Euphytica 27 (1978) 211–218

MORPHOLOGICAL AND PHYSIOLOGICAL CHARACTERS AFFECTING FLOWER DROP AND FRUIT SET OF TOMATOES AT HIGH TEMPERATURES

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Received 5 April 1977

INDEX WORDS

Lycopersicon esculentum, tomato, flower drop, fruit set, high temperatures.

SUMMARY

Seven tomato cultivars and lines were studied under high temperature conditions. Fruit set varied between 77.3% in the heat tolerant cv. Hotset, 62% in cv. Gamad and 16.3% in the most sensitive cv. Hosen-Eilon. The characters contributing to low fruit set were bud drop, splitting of the antheridial cone, style exsertion and reduction of the quantity and/or functionality of the gametes. Employing the above characters as criteria for selection, fruit set of an F_4 line, phenotypically similar to the sensitive parent, was improved to 63.1%. Improved fruit set, 87.6%, was also obtained in an F_1 hybrid between 'Hotset' and 'Gamad'. The importance is discussed of various easily recognizable flower components contributing to satisfactory fruit set under high temperatures and their possible use in breeding is elaborated.

INTRODUCTION

High temperatures induce drop of buds and flowers in the tomato (RADSPINNER, 1932; SMITH, 1935; LEOPOLD & SCOTT, 1952; SAITO & ITO, 1967; ABDALLA & VERKERK, 1968). Flower drop is essentially a result of lack of fertilization which, in turn, is affected by a number of factors. Under high temperatures, gametogenesis is disturbed, gamete viability is reduced (IWAHORI & TAKAHASHI, 1964; IWAHORI, 1965, 1966) and less pollen is produced in the flower (ABDALLA & VERKERK, 1968). High temperatures can also affect the germination and the elongation of the pollen tube into the style and thus inhibit fertilization (SMITH, 1935; SMITH & COCHRAN, 1935; IWAHORI & TAKAHASHI, 1964; IWAHORI, 1967).

Tomatoes are self-pollinated at a rate of 98% or more (DONALD, 1916; LESLEY, 1924). Under high temperatures, morphological changes in the flower structure such as style exsertion out of the antheridial-cone (SMITH, 1932; SAITO & ITO, 1967; ABDALLA & VERKERK, 1968), browning and drying of the stigma (YOUNG, 1963; ABDALLA & VERKERK, 1968) are observed. Any of these changes may prevent or reduce self-pollination, resulting in low rates of fruit set.

Differences between cultivars in fruit set under high temperatures have been reported (LOCKE, 1952; SCHAIBLE, 1962; OGNYANOVA & SHUKAROV, 1970). Some

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works were concerned with the general reaction to high temperature (IWAHORI & TAKAHASHI, 1964; IWAHORI, 1965, 1966, 1967; ABDALLA & VERKERK, 1968) while others dealt with differences between genotypes in one or more of the specific mechanisms affected (SCHAIBLE, 1962; ABDALLA & VERKERK, 1968; OGNYANOVA & SHUKAROV, 1970; CHARLES & HARRIS, 1972). However, until now, the relative contribution of each of the above characters for fruit set has not been established. Knowledge of the relative importance of such factors is imperative for elaborating an ideotype characterised by maximum fruit set under high temperature conditions.

