

18. Ishibashi, M. and Terashima, I., Effects of continuous leaf wetness on photosynthesis: adverse aspects of rainfall. *Plant Cell Environ.*, 1995, **18**, 431–438.
19. Ishibashi, M., Usuda, H. and Terashima, I., The loss of ribulose-1, 5-bisphosphate carboxylase/oxygenase caused by 24-hour rain treatment fully explains the decrease in the photosynthetic rate in bean leaves. *Plant Physiol.*, 1996, **111**, 635–640.
20. VonCaemmerer, S. and Farquhar, G. D., Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta*, 1981, **153**, 376–387.
21. Mather, K., *Statistical Analysis in Biology*, Chapman and Hall, London, 1973.
22. Joshi, S. C., Species specific diurnal changes in chlorophyll fluorescence in tropical deciduous evergreen plants growing in the field during summer. *Photosynthetica*, 1995, **31**, 549–557.
23. Joshi, S. C., Chandra, S. and Palni, L. M. S., Differences in photosynthetic characteristics and accumulation of osmoprotectants in saplings of evergreen plants grown inside and outside a glasshouse during the winter season. *Photosynthetica*, 2007, **45**, 594–600.
24. Weatherley, P. E., Studies in the water relations of the cotton plants. I. The field measurements of water deficits in leaves. *New Phytol.*, 1950, **49**, 81–97.
25. Dabral, B. G., Bali, H. K. and Bhalla, H. K. L., Dew studies under forest plantations at new forest, Dehradun. *Indian For.*, 1964, **90**, 169–170.
26. Zangvil, A., Six years of dew observations in the Negev desert, Israel. *J. Arid Environ.*, 1996, **32**, 361–371.
27. Gindell, I., *A New Ecophysiological Approach to Forest-Water Relationships in Arid Climates*, Junk Publishers, The Hague, 1973.
28. Jones, R. L., The effect of surface wetting on the transpiration of leaves. *Physiol. Plant.*, 1957, **10**, 281–288.
29. Boyer, J. S., Advances in drought tolerance in plants. In *Advances in Agronomy* (ed. Sparks, D. L.), Academic Press, New York, 1996, vol. 56, pp. 187–218.
30. Monclus, R. et al., Impact of drought on productivity and water use efficiency in 29 genotypes of *Populus deltoids* × *Populus nigra*. *New Phytol.*, 2006, **169**, 765–777.
31. Jones, H. G., *Plants and Microclimate: Quantitative Approach to Environmental Plant Physiology*, Cambridge University Press, Cambridge, 1992.
32. Zhang, J. W., Marshall, J. D. and Fins, L., Correlated population differences in dry matter accumulation, allocation and water use efficiency in three sympatric conifer species. *For. Sci.*, 1996, **42**, 242–249.
33. Stone, E. C. and Fowells, H. A., The survival value of dew as determined under laboratory conditions with *Pinus ponderosa*. *For. Sci.*, 1955, **1**, 183–188.
34. Alexander, J. D., Donnelly, J. R. and Shane, J. B., Photosynthetic and transpirational responses of red spruce understory tree to light and temperature. *Tree Physiol.*, 1995, **15**, 393–398.
35. Thornton, M. K., Malik, N. J. and Dwelle, R. B., Relationship between leaf gas exchange characteristics and productivity of potato clones grown at different temperatures. *Am. Potato J.*, 1995, **73**, 63–77.
36. Vyas, P., Bisht, M. S., Bhuchar, S., Sharma, S. and Palni, L. M. S., Polypit: an improved technique for raising nursery plants. *J. Sustain. For.*, 1999, **8**, 43–59.
37. Flexas, J. and Medrano, H., Drought-inhibition of photosynthesis in C₃ plants: stomatal and non-stomatal limitations revisited. *Ann. Bot.*, 2002, **89**, 183–189.
38. Smith, W. F. and McClean, T. M., Adaptive relationship between leaf water repellency, stomatal distribution, gas exchange. *Am. J. Bot.*, 1989, **76**, 465–469.
39. Jones, H. G., Partitioning stomatal and non-stomatal limitations to photosynthesis. *Plant Cell Environ.*, 1985, **8**, 95–104.
40. Strand, M. and Oquist, G., Inhibition of photosynthesis by freezing temperatures and high light levels in cold-acclimated seedlings of Scots pine (*Pinus sylvestris* L.). II. Effects on chlorophyll fluorescence at room temperature and 77 K. *Physiol. Plant.*, 1985, **65**, 117–123.
41. Bolhar-Nordenkamp, H. R. and Lechner, E. G., Temperature and light dependent modifications of chlorophyll fluorescence kinetics in spruce needles during winter. *Photosynth. Res.*, 1988, **18**, 287–298.

