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FLORAL ABSCISSION AND CHANGES IN SUCROSE PHOSPHATE SYNTHASE AND INVERTASE ACTIVITIES IN WATER DEFICIENT TOMATO

R.M. BHATT*, N.K. SRINIVASA RAO, K.K. UPRETI AND H.S. SHOBHA

Division of Plant Physiology and Biochemistry, Indian Institute of Horticultural Research, Hessaraghatta Lake P.O., Bangalore-560 089

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SUMMARY

A study was conducted to determine the photosynthesis, sucrose phosphate synthase and invertase activities in four tomato (*Lycopersicon esculentum* Mill) cultivars, e.g. Mruthyunjaya, Pusa early dwarf (PED), Arka Ahuthi and Pusa Ruby exhibiting differential response in floral abscission under water stress. Among the four cultivars, Arka Ahuthi and Pusa Ruby were found to be more susceptible to abscission under water stress as indicated by more than 55.0% abscission of flower buds and flowers in these cultivars. Water stress caused a substantial decrease in photosynthesis in all the cultivars, although the degree of decrease varied with cultivars. In the cultivars where the abscission of flowers and flower buds was more (Arka Ahuthi and Pusa Ruby), the reduction in photosynthesis was more (53 - 61.5%) compared to the cultivars where the abscission was relatively less (Mruthyunjaya and PED) (39.0-53.0%) during stress. There was a considerable decrease in SPS activity during stress in susceptible cultivars. In susceptible cultivars, the invertase activity in reproductive organs as well as leaf and developing young fruits decreased under stress. The decrease in photosynthesis along with a reduction in invertase activity may be important contributing factors for the abscission of flower and flower buds in abscission susceptible tomato cultivars under water stress.

Key words **: Invertase activity, photosynthesis, sucrose phosphate synthase, tomato.**

INTRODUCTION

In solanaceous vegetable crops, flower retention and fruit set are highly sensitive to environmental stresses (Aloni *et al*.1991a & b, Aloni *et al.* 1996, Kokubun *et al*. 2001). Abscission of reproductive organs (flower buds and flowers) is a major yield limiting factor in vegetable crops (Wein *et al*.1989a). The abscission of floral organs during stresses has been associated with the changes in physiological processes (Macleod and Duffus 1988, Aloni *et al.* 1991a, Ofir *et al*.1993, Turner and Wien 1994, Aloni *et al.* 1996). It has been suggested that water stress imposed during flowering reduces photosynthesis and the amount of photosynthetic assimilates allocated to floral organs, and might thereby increase the rate of abscission. Aloni *et al.* (1996) found that in pepper, abscission might also be the result of reduced assimilate availability and metabolic activities of the flower and flower buds. Some workers are of the opinion that the abortion of reproductive organs is not solely due to a shortage of assimilate supply but also due to other factors such as assimilate utilization (Ruiz and Guardiola 1994, Aloni *et al.* 1996). Though different views were proposed for the flower and flower bud abortion under water stress, the physiological mechanism controlling reproductive abortion, however, remains unclear. Majority of work on the flower abscission was reported in relation to high temperature and limiting light intensities (shade), little information is available on floral abscission in relation to water stress in solanaceous

*Corresponding author, E-mail: rmbt@iihr.ernet.in

vegetable crops, and tomato in particular. The present study was conducted to determine the metabolic responses of tomato cultivars exhibiting differential response in floral abscission under water stress.

MATERIALS AND METHODS

Plant material and growth conditions: The seedlings of four genotypes, e.g. Mruthyunjaya, Pusa Early Dwarf (PED), Pusa Ruby and Arka Ahuthi of tomato *(Lycopersicon esculentum* Mill.) were raised in the seed beds. Four weeks old uniform seedlings were transplanted in the field. After transplanting, the plants were regularly irrigated until flower bud formation (40 days from transplanting). Water stress was imposed at flowering stage of the plants for a period of one month by withholding irrigation. Soil moisture content as measured gravimetrically was 20-22% in the control and 12-14% under the stress. The minimum and maximum temperatures varied from 19 to 21 ^{0}C and 35 to 37 ^{0}C, respectively. During the stress period, the observations were made on the pattern of flower and flower bud drop, the photosynthetic rate, sucrose phosphate synthase (SPS) and invertase activity in the flower and flower buds.

Abscission measurements: Abscission measurements were made by recording the number of abscised reproductive organs every alternative day from the onset of water stress treatments both in control and stressed plants.