MATERIALS AND METHODS

The responses of various components of the reproductive process to the effect of high temperatures were studied in two sets of experiments. Plants with 6–7 true leaves of seven cultivars and crosses (Table 1) were transplanted in July from an open nursery to the experimental field. At this stage of development, no flower bud primordia were visible. Day length decreased progressively from 14.07 hours on the day of planting to 12.00 hours in September. During flower development, the daily maximum and minimum temperatures in the field varied between 36.5°C to 38.7°C and 16.5°C to 20.0°C, respectively. Style length was scored at anthesis in the first three flowers of the first three clusters on a scale of three grades (see Table 1 for details). The percent of fruit set was determined two weeks after anthesis, counting ovaries which had reached a diameter of 1 cm or more. The relations between style length and flower drop was established by contingency test (SNEDECOR & COCHRAN, 1969). A second experiment with the two cultivars Hotset and Hosen-Eilon was conducted under controlled conditions. Fifty plants of each of the two cultivars were grown in 10-liter pots. The photoperiod was 12 hours and a combination of fluorescent and incandescent lamps maintained light intensity of 4000 ft-c at the growing points. Day and night temperatures were: normal, 23 ± 3°C and 17 ± 3°C (ABDALLA & VERKERK, 1968) and hot, 33 ± 2°C and 23 ± 2°C, respectively. Bud drop, style exsertion, splitting of the antheridial-cone and fruit set of the first three flowers of the first three inflorescences were determined. All the lateral branches except the first one below the first truss were removed. Crosses were made with and pollen samples were taken from flowers of this lateral branch. Pollen was collected by an electric shaker and mean pollen weight was determined on each of 10–20 flowers at anthesis. Pollen viability was measured following germination on BREWBAKER & KWACK (1963) medium for one hour at 25°C under illumination. About 100 pollen grains were observed in each sample. Germinated pollen was classified into two grades according to their tube lengths: a) up to 0.15 mm; b) longer than 0.15 mm.

RESULTS

The cultivars and crosses studied under field conditions varied in their reaction to high temperatures. Differences were found in style exsertion and flower drop, with cv. Hosen-Eilon reaching the highest values (Table 1). Hotset and its F_1 cross with cv. Gamad were the least affected. Within each line, a strong relationship was found between style exsertion and flower drop (Table 1). However, flower drop also occurred

Table 1. Fruit set and grade of style exsertion in tomato cultivars and lines under field conditions.

Cultivar and origin	Grade of style exsertion[1]	Total number of flowers	% flower drop	χ^2 [2]	% flowers with exserted style (grades 2 and 3)	% fruit set (total)
Roma	1	241	33.6	63.84	25.6	53.4
	2	83	84.3	P<0.001		
	3	0	0			
Hotset (ANONYMOUS,	1	180	9.4	89.76	20.0	77.3
1958)	2	45	75.6	P<0.001		
	3	0	0			
Gamad	1	168	23.2	56.85	28.2	62.0
(RETIG & KEDAR,	2	61	73.8	P<0.001		
1968)	3	5	100.0			
F_1 (Hotset ×	1	205	5.9	65.15	12.4	87.6
GAMAD)	2	29	58.6	P<0.001		
	3	0	0			
F_2 (Hotset ×	1	327	15.0	130.97	31.4	69.2
Gamad)	2	136	61.8	P<0.001		
	3	14	100.0			
Hosen-Eilon[3]	1	32	50.0	34.81	79.1	16.3
	2	96	90.6	P<0.001		
	3	25	100.0			
F_4 line (Hotset ×	1	160	23.7	43.75	28.9	63.1
Hosen-Eilon)	2	59	66.1	P<0.001		
	3	6	100.0			

[1] Grade 1: style at antheridial-cone level or below; 2: style exserted up to 1 mm out of the antheridial cone; 3: style exserted more than 1 mm out of the antheridial-cone.
[2] Examining dependence between grade of style exsertion and flower drop.
[3] Local semi-determinate cv. with large oblate fruits.

in flowers with normal styles (grade 1).

In the following experiment under controlled conditions we tried to evaluate the importance of additional mechanisms involved in the response to high temperatures (Table 2). High temperature treatment induced drop of flower buds, reduced the quantity of viable pollen and caused style exsertion. These responses were much more pronounced in the susceptible cv. Hosen-Eilon than that in the heat tolerant cv. Hotset. Another symptom occurring in 'Hosen-Eilon' only, was splitting of the antheridial-cone (Fig. 1). Such a change, found under high temperatures in nearly 40% of the flowers with exserted styles, constitutes another mechanical barrier to self-pollination. Each flower with a split antheridial-cone has dropped. The differential sensitivity to high temperatures of male and female gametes was studied by reciprocal crosses within the two cultivars between plants grown under the two temperature regimes (Table 3). The functionality of both types of gametes was reduced by high temperatures as expressed by the reduced rates of fruit set. Microspores,

Table 2. The effect of high temperatures on some components affecting fruit-set. Twenty-five plants of each cultivar were grown under each temperature regime.