ACKNOWLEDGEMENT. We thank the Director, High Altitude Plant Physiology Research Centre, HNB Garhwal University, Srinagar-Garhwal for providing necessary facilities and encouragement.

Received 1 October 2009; accepted 26 August 2010

Altered gibberellin and auxin levels in the ovaries in the manifestation of genetic parthenocarpy in tomato (*Solanum lycopersicum*)

P. Hazra^{1*}, A. K. Dutta² and Padma Chatterjee³

¹Department of Vegetable Crops, Bidhan Chandra Krishi Viswavidyalaya, Mohanpur 741 252, India

²Integrated Rural and Tribal Development and Management Faculty, Ramkrishna Mission Vivekananda University, Morabadi, Ranchi 834 008, India

³Department of Botany, University of Kalyani, Kalyani 741 235, India

Precocious ovary development and altered gibberellin (GA) and auxin levels in the ovary of the *pat-2* gene-induced facultative parthenocarpic line of tomato (*Solanum lycopersicum* L.) Oregon Pride was studied. Unpollinated 'Oregon Pride' ovaries showed marked development with 2.78-fold higher GA content at anthesis and 10.48-fold higher auxin content at 2–3 days before anthesis stage, than the ovaries of the non-parthenocarpic line Patharkuchi at the corresponding stages of the flower which might have triggered the precocious onset of cell division and elongation in the pericarp. Very low selfed and crossed seeds in the fruits of Oregon Pride indicated that marked higher GA and auxin concentration in the ovary leading to anticipated ovary growth and parthenocarpy might have resulted in impaired fertilization by either enhancing ovule abortion or reducing the pollen tube growth.

Keywords: Auxin, facultative parthenocarpy, gibberellic acid, ovary, tomato.

PARTHENOCARPY, the alternative pathway to normal fruit-set and development, has a genetic basis and in tomato it

*For correspondence. (e-mail: hazra.pranab05@gmail.com)

is known to be controlled by one or more recessive gene(s)¹⁻⁸. Among the different sources of natural parthenocarp, the Russian cultivar Severianin is of particular interest because of its strong expressivity, its facultative character and its simple genetic control². The capability of the cultivar Severianin to set seedless fruits with complete locule fill under unfavourable environmental conditions is mainly due to the *pat-2* gene^{5,9}, which induces a different protein in the ovary after anthesis¹⁰. Three facultative parthenocarpic lines, viz. Oregon Pride, Oregon Star and Siletz have been developed in USA through introgression of *pat-2* gene from the cultivar Severianin^{11,12}. The analysis by two-dimensional PAGE of *in vitro* translation products of RNAs from flowers and ovaries before anthesis shows a differential expression associated with *pat-2*-induced parthenocarp¹³. Elevated endogenous phytohormone levels have been observed during parthenocarpic fruit set^{3,14-17}. The present work was thus aimed at studying the precocious ovary development concomitant with assaying the endogenous levels of gibberellic acid (GA₃) and auxin in the developing tomato ovaries of both parthenocarpic and non-parthenocarpic lines (wild type) at anthesis and pre-anthesis stages, to correlate the endogenous phytohormone level and low seededness in the facultative parthenocarpic tomato line Oregon Pride.