Photosynthesis measurement: The observations on photosynthesis were recorded at 10 days intervals between 10.00 and 11.30 hr. The day temperature varied from 34 to 37 ^{0}C, irradiance varied from 12000 to 16000 µmol m^{-2} s^{-1} and the carbon dioxide concentration ranged between 330 and 340 ppm during the observations. Photosynthesis rate was measured on fully expanded leaves using ADC open portable Photosynthesis Analysis System (Model LCA 3, Analytical Development Corporation, Huddesdon, U.K).

Determination of sucrose phosphate synthase (SPS) activity: Sucrose phosphate synthase activity was determined as described by Pavlinova *et al* (2002). Sucrose was measured using anthrone reagent as modified by Ashwell (1957). Samples of leaf, flower, flower buds and young fruits (500 mg) were ground in an ice cold extracting medium (2 ml) containing 50 mM Hepes-NaOH (pH 7.5), 5 mM $MgCl_2$, 1 mM EDTA and 2.5 mM DTT (Dithiothreitol). The homogenate was centrifuged at 10,000 rpm for 10 minutes. To determine SPS activity, an incubation mixture (0.2 ml) contained 8mM UDPG, 8 mM fructose-6-phosphate, 15 mM $MgCl_2$, 40 mM Hepes-NaOH (pH 7.5) and 0.1 ml of enzyme preparation. The control sample contained no UDPG. The reaction mixture was incubated for 30 minutes at 30 ^{0}C. The reaction was stopped by immersing the tubes into boiling water bath for 1 minute. After cooling, 0.2 ml of 0.5 N KOH was added and kept in boiling water bath for 10 minutes in order to break down the excess fructose-6-phosphate, which remained unutilized in the reaction. The enzyme activity was determined from the amount of sucrose synthesized by adding 2 ml of cold anthrone reagent slowly. Absorbance was measured at 630 nm and the activity was expressed in mg sucrose/mg protein/hr.

Determination of invertase activity: The invertase activity was determined in the young leaves, flowers, flower buds and young fruits (average fruit fresh weight 1.0 g). Samples (500 mg) were homogenized in 2 ml ice cold 100 mM acetate buffer pH 5.0 and centrifuged at 2500 g for 20 minutes at 4 ^{0}C. Soluble acid invertase was assayed by incubating 0.2 ml of aliquat (supernatant) with 0.8 ml of 0.1 M sucrose for 30 minutes at 30 ^{0}C. Reaction was stopped by adding 1 ml Somogyi's copper reagent and boiled for 10 minutes. Sucrose was added to control sample just before boiling. Blank sample had no sucrose. Reaction mixture was cooled and 1 ml arsenomolybdate was added. The absorbance was read at 630 nm. The enzyme activity was estimated as described by Morris and Arthur (1984). The soluble protein was determined by Lowry method (Lowry *et al*. 1951) using bovine serum albumin as the standard.

RESULTS

Abscission of flower buds and flowers: Water stress enhanced the abscission of flowers and flower buds in all the cultivars of tomato (Fig. 1). The effect of water stress was more on the flower buds compared to the flowers as indicated by 46.0 to 67.0% of flower bud

and 34.0 to 61.0% of flower abscission in different cultivars during stress. During first 10 days, there was 1.5 to 15.3% abscission of flower buds and 5.3 to 24.0% of flowers in different cultivars. Thereafter, there was a substantial increase in abscission both in flower buds and flowers. Among the four cultivars, Arka Ahuthi and Pusa Ruby were found to be more susceptible to abscission under water stress as indicated by more than 55.0% abscission of flower buds and flowers in these two cultivars. However, cvs. Mruthyunjaya and PED had 46.0 to 48.0 % abscission of flower buds and 34.0 to 46.0 % of flowers under stress. In the control plants, there was 10.0 to 48.0% abscission of flower buds and 14.0 to 34.0 % of flowers in different cultivars. The variation in abscission percentage of reproductive organs shows the differential abscission susceptibility of flowers and flower buds during water stress in tomato cultivars.