Cultivar	Temp. (°C) day	Temp. (°C) night	Drop of flower buds (%)	Pollen weight/ flower (mg)	Pollen germination, (%)	% pollen with tubes longer than 0.15 mm	Average grade of style exsertion[1]	% set
Hosen-	23	17	12.2 b	1.21	67.7 a	18.3 a	2.1 b	31.8 b
Eilon	33	23	66.2 a	0.45	48.6 b	4.6 b	2.8 a	5.8 c
Hotset	23	17	2.1 b	0.60	73.4 a	20.0 a	1.2 d	78.8 a
	33	23	10.0 b	0.54	66.0 a	17.5 a	1.6 c	63.0 a

[1] See Table 1.
Values within a column not followed by the same letters are significantly different at the 5% level.

Table 3. Effect of temperature treatments of female and male parents on fruit set. Twenty-five plants of each cultivar were grown under each temperature regime.

Female parent	Day/night temp. (°C)	Pollinator	Day/night temp. (°C) 23/17	Day/night temp. (°C) 33/23
Hotset	23/17	Hotset	100[1]	78.8
	33/23		84.7	69.8
Hosen-Eilon	23/17	Hosen-Eilon	100[1]	31.6
	33/23		45.3	20.9

[1] The considered 100% absolute rates of fruit set were 89.5% and 73.1% in Hotset and Hosen-Eilon, respectively, at 23/17 °C.

however, were more affected than macrospores. There were also marked differences between the two cultivars in this respect. The combined effect of high temperatures treatment of both the male and female parents resulted in about 70% and 21% fruit set in 'Hotset' and 'Hosen-Eilon', respectively, when compared to normal temperature controls.

DISCUSSION AND CONCLUSIONS

While the effect of temperature on flower bud drop has been reported earlier (RADSPINNER, 1932; SMITH, 1932), the relative importance of this phenomenon has not been established. Flower bud drop under high temperature was 66% of all buds produced in cv. Hosen-Eilon as compared to 10% only in cv. Hotset (Table 2). Such a high rate of bud drop may result in a drastic reduction of the yield and may be critical in cultivars for single harvest. The great difference between 'Hosen-Eilon' and 'Hotset' in the rate of bud drop suggests the possibility of using breeding techniques to overcome this problem.

Many studies have shown that high temperatures disturb the process of gametogenesis and the efficiency of the fertilization process (SMITH & COCHRAN, 1935; JOHNSON & HALL, 1952; IWAHORI & TAKAHASHI, 1964; IWAHORI, 1965, 1966, 1967).

Fig. 1. Splitting of the antheridial-cone, C. V. Hosen-Eilon.

The viability of both pollen and ovules was reduced (ABDALLA & VERKERK, 1968) but microsporogenesis was more affected (IWAHORI & TAKAHASHI, 1964). CHARLES & HARRIS (1972) however, reported that under their experimental conditions stigma receptivity was affected. In the present work it was found that high temperatures during development of the flowers in the sensitive cv. Hosen-Eilon strongly affected the quantity of pollen, its viability and the growth rate of the pollen tubes when examined in vitro at 25°C (Table 2); the cv. Hotset was found to be less sensitive. DEMPSEY (1970) found that following pollination of excised flowers which had developed under optimum conditions, high temperature caused a marked decrease in pollen germination in vivo.