Oregon Pride developed at the Department of Horticulture, Oregon State University, USA, and received from the Indian Institute of Vegetable Research, Varanasi, India, was utilized in this study. Plants of Oregon Pride along with the non-parthenocarpic line Patharkuchi were grown in three plantings over 12 months in the rainy-autumn season (June–October) under open-sided poly sheds; early winter (October–March) and late winter (December–May) in the field at the Central Research Farm, Gayeshpur, Bidhan Chandra Krishi Viswavidyalaya, Mohanpur, situated at 22°57'N lat. and 88°20'E long. with an average altitude of 9.75 m amsl. There were 20 plants in each planting. The site is in the Gangetic new alluvial plains of West Bengal, India, with sandy loam soil (organic carbon, 0.57%; available N:P:K, 257, 29 and 92 kg ha⁻¹ respectively, with pH 6.5). The seedlings of Oregon Pride and Patharkuchi were produced on a raised seedbed under low polyethylene tunnel. The 30-day-old seedlings were transplanted in flat beds. Seeds were counted from all harvested fruits and averaged. Percentage of parthenocarpic fruit and seed/fruit was averaged over 20 plants from each planting. Total fruit weight, seed number and parthenocarpic expression were recorded.

Ovary growth in diameter (mm) and weight (mg) was studied by sampling five random flower buds/flowers from each plants of both parthenocarpic and non-parthenocarpic lines at four stages: S₃ (three days before anthesis), S₂ (two days before anthesis), S₁ (one day before anthesis) and S₀ (the day of anthesis), and then

averaged. Fruit set and parthenocarpic expression through seed number/fruit was recorded when flowers were selfed and mechanically cross-pollinated following emasculation. Selfing was done in three environments by protecting the flower buds on the day before anthesis using thin cotton wad and then hand-pollination on the day of anthesis. The flower buds to be cross-pollinated by three widely divergent pollen parents, viz. BCT-115, CLN 2116 B and BCps only in early winter season were emasculated in the afternoon hours on the previous day before anthesis and cross-pollinated in the morning hours of the next day. These widely divergent pollen parents possessed marker genes, viz. BCT-15 (*aw*⁺, *c*⁺ and *sp*), CLN-2116B (*c*⁺ and *sp*⁺) and BCps (*aw*, *c* and *sp*⁺). Only matured fruits resulting from selfing and crossings were considered to record fruit-set percentage and seeds per fruit.

Concentration of gibberellin (GA) and auxin (μg/g fr wt) in the ovary of the four floral stages (S₃, S₂, S₁ and S₀) from the plants of Oregon Pride and Patharkuchi grown in the rainy-autumn season, having highest parthenocarpic expression was estimated by plant hormonal assay.

Composite ovary sample of 200 mg was macerated in 95% ethanol. The macerated sample was kept in a volumetric flask for 3 days in the dark. The macerate was then filtered under low pressure and cell debris was washed twice with 95% ethanol. Ethanol was distilled-off under low pressure to leave an aqueous residue. Next 100 ml of distilled water was added and pH adjusted to 3.0 using H₃PO₄. The residue was extracted three times with 50 ml ethyl acetate using a separating funnel. The upper portion of the separating funnel, i.e. ethyl acetate phase contained auxins and GAs (acid phase). The lower portion of the separating funnel, i.e. the aqueous phase contained cytokinins (basic phase). The pooled ethyl acetate phase was dried over anhydrous Na₂SO₄. The conical flask/beaker with the extract and Na₂SO₄ was kept overnight. The decant was taken the next day. The pooled ethyl acetate fraction at pH 3.0 was purified by partitioning three times with 5% NaHCO₃. The acidic substances were removed from the NaHCO₃ fraction by adding H₃PO₄ to obtain pH 3.0. Then the upper portion of the separating funnel was partitioned three times with ethyl acetate. The ethyl acetate extract was then dried over anhydrous Na₂SO₄ and kept overnight. The decant of ethyl acetate fraction that contains auxins and GAs was taken.