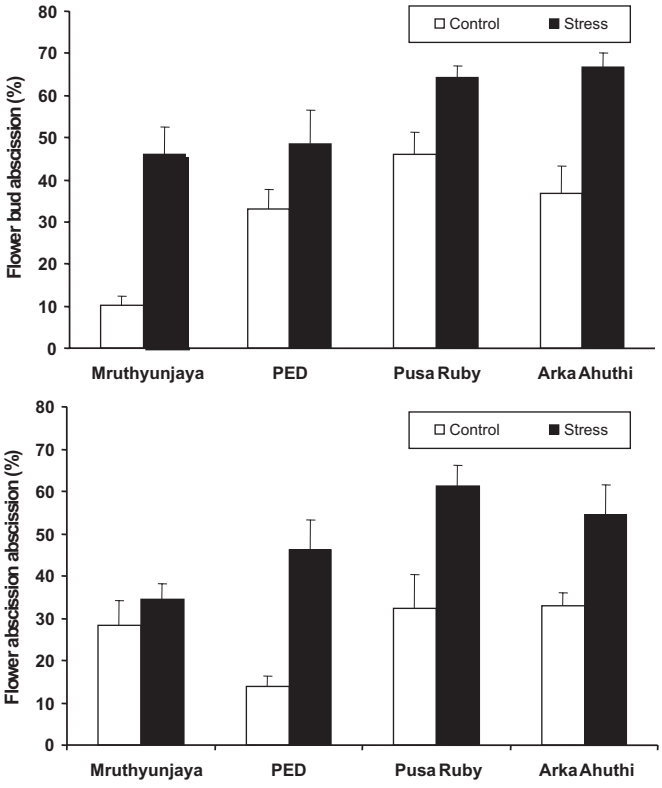

Fig. 1. Abscission of flower buds and flowers under water stress

Photosynthetic response: In the control plants, the photosynthetic rate varied from 18.2 to 22.8 µmol m^{-2} s^{-1} in different cultivars (Fig. 2). However, the water stress caused a substantial decrease in photosynthesis in all the cultivars. For the first 10 days, the decrease ranged from 12.0 % in Mruthyunjaya to 32.5 % in Arka Ahuthi. There was further decrease in photosynthesis with the increase of stress and it reached to the level of 7.6 µmol m^{-2} s^{-1} in Arka Ahuthi and 13.4 µmol m^{-2} s^{-1} in Mruthyunjaya by 30 days stress.

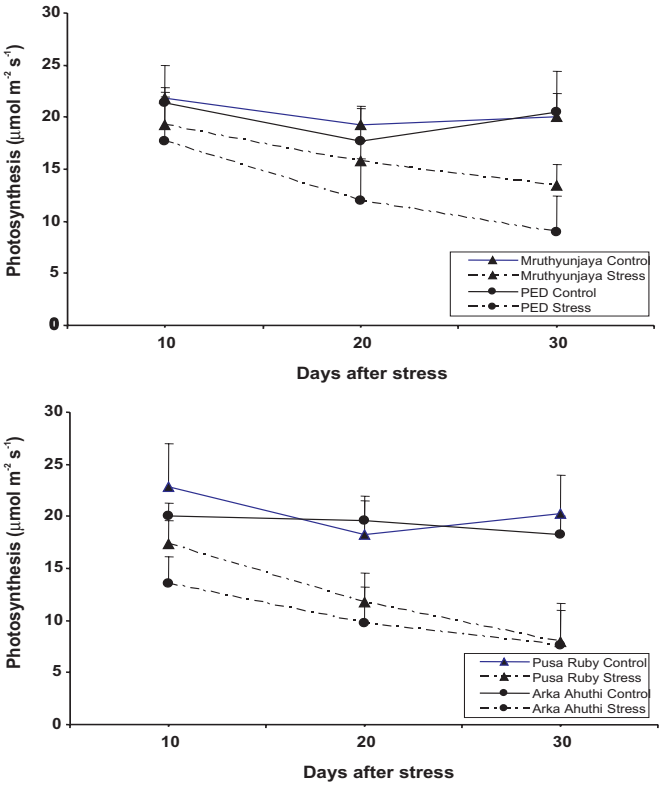

Fig. 2. Photosynthetic rate as affected by water stress in tomato cultivars

Sucrose phosphate synthase activity: In reproductive organs and developing leaves the sucrose phosphate synthase (SPS) activity was determined at 15 and 30 days stress (Table 1). In general, there was a reduction in SPS activity under the stress condition. In Pusa Ruby and Arka Ahuthi (susceptible cultivars), the reduction in SPS activity was 47.6 – 53.0% in flower buds, 13.0 – 74.0% in flowers, 43.5 – 56.0% in young fruits and 25 – 90.0% in leaves at 15 days stress. In Mruthyunjaya and PED (less susceptible cultivars), the decrease was 46.7 – 51.0% in flower buds, 3.3 – 53.0% in flowers, 11.5 – 83.3 % in fruits and 21.0 – 57.7% in leaves at 15 days

Table 1. Stress induced changes in sucrose phosphate synthase activity (mg sucrose/mg protein/hr) in flower buds and flowers, young fruits and leaves in tomato cultivars.

