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Influence of High Temperatures on Gas Exchange Rate and Growth of Eight Tomato Cultivars under Controlled Heat Stress Conditions

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Summary

Eight tomato cultivars of different origin were evaluated for heat tolerance. Plants were grown in growth chambers under two temperature regimes (37/27 °C or 37/22 °C day/night). Variations in leaf gas exchange rate as well as the vegetative growth and reproductive development in response to heat stress were investigated. Heat tolerant cultivars showed higher photosynthetic rate under heat stress conditions at the different growth stages in comparison to the heat sensitive ones. Photosynthetic rate increases from the vegetative stage, peaks at the flowering and declines at the late fruiting stage. The reproductive processes in tomato were more sensitive to high temperatures than the vegetative ones. Number of pollen grains, fruit set percentage and fruits fresh weight produced by the heat tolerant cultivars were higher than those produced by the heat sensitive ones. Night temperature had an effect on the number of pollen grains produced and released and fruit set percentage. A positive correlation between the photosynthetic rate and fruit set was observed.

Key words. Fruit set – photosynthetic rate – pollen grains production – growth temperature

Introduction

Heat stress is a major abiotic factor that limits tomato production during the summer season in the arid tropics of the Sudan. This environmental factor influences various physiological processes such as photosynthetic activities, transpiration, photorespiration and dark respiration as well as vegetative growth and reproductive development. Therefore, studies aimed at better understanding how heat affects photosynthesis are, in the context of global warming, of increasing importance (Sharkey 2000).

It has been reported that heat stress can occur at temperatures just a few degrees above optimal (mean daily temperatures of 27 and 29 °C) (Peet et al. 1997). Such moderately elevated temperature stress may not disrupt biochemical reactions fundamental for normal cell functioning. However, an impairment of pollen and anther development by elevated temperature contributes to decreased fruit set in tomato (Sato et al. 2000).

According to Moore and Thomas (1952) tomato production is limited primarily by high night time temperature. Furthermore, Dinar and Rudich (1985) reported that in tomato plants, high temperatures affect several physiological and biochemical processes resulting in yield reduction. Possible biochemical and/or physiological processes affected by temperature are photosynthetic enzyme activity, membrane integrity, photophosphorylation, and electron transport in chloroplast, stomatal conductance to CO_2 diffusion and photoassimilate translocation. Willits and Peet (1998) found that yield reductions result when night time temperatures are over 22 °C.

The mechanisms of heat tolerance, their interactive effects, and associated morphological and physiological modifications and symptoms have not been fully identified and/or understood by plant breeders and plant physiologists. Hence, the study of high temperature limitation on productivity and the potential variability in thermo-sensitivity and acclimation capacity among crop cultivars has been an active field of research and different cultivars of tomato exhibited considerable variation in their sensitivity to heat stress (Rainwater et al. 1996).

In addition, little information is known concerning the effect of temperature on leaf gas exchange and differences in gas exchange physiology. No published data are available for the local Sudanese tomato cultivars. With this consideration in mind, this study was carried out to fulfil the following objectives:

1. To study the effect of two temperature regimes (37/27 °C and 37/22 °C) on the growth and development of different tomato cultivars. The temperature regimes selected to match natural temperature regime in a given time of the year in Sudan, so that any possible practical results can be readily used.
2. To assess the cultivar differences in photosynthetic capacity as well as in growth and development.
3. To make a comparative study of local as well as exotic cultivars of tomatoes for screening high yielding cultivars suitable to agro-climatic conditions of Sudan.

Materials and Methods

Eight tomato genotypes with known differences in sensitivity to heat stress were used: 'Strain B' (tolerant), 'Peto 86' (sensitive) and 'UC 82-B' (sensitive) from Peto Seed, Co. Inc (USA). 'Maverick F_1' (tolerant), 'Kervic F_1' (tolerant) and 'Drd 85 F_1' (tolerant) from De Ruiter Seed Company, the Netherlands. 'Summerset' (tolerant) and 'Omdurman' (tolerant) as local cultivars bred by the National Institute for Exports of Horticultural Crops, University of Gezira, Sudan.

They were sown in flat trays filled with a standard peat mixture substrate for germination (C200) from Stender AG, Company, Germany. Substrate contains 0.5 g l^{-1} NPK fertiliser and had an electrical conductivity (EC) of 0.25 dS m^{-1} and pH 5.0–6.0. Fifteen days after sowing (DAS), the seedlings were transplanted into 9 cm containers filled with standard peat mixture substrate (B700) from the same company. Substrate contains 1 g l^{-1} NPK fertilizer, with an EC of 0.53 dS m^{-1} and pH 5.8. The transplants were grown in the greenhouse of the Department of Vegetable Crops, Institute for Horticultural Sciences, Humboldt University of Berlin (Latitude 52° 30' N, Longitude 13° 25' E).