Bioassay of GA₃ was done through induction of α-amylase synthesis in aleurone cells of wheat using GA₃. As embryo produces GA₃, embryo-less half of wheat grains was taken for the bioassay and placed in different petri dishes along with the test solutions (different concentrations of GA₃ and control) and sample solutions. The covered petri dishes were kept in the dark at 25°C for 24 h. The endosperms after 24 h of incubation were crushed in 5 ml 0.5 (M) NaCl solution. The crushed

endosperm with NaCl solution was homogenized and centrifuged and the supernatant was tested for α -amylase activity with soluble starch (0.1%) as substrate. Then 2 ml of the supernatant was added to 2 ml of 0.1% starch solution in a test tube, kept for 10 min at room temperature and then heated with boiling water for 5 min. After cooling, two drops of iodine was added to each test tube and OD values were observed at 620 nm wavelength using a spectrophotometer. The amount of α -amylase formed is directly proportional to the amount of GA supplied over a wide range of concentrations.

Bioassay of auxin was done through wheat coleoptiles elongation test, which shows a quantitative relation between growth and concentration of the auxin. Viable wheat seeds were treated with 20% formalin for 15 min and then rinsed several times with sterile water. The treated seeds were spread on a filter paper, covered with another filter paper and kept in the dark. After 48 h, when the shoots had developed the coleoptiles of 6 mm size were taken, but 1 mm from the apical portion was discarded. Indoleacetic acid (IAA) solution of different concentrations was prepared in phosphate buffer at pH 7.0. Two sets of petri dishes for each concentration of IAA along with one control set that contained only 3 ml phosphate buffer and two sets of petri dishes each for different unknown samples were arranged. Ten pieces of coleoptiles were taken in the petri dish for each test. Then 3 ml of test solution was added in each petri dish and the same volume of unknown solution was added separately in different petri dishes, covered and kept in the dark for 24 h. The growth in length for each concentration of IAA along with the unknown samples was measured and calculation was made according to increment of length over the control. The coleoptile length increment was recorded for the known concentrations of IAA solution and results plotted on a graph paper to draw a standard curve from which the approximate values of unknown samples were calculated by plotting their respective increments of coleoptile length over the control.

Precocious ovary development (Figure 1 *a*) leading to parthenocarpic fruit set was concomitant with persistent style with the developed fruit (Figure 1 *b*). The expression was facultative in nature with seedless (Figure 1 *c*), very less seeded (1–20 seed(s)/fruit) as well as normal seeded fruits produced on the same plant in its total growing span when all the flower trusses of the plant were considered.

Maximum expression of parthenocarpy was related to high temperature stress above the daily mean optimal of 24°–25°C during rainy–autumn season (Table 1). However, in all three environments, parthenocarpy in Oregon Pride was manifested through enhanced ovary growth rate at and before anthesis. In the parthenocarpic line, the ovary was precociously the biggest in the high-temperature condition of rainy–autumn followed by in late winter season, but comparatively smaller in the early

winter season when congenial temperature for fruit set and development prevailed (Table 2).

The bioassays techniques may not quantify the hormonal level accurately, but they could adequately address the large difference between the parthenocarpic and non-parthenocarpic lines of tomato serving the very purpose of the study. In the non-parthenocarpic ovaries of Patharkuchi, the lowest GA concentration (659 $\mu\text{g/g}$ fr wt)



Figure 1. *a*, Precocious ovary development at anthesis. *b*, Parthenocarpic fruit set with persistent style. *c*, Parthenocarpic seedless fruit.

