectation. It may be that the second gene “$ii$” in heterozygous condition influenced the three heterozygous pat-2 pat-2” segregates of the two crosses to set parthenocarpic fruits.
### Table 2. Association between stem pigmentation and parthenocarpy in two crosses.

<table>
<thead>
<tr>
<th>Population</th>
<th>Joint segregation of stem pigmentation (pig) and parthenocarpy (pat)</th>
<th>Expected ratio</th>
<th>$\chi^2$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Pig non-pat</td>
<td>Pig/pat</td>
<td>Non-pig/non-pat</td>
<td>Non-pig/pat</td>
</tr>
<tr>
<td>$F_2$ Oregon Pride × CLN 2116 B</td>
<td>65</td>
<td>5</td>
<td>20</td>
<td>0</td>
</tr>
<tr>
<td>BC-Oregon Pride</td>
<td>58</td>
<td>7</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>BC-CLN 2116 B</td>
<td>30</td>
<td>1</td>
<td>29</td>
<td>0</td>
</tr>
<tr>
<td>$F_2$ Oregon Pride × BC ps</td>
<td>52</td>
<td>7</td>
<td>23</td>
<td>0</td>
</tr>
<tr>
<td>BC-Oregon Pride</td>
<td>64</td>
<td>8</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>BC-BC ps</td>
<td>30</td>
<td>2</td>
<td>28</td>
<td>0</td>
</tr>
</tbody>
</table>

The corresponding probability value $p$ is used to interpret the $\chi^2$ value and values of 0.05 to 1.0 allow the null hypothesis to be accepted.

### Association between parthenocarpy and stem pigmentation

**Oregon Pride × CLN 2116 B**

The hypothesis that the inheritance of stem pigmentation in Oregon Pride was controlled by single dominant gene “aw+” was supported by results from the $F_2$ and BC segregation data (Table 2). The trihybrid ratio in the present investigation is the product of one dihybrid and one monohybrid ratio in terms of phenotypic class, provided each of the three gene pairs (two pairs for parthenocarpy and one pair for stem pigmentation) must have been segregated independently at the time of gamete formation. The two independent phenotypic classes, 15 non-parthenocarpic:1 parthenocarpic and 3 stem pigmented:1 non-pigmented, four phenotypic classes are expected $[(15+1) \times (3+1)]$ in the ratio of 45/64 pigmented and non-parthenocarpic, 3/64 pigmented and parthenocarpic, 15/64 non-pigmented, and non-parthenocarpic and 1/64 non-pigmented and parthenocarpic. The chi-square analysis of four phenotypic classes in the $F_2$ population indicated that two traits did segregate independently. The $\chi^2$ value for the $F_2$ was 1.58 (Table 2) which highly supported the hypothesis of independent segregation of non-parthenocarpic versus parthenocarpic plants in a 15:1 ratio and pigmented versus non-pigmented plants in a 3:1 ratio in the $F_2$ population. Non-pigmented plants with parthenocarpic fruit could not be recovered which might be due to small population size. The $X^2$ analysis (Table 2) of the expected two phenotypic classes in BC-Oregon Pride population, 12/16 pigmented and non-parthenocarpic, and 4/16 pigmented and parthenocarpic $[(3+1) \times (4+0)]$ did not fully support the expected independent segregation of traits because of deficiency of parthenocarpic segregates. The chi-square analysis of the two expected phenotypic classes in BC-CLN 2116 B population, $\frac{1}{2}$ pigmented and non-parthenocarpic, and $\frac{1}{2}$ non-pigmented and non-parthenocarpic $[(16+0) \times (1+1)]$, demonstrated that the two traits segregated independently. The chi-square value was 0.03 with very high probability of 0.88.

**Oregon Pride × BC ps**

In this cross parthenocarpy and stem pigmentation exhibited individual digenic and monogenic segregation. However, a genetic linkage between parthenocarpic and stem pigmentation could not be established. The three genes for the two characters segregated independently at gamete formation, and it is expected that the three genes are located in three different chromosomes.