Tomato plants at 25 DAS were transferred into 14 cm diameter pots filled with the same substrate. At 35 DAS they were transferred into Tube-like single-plant-pots 50 cm long by 25 cm diameter. The pots were closed at one end by perforated cover, which allowed free drainage of excess water. The pots had a volume of 8 l each, which were filled with the same substrate. The plants then were transferred to the reach-in growth chamber at the Institute of Crop Sciences of the Humboldt University of Berlin. The transplants of each cultivar were divided into two sets, one set was transferred to the reach-in growth chamber (installed by BBC-York, York International Company) at 37/22 °C (day/night) for 13/11 h. Another set was transferred to a second growth chamber at 37/27 °C (day/night) for 13/11 h. During the day, 500 µmol m^{-2} s^{-1} irradiance from cool white fluorescent lamps (TLM 140 W/33 RS Double Flux) were provided for each set, on the top of the plants. Relative humidity was 45/55 % (day/night). Temperature and relative humidity were continuously recorded using hygrothermographs (Belfort Instrument, Baltimore, MD). Tomato plants were watered daily. Twice a week 40 ml of 0.2 % soluble fertilizer (12N-4P-6K) were applied to each pot. Plants were relocated randomly within chambers weekly to reduce possible position effects. All plants were harvested at 115 DAS.

Data collected

Leaf area (cm^2), leaf fresh weight, leaf dry weight, stem fresh weight, stem dry weight, fruit fresh weight (g $plant^{-1}$), number of pollen grains per flower, and percent of fruit set were recorded according to Abdelmageed and Gruda (2007). In addition, leaf gas exchange was measured.

Leaf gas exchange was measured using either the 4th or 5th uppermost youngest fully expanded leaf from the apex at the time of measurement, with a portable leaf chamber compact CO_2/H_2O porometer (CQP 130, WALZ Mess- und Regeltechnik, Effeltrich, Germany) during vegetative (45 DAS), flowering (55–65 DAS) and late fruit development stage (95–100 DAS). CO_2 and H_2O differential measurements were made in an open system under steady state condition using an infrared high sensitive gas analyzer incorporated in the compact porometer as described by Anyia and Herzog (2004). An external light source was connected with the leaf chamber during leaf gas exchange measurements, such that all measurements were made at a defined light intensity (800 µmol m^{-2} s^{-1}). According to Jun et al. (1988) this values are near to a saturation light intensity for tomatoes. CO_2 assimilation rate, transpiration rate, stomatal conductance to CO_2, and internal CO_2 concentration of the leaves were calculated from the gas-exchange measurement according to von Caemmerer and Farquhar (1981). All measurements of photosynthesis were carried out between 11:00 and 14:00 h.

Statistical analysis

Collected data were analyzed using the SPSS statistical package software version 10.0. (Chicago, USA). Data were subjected, when appropriate, to two-way factorial analysis of variance (ANOVA) for temperature and cultivar. Differences between means ($P \leq 0.05$) were separated by Duncan's multiple range tests for both temperature regimes separately to determine the significance of variation among the different cultivars. Association among recorded parameters was examined by simple correlation analysis.

Results

Leaf gas exchange rate

The leaf gas exchange rate of the eight cultivars was measured at vegetative, flowering and late fruit development stage at two temperature regimes (37/27 °C and 37/22 °C day/night). The pooled CO_2 assimilation rate (A) increases from the vegetative stage, peaks at the flowering and declines at the late fruiting stage. Significant genotypic variations were detected in A at the different growth stages. Under both temperature regimes, the pooled A decreased slightly from vegetative to late fruit development stage (Table 1).

At vegetative stage, the A varied significantly among the cultivars at both temperature regimes. At 37/27 °C regime 'Maverick F_1' and 'Summerset' had the highest A respectively and 'Strain B', 'Kervic F_1', 'Omdurman', 'UC 82-B' and 'Peto 86' had the lowest values. 'Drd 85 F_1' was intermediate. While, at 37/22 °C regime at the same growth stage, 'Maverick F_1' and 'Summerset' had the highest values of A. 'UC 82-B' and 'Omdurman' had the lowest values (Table 1). A at vegetative and flowering growth stages was significantly affected by both temperature and cultivar but not by the interaction (temperature x cultivar) (Table 1).

During flowering stage, under high day/high night temperatures (37/27 °C), A was higher in 'Kervic F_1', 'Summerset', 'Maverick F_1', and 'Drd 85 F_1' and was lower in 'Omdurman', 'Peto 86', and 'UC 82-B'. Other cultivars were intermediate. While, under high day/intermediate night temperatures (37/22 °C) at the same growth stage, 'Summerset' had the highest value. 'UC 82-B' and 'Peto 86' had the lowest ones (Table 1).

At late fruit development stage, among the cultivars used, 'Summerset' showed the highest value and 'UC

Table 1. Assimilation rate (A) and transpiration rate (E) of tomatoes at different growth stages grown under two temperature regimes.

	Assimilation rate (A) [µmol CO_2 m^{-2} s^{-1}]					
Growth stage	Vegetative		Flowering		Late fruiting	
Temperature [day/night (°C)]	37/27	37/22	37/27	37/22	37/27	37/22
Cultivar						
'Peto 86'	7.46 B†	9.41 ab	5.91 D	7.40 d	4.56 CD	6.35 cd
'