Cultivar	Flower buds		Flowers		Young fruits		Leaves	
	Days after stress		Days after stress		Days after stress		Days after stress	
	15	30	15	30	15	30	15	30
Mruthyunjaya								
Control	2.28±0.162	0.62±0.069	2.58±0.335	0.11±0.029	0.60±0.115	0.44±0.012	2.73±0.421	0.09±0.010
Stress	0.12±0.012	0.04±0.016	1.21±0.016	0.07±0.010	0.10±0.015	0.39±0.023	2.15±0.100	0.12±0.010
P E D								
Control	0.92±0.010	0.50±0.017	0.61±0.010	0.19±0.015	0.61±0.010	0.54±0.100	1.04±0.026	0.24±0.032
Stress	0.49±0.012	0.49±0.010	0.59±0.052	0.22±0.012	0.42±0.012	0.20±0.012	0.44±0.015	0.75±0.032
Pusa Ruby								
Control	0.21±0.020	0.70±0.032	0.54±0.026	0.92±0.012	1.31±0.180	0.74±0.052	0.89±0.010	0.28±0.046
Stress	0.11 ±0.013	0.17±0.036	0.47 ±0.020	0.02±0.032	0.59±0.015	0.45±0.017	0.09±0.010	0.66±0.009
Arka Ahuthi								
Control	0.17±0.026	0.35±0.036	0.23±0.020	0.21±0.032	0.25±0.015	0.13±0.017	0.04±0.010	0.08±0.010
Stress	0.08±0.015	0.30±0.038	0.06±0.010	0.87±0.040	0.11± 0.016	0.62±0.021	0.03±0.011	0.13±0.014

stress. At 30 days stress, the SPS activity decreased 67.3 – 80% in flower buds, 65.2 – 78.4% in flowers and 23.7 – 79.0% in young fruits. In less susceptible cultivars, the decrease in SPS activity was 22 – 30.6% in flower buds, 13.6 – 36.4% in flowers and 11.4 – 52.4% in young fruits.

Invertase activity: There was considerable reduction in invertase activity in all the cultivars and it was relatively

Table 2. Stress induced changes in invertase activity (mg glucose/mg protein/hr) in flower buds, flowers, young fruits and leaves in tomato cultivars.

Cultivar	Flower buds		Flowers		Young fruits		Leaves	
	Days after stress		Days after stress		Days after stress		Days after stress	
	15	30	15	30	15	30	15	30
Mruthyunjaya								
Control	1.74 ±0.427	0.96 ±0.035	0.64 ± 0.026	1.45 ±0.020	1.87 ±0.214	2.06 ±0.035	1.94 ± 0.485	0.97 ±0.041
Stress	1.58 ±0.323	0.81±0.064	0.54 ±0.066	1.14 ±0.084	0.04 ±0.012	1.09 ±0.058	1.29 ±0.055	0.35 ±0.032
P E D								
Control	0.93 ±0.133	1.39 ±0.139	3.81 ±0.468	3.30 ±0.090	1.00 ±0.141	0.25 ±0.043	1.51 ±0.092	1.63 ±0.021
Stress	0.79 ±0.042	1.07 ±0.035	3.41 ±0.196	1.18 ±0.0.87	0.43 ±0.010	0.22 ±0.021	0.75 ±0.026	0.04 ±0.001
Pusa Ruby								
Control	2.51 ±0.294	1.55 ±0.118	3.91 ±0.814	1.69 ±0.707	0.18 ±0.016	2.90 ±0.231	3.91 ±0.237	1.91 ±0.064
Stress	1.46 ±0.020	0.81 ±0.035	1.36 ±0.035	0.06 ±0.023	0.04 ±0.009	0.79 ±0.003	1.64 ±0.089	1.27 ±0.040
Arka Ahuthi								
Control	0.69 ±0.083	2.10 ±0.061	4.00 ±0.583	2.95 ±0.087	0.82 ±0.040	1.16 ±0.095	0.45 ±0200	0.60 ±0.061
Stress	0.35 ±0.021	1.09 ±0.550	1.05 ±0.032	2.23 ±0.020	0.04 ±0.015	0.91 ±0.035	0.38 ±0.046	0.34 ±0.026

more in the abscission susceptible cultivars. In Pusa Ruby and Arka Ahuthi (susceptible cultivars), the reduction in invertase activity was 42.0 – 49.0% in flower buds, 65.2 – 73.7% in flowers, 78.0 – 95.0% in young fruits and 15.5 – 58.0% in leaves at 15 days stress. In Mruthyunjaya and PED (less susceptible cultivars), the decrease in invertase activity was 15.6 – 23.0% in flower buds, 10.5 – 21.4% in flowers, 57.0 – 97.0 % in fruits and 33.5 – 50.3% in leaves at 15 days stress. At 30 days stress, the invertase activity decreased 47.8 – 48.0% in flower buds, 24.4 – 96.4% in flowers, 21.5 – 72.7% in young fruits and 33.5 – 43.0% in leaves in susceptible cultivars. In less susceptible cultivars, the decrease in invertase activity was 15.6 – 23.0% in flower buds, 21.4 – 64.2% in flowers, 12.0 – 47.0% in young fruits and 64.0 – 97.5% in leaves.