### Association between parthenocarpy and leaf character

**Oregon Pride × BC ps**

Segregation data (Table 3) for leaf character (cut and potato leaf) in the $F_2$ and BC-populations demonstrated
that cut leaf (c+) of ‘Oregon Pride’ was monogenically dominant over potato leaf (c) of BC ps. The \( \chi^2 \) values for \( F_2 \) and BC-BC ps populations were 0.25 and 0.27, respectively, with high probabilities of 0.67 to 0.69 (Table 3). The expected 3:1 segregation of cut and potato leaves in the \( F_2 \) population and 1:1 segregation of cut and potato leaf characters in BC-BC ps populations amply supported the hypothesis of monogenic inheritance of leaf type. It could be that if two genes for parthenocarpy and one gene for leaf character segregated independently at gamete formation, four phenotypic classes with the respective ratio would emerge in the \( F_2 \) segregation, 45/64 cut leaf with non-parthenocarpy, 3/64 cut leaf with parthenocarpy, 15/64 potato leaf with non-parthenocarpy, and 1/64 potato leaf with parthenocarpy. Chi-square analysis demonstrated that the traits segregated independently with a high probability of 0.60 (Table 3). In the BC-Oregon Pride population, both the expected phenotypic classes, cut leaf with non-parthenocarpy, and cut leaf with parthenocarpy emerged, but the probability of the segregation in the expected ratio of 12:4 ratio was low (0.005) because of deficiency of parthenocarpic segregates. The \( \chi^2 \) analysis for two expected phenotypic classes in BC-BC ps, ½ cut leaf with non-parthenocarpy, ½ potato leaf with non-parthenocarpy, demonstrated that the two traits segregated independently. There did not appear to be a genetic linkage between parthenocarpy and cut/potato leaf character.

DISCUSSION

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 \( \text{pat-2} \) gene had been derived, to develop ‘Oregon Pride’ (Baggett et al., 1995; Baggett et al., 1997) was also facultative in parthenocarpic expression (Lin et al., 1984; Dutta, 2010). Small numbers of seed production, up to 30 seed in 5% of plants of the parthenocarpic line was also recorded by Mazzucato et al. (1998). Facultative parthenocarpy in ‘Oregon Pride’ was manifested when the genes were in a homozygous recessive condition \( \text{pat-2} \text{pat-2} ii ii \) which did not support earlier findings of Lin et al. (1984) where it was reported that parthenocarpy in ‘Severianin’ was controlled by a single recessive gene, \( \text{pat-2} \). However, our findings agree with Vardy et al. (1989) regarding their inference of involvement of two recessive genes for expression of parthenocarpy in ‘Severianin’ in low temperature. Philouze (1989) suggested polygenic inheritance of parthenicary in other tomato lines. Gorguet et al. (2008) studied the genetics of parthenocarpy in the lines ‘IL5-1’ and ‘IVT-line 1’, both of which carry \( S. habrochaites \) \( (L. hirsutum) \) chromosome segments. Parthenocarpy in ‘IL5-1’ is controlled by two QTLs; one on chromosome 4 \( (\text{pat4.1}) \) and one on chromosome 5 \( (\text{pat5.1}) \). The ‘IVT-line 1’ contains two parthenocarpic QTLs; one on chromosome 4 \( (\text{pat4.2}) \) and one on chromosome 9 \( (\text{pat9.1}) \).

The \( \text{pat-2} \) and the other proposed gene designated as “ii” segregated independently as evidenced from \( F_2 \) and BC segregations for parthenocarpy. Gene mapping localized the \( \text{pat-2} \) gene in chromosome 3 (Vardy et al., 1989; Beraldi et al., 2004) and with the probability the proposed second gene for parthenocarpy “ii” might be located in another chromosome.

Genetic linkages between parthenocarpy \( (\text{pat-2} \text{pat-2} ii ii) \) and two marker genes: stem pigmentation \( (aw+/aw) \) and leaf character \( (c+/c) \) could not detected.

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