A great difference was found in vivo between the two genotypes in the sensitivity of their male and female gametophytes (Table 3). In the cv. Hotset, the rate of fruit set was about twice or more that of 'Hosen-Eilon', when either the male or the female parent was subjected to high temperatures. When both parents were grown under the high temperature regime, the rate of fruit set in 'Hotset' was three times that of the sensitive cultivar. The reduction in fruit set after exposure of the female parent to high temperatures might be caused by damage to the ovules (IWAHORI, 1966; ABDALLA & VERKERK, 1968) as well as by reduced stigma receptivity (CHARLES & HARRIS, 1972).

Another important character affecting fruit set under high temperatures (BURK, 1929) or soil moisture stress (COYNE, 1968) is the stigma position relative to the antheridial-cone. Pollination was prevented or reduced when the stigma extended beyond the top of the antheridial-cone (BURK, 1929; SMITH, 1932; WARNER, 1939; YOUNG, 1963). No style elongation was observed in several cultivars (CHARLES & HARRIS, 1972) while a great variability in this respect between cultivars was shown in other studies under high temperatures (JOHNSON & HALL, 1953). The present work confirmed the wide genotypic variation in style exsertion. The frequency of such distorted flowers ranged from 12.5% to 80% of all the flowers in the hybrid 'Hotset' × 'Gamad' and in 'Hosen-Eilon', respectively(Table 1). A strong relationship was found between style exsertion and flower drop. No fruit set was ever observed of flowers with style protruding more than 1 mm out of the antheridial-cone. In flowers with style exserting up to 1 mm, flower drop ranged between 60% in the 'Hotset' × 'Gamad' hybrid to 90% in 'Hosen-Eilon'. Splitting of the antheridial-cone is probably another mechanical barrier preventing self pollination. This character was not found in 'Hotset', whereas in 'Hosen-Eilon', its frequency reached 40% of all flowers with exserted style.

The relative importance of the factors responsible for fruit-set under high temperature conditions could be estimated as follows: About two thirds of the flower buds of the heat sensitive cv. Hosen-Eilon aborted (Table 2). Amongst the remaining buds which developed into flowers, almost 80% were malformed and most of them did not set fruit (Table 1). The combined effect of the above components resulted in a fruit set of only 6% (Table 2). Fruit set was increased to 45% when the mechanical barriers to self-pollination and the effect of heat on microsporogenesis were overcome by hand pollination with normal pollen (Table 3).

The heritability (KAMPTHORNE, 1969) in style exsertion in our experiments was estimated from the variances measured in the cvs. Hotset and Gamad and in the F_1 and F_2 generations of the cross between them. The relatively high value found ($H = 43\%$) is in accordance with other reports (RICK & DEMPSEY, 1969) and indicates the practical possibilities for selecting lines with normal style position under high temperatures.

The marked differences between cultivars in their sensitivity to high temperatures as expressed by bud drop, style exsertion and splitting of the antheridial-cone might be employed as visual parameters for breeding of better adapted lines. Indeed, such criteria were applied on a cross between 'Hotset' and 'Hosen-Eilon'. After only two generations of selection, rate of fruit set of an F_4 line with a phenotype similar to the sensitive parent, reached a value of 63% as compared with only 16.3% of the sensitive cultivar (Table 1). A more sophisticated method is needed to select for improved functionality of the gametes under high temperature stress. The genetic material with such desirable characters is readily available (JOHNSON & HALL, 1953; SCHAIBLE, 1962; ABDALLA & VERKERK, 1968; OGNYANOVA & SHUKAROV, 1970; CHARLES & HARRIS, 1972; ANONYMOUS, 1974; and Tables 1, 2, 3).

A comparison between the standard cv. Gamad, the heat-tolerant cv. Hotset and their F_1 cross shows that the rate of flowers with exserted style was the lowest and fruit set was the highest in the F_1 hybrid (Table 1). This might indicate that improved fruit set can be obtained also by choosing the adequate parent combination for F_1 hybrids.

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