Table 1. Percentage parthenocarpic fruit in Oregon Pride under three environmental conditions

Season	Percentage parthenocarpy (up to 20 seeds/fruit)	Average fruit weight (g)
Rainy season	100.0	36.12
Early over-winter	94.57	81.00
Late over-winter	98.20	57.41

Table 2. Concentration of gibberellin (GA) in the ovary of Oregon Pride and Patharkuchi during rainy–autumn season

Stage of ovary	Average ovary weight (mg)		GA concentration ($\mu\text{g/g}$ of fr wt)	
	Oregon Pride	Patharkuchi	Oregon Pride	Patharkuchi
S_0	98.57 ± 7.82	5.04 ± 1.78	49320	17770
S_1	52.80 ± 6.78	4.55 ± 1.64	24880	20290
S_2	8.52 ± 2.56	3.56 ± 1.35	2514	27803
S_3	2.91 ± 1.52	2.65 ± 0.78	920	659

Table 3. Concentration of auxin in the ovary of Oregon Pride and Patharkuchi during rainy–autumn season

Stage of ovary	Average ovary weight (mg)		Auxin concentration ($\mu\text{g/g}$ of fr wt)	
	Oregon Pride	Patharkuchi	Oregon Pride	Patharkuchi
S_0	98.57 ± 7.82	5.04 ± 1.78	677.30	4640.60
S_1	52.80 ± 6.78	4.55 ± 1.64	6410.00	1625.00
S_2	8.52 ± 2.56	3.56 ± 1.35	7510.00	2023.00
S_3	2.91 ± 1.52	2.65 ± 0.78	7610.00	726.00

Table 4. Seed set by selfing in Oregon Pride under three environments

Season	Number of selfed buds	Number of fruits developed up to maturity	Fruit set percentage	Percentage of seeded fruits	Average seeds per fruit
Rainy–autumn	60	21	35.0	28.6	5.4 ± 0.82
Early winter	100	43	43.0	62.7	12.8 ± 1.46
Late winter	50	19	38.0	47.4	8.1 ± 0.83

was recorded at S_3 and the highest ($27803 \mu\text{g/g}$ fr wt) at S_2 , and it decreased progressively and markedly during further ovary development (Table 2). In contrast, the level of GA increased progressively and significantly during ovary development in the parthenocarpic ovaries of Oregon Pride, being $49320 \mu\text{g/g}$ fr wt at anthesis which was 2.78-fold higher than the non-parthenocarpic ovaries of Patharkuchi. Contrary to this, the highest auxin concentration ($7610 \mu\text{g/g}$ fr wt) was recorded at S_3 of Oregon Pride, which decreased progressively during ovary development with the lowest concentration of $677.3 \mu\text{g/g}$ fr wt at S_0 . However, in the non-parthenocarpic ovaries auxin content was the lowest ($726 \mu\text{g/g}$ fr wt) at S_3 and highest ($4640.6 \mu\text{g/g}$ fr wt) at S_0 (Table 3). This clearly suggested that both GA and auxin biosyntheses were markedly higher in the parthenocarpic ovaries.

Ovary development in the non-parthenocarpic tomato lines is generally triggered two days post-anthesis when a mature embryo sac has been formed, pollination has occurred and fertilization has taken place¹⁸, which marks the synchronous beginning of pericarp cell division, elongation placenta growth and ovule development⁶. All these processes, which ultimately initiate ovary growth, were precocious in the ovary of Oregon Pride, which suggested that in parthenocarpic lines the complete machinery for fruit set and development is switched on

before and independently from pollen shedding, pollination and fertilization, and correlates with the expression of parthenocarp in plants carrying *pat-2* gene^{6,13,16}.