DISCUSSION

The results showed that water stress increased the abscission of reproductive organs in tomato. However, there was differential susceptibility to abscission of flowers and flower buds during stress in tomato cultivars. This supports the earlier findings that the environmental stress enhances the flower and flower bud abscission (Wein *et al.*1989, Aloni *et al.* 1996, Marcelis and Bann Hofman-Eijer 1997, Marcelis *et al* 2004). The abscission of reproductive organs caused by abiotic stresses was associated with the changes in different physiological processes. In the present study, a substantial reduction in photosynthesis was found during water stress. However, there was cultivar variation in photosynthetic response to water stress. In the cultivars where the abscission of flowers and flower buds was more (Arka Ahuthi and Pusa Ruby), the reduction in photosynthesis was more (53 - 61.5%) compared to the cultivars where the abscission was relatively less (Mruthyunjaya and PED) (39.0-53.0%) during stress. The decrease in photosynthesis in more susceptible cultivars may lead to a limitation of carbon supply and also influence the biochemical capacity of the plants for carbon assimilation and its utilization during water stress. The reduction in photosynthesis during stress may decrease the availability of assimilates to the developing floral organs and leads to the abscission of flowers and flower buds in susceptible cultivars. The reduction in photosynthesis during water stress in different cultivars may be an important physiological factors for enhancing the abscission of reproductive organs in abscission susceptible cultivars of tomato. Apart from the limited carbon supply through reducing the photosynthesis, the biochemical capacity was also affected differentially as indicated by SPS and invertase activities in different cultivars under stress. The reduced photosynthesis during water stress may also lead to a reduction in the capacity for both starch and sucrose synthesis. Water stress cause a decline in the starch formation and in SPS activity (Vessey and Sharkey 1989).

Furthermore, the biochemical capacity was also affected by the water stress as indicated by a decrease in SPS and invertase activities which may affect the availability and utilization of sucrose. The SPS is considered to play a major role in the re-synthesis of sucrose (Whittingham *et al.* 1979, Wardlaw and Willenbrink 1994) and sustain the assimilatory carbon flux from source to developing sink (Isopp *et al.* 2000). The activation of SPS by water stress may lead to an increase in rate of sucrose accumulation (Hubbard *et al.* 1989, Miron and Schaffer 1991, Huber and Huber 1996). However, the increase was more in the abscission susceptible cultivars. Though there was an increase in SPS activity in the reproductive organs of all the cultivars, the utilization of sucrose was also affected by water stress as indicated by a decrease in invertase activity in floral organs and developing leaves. The invertase activity indicates the sink activity. It is involved in the supply of hexose for respiration, establishment of sucrose gradients and the vacuolar osmotic-turgor related cell expansion (Hawker 1985) Though the carbohydrate level may increase under stress condition as shown by higher SPS activity, the allocation of assimilates is regulated to a large extent by the relative activities of each of the plant's sink organs which compete for the common pool of photosynthates. There was a decrease in invertase activity during water stress and it was more in abscission susceptible cultivars indicating a decrease in sink activity. Castrillo (1992) also found a decrease in invertase activity under water stress. The decreased invertase activity might affect the ability to utilize sucrose (Liu *et al.* 2004) and also result

in reduced ovary growth and reduced concentration of hexoses (Anderson *et al.* 2002). In several other studies, invertase has been suggested to be part of mechanism by which sinks maintain sucrose import. There are contrasting observations about the sink strength of reproductive organs (Walker and Hawker 1976, Aloni *et al.* 1991b). Aloni *et al*. (1996) suggested that the flower capacity to accumulate sugars and starch during the day is important factor for the flower retention and fruit set. The data supports the earlier findings that the abscission susceptible cultivars affected more during stress which may be associated with a substantial reduction in photosynthesis during stress.

The results indicate that the water stress negatively affect the reproductive sink activity in the abscission susceptible cultivars. Our results indicated that the decrease in photosynthesis along with a reduction in invertase activity may be important contributing factors for the abscission of flower and flower buds in abscission susceptible tomato cultivars under water stress. However, the role of other physiological factors may not be ruled out (Bhatt *et al.* 2009).

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