The results suggested the dependence of parthenocarp in Oregon Pride tomato on markedly elevated GA concentration in the early stages of ovary development, which agreed well with earlier works^{15–17,19}. GA may be synthesized in the ovary itself, because genes coding for GA biosynthesis enzymes (Copalyl diphosphate synthase, GA_{20} oxydase and GA 3β -hydroxylase) are expressed in developing tomato fruits and flowers²⁰. The *pat-2* mutation might have increased GA_{20} oxydase activity in unpollinated ovaries, leading to a higher synthesis of GA_{20} , the precursor of an active GA¹⁷. A link between auxin and GA level in the parthenocarpic ovaries of Oregon Pride is supported by the partial dependence of *orf 8* parthenocarp on GA activity²¹, and by a study with garden peas suggesting that seeds produce a modified auxin which stimulates GA production in the surrounding carpel tissues²². It was also recorded earlier that tomato fruits induced by the application of 4-chlorophenoxyacetic acid (an auxin) also contain high levels of GA²³.

Fruit set in Oregon Pride by selfing ranged from 35.0% to 43.0%, the highest being in early winter season with very low selfed seed ranging from 5.4 ± 0.82 in rainy–autumn to 12.8 ± 1.46 in early winter season (Table 4).

Table 5. Crossing success in Oregon Pride in early winter season

Cross combination	Number of crossed buds	Number of fruits developed up to maturity	Fruit set percentage	Percentage of seeded fruits	Average seeds per fruit
Oregon Pride × BCT-115	40	19	47.5	52.2	19.5 ± 3.62
Oregon Pride × CLN 2116 B	60	28	46.6	64.8	20.6 ± 1.39
Oregon Pride × BCps	50	22	44.0	55.2	18.6 ± 2.51

Average crossing success involving three pollen parents was slightly higher (46%) than the selfing success (43%), with marginally higher number of crossed seeds (16.2) over the selfed seeds (12.8) under early winter season (Tables 4 and 5). It appeared that marked higher GA and auxin concentration in the ovary leading to anticipated ovary growth and parthenocarpy might have resulted in impaired fertilization by either enhancing ovule abortion or reducing the pollen tube growth because pollen viability did not vary significantly between the parthenocarpic and non-parthenocarpic lines²⁴. However, a study on pollen tube growth as well as anatomy of the ovules could have fortified this proposition. Application of GA₃ (10 mg l⁻¹) on the days around anthesis impaired fertilization in Clementine mandarin by either enhancing ovule abortion or reducing pollen tube growth under cross-pollination conditions²⁵, thus supporting our proposition.

- Soressi, G. P. and Salamini, F., A monomendelian gene inducing parthenocarpic fruits. *Rep. Tomato Genet. Coop.*, 1975, **25**, 22.
- Philouze, J., Parthenocarpic naturelle chez la tomate. II-Eluded'une collection varietale. *Agronomie*, 1985, **5**, 47–54.
- George, W. L., Scott, J. W. and Splittstoesser, W. E., Parthenocarpy in tomato. *Hortic. Rev.*, 1984, **6**, 65–84.
- Lin, S., George, W. L. and Splittstoesser, W. E., Expression and inheritance of parthenocarpy in 'Severianin' tomato. *J. Hered.*, 1984, **75**, 62–66.
- Vardy, E., Lapushner, D., Genizi, A. and Hewitt, J., Genetics of parthenocarpy in tomato under a low temperature regime: II Cultivar 'Severianin'. *Euphytica*, 1989, **41**, 9–15.
- Mazzucato, A., Taddel, A. R. and Soressi, G. P., The parthenocarpic fruit (*pat*) mutant of tomato (*Lycopersicon esculentum* Mill.) sets seedless fruits has aberrant anther and ovule development. *Development*, 1998, **125**, 107–114.
- Gorguet, B. *et al.*, Mapping and characterization of novel parthenocarpy QTLs in tomato. *Theor. Appl. Genet.*, 2008, **116**, 755–767.
- Gorguet, B., Van Heusden, A. W. and Lindhout, P., Parthenocarpic fruit development in tomato. *Plant Biol.*, 2005, **7**, 131–139.
- Philouze, J. and Maisonneuve, B., Heredity of the natural ability to set parthenocarpic fruits in the Soviet variety Severianin. *Rep. Tomato Genet. Coop.*, 1978, **28**, 12.
- Barg, R., Salts, Y., Lapushner, D., Frankel, R. and Meir, E., Differential regulation of a fruit specific 62 kDa protein in developing parthenocarpic (*pat2/pat2*) and seeded tomato fruits. In Proceedings of the XI Eucarpia Meeting on Tomato Genetics and Breeding (eds Gomez, C. J., Guillaumon, M. L. and Fernandez-Munoz, R.), 1990, p. 143.
- Baggett, J. R., Kean, D. and Mansour, N. S., 'Siletz' parthenocarpic tomato. *Hortic. Sci.*, 1997, **32**, 1299–1300.
- Baggett, J. R., Mansour, N. S. and Kean, D., 'Oregon Star' and 'Oregon Pride' parthenocarpic tomatoes. *Hortic. Sci.*, 1995, **30**, 649–650.
- Fos, M. and Nuez, F., Molecular expression of genes involved in parthenocarpic fruit set in tomato. *Physiol. Plant.*, 1996, **98**, 165–171.
- Talon, M., Zacarias, L. and Primo-Millo, E., Gibberellins and parthenocarpic ability in developing ovaries of seedless mandarins. *Plant Physiol.*, 1992, **99**, 1575–1581.
- Hassan, A. A., Marghany, M. M. and Sims, W. L., Genetics and physiology of parthenocarpy in tomato. *Acta Hortic.*, 1987, **200**, 173–184.
- Mapelli, S., Frota, C., Torti, G. and Soressi, G. P., Relationship between set, development and activities of growth regulators in tomato fruits. *Plant Cell Physiol.*, 1978, **19**, 1281–1288.
- Fos, M., Nuez, F. and Garcia Martínez, J. L., The gene *pat-2*, which induces natural parthenocarpy, alters the gibberellin content in unpollinated tomato ovaries. *Plant Physiol.*, 2000, **122**, 471–480.
- Rick, C. M., Tomato. In *Hybridization of Crop Plants* (eds Fehr, W. R. and Hadley, H. H.), American Society of Agronomy, Madison, USA, 1980, pp. 669–680.
- Fos, M., Proano, K., Nuez, F. and Garcia Martinez, J. L., Role of gibberellins in parthenocarpic fruit development induced by the genetic system *pat-3/pat-4* in tomato. *Physiol. Plant.*, 2001, **111**, 545–550.
- Rebers, M. *et al.*, Regulation of gibberellin biosynthesis gene during flower and early fruit development of tomato. *Plant J.*, 1999, **17**, 241–250.
- Vivian Smith, A., Luo, M., Chaudhury, A. and Koltunow, A., Fruit development is actively restricted in the absence of fertilization in *Arabidopsis*. *Development*, 2001, **128**, 2321–2331.
- Ozga, J. A., Yu, J. and Reinecke, D. M., Pollination, development, and auxin specific regulation of gibberellin 3 β -hydroxylase gene expression in pea fruit and seed. *Plant Physiol.*, 2003, **131**, 1137–1146.
- Koshioka, M., Nishijima, T., Yamazaki, H., Nonake, M. and Mander, L. N., Analysis of gibberellins in growing fruits of *Lycopersicon esculentum* after pollination or treatment with 4-chlorophenoxy acetic acid. *J. Hortic. Sci.*, 1994, **69**, 171–179.
- Hazra, P. and Dutta, A., Expression of parthenocarpy in tomato due to temperature and pollination treatment. *Int. J. Veg. Sci.*, 2010, **16**, 222–232.
- Mesejo, C., Martínez-Fuentes, A., Reig, C. and Agustí, M., Gibberellic acid impairs fertilization in Clementine mandarin under cross-pollination conditions. *Plant Sci.*, 2008, **175**, 267–271.

ACKNOWLEDGEMENT. We thank the Director, Indian Institute of Vegetable Research, Varanasi, for providing the seeds of Oregon Pride for this study.

Received 21 January 2010; revised accepted 22 September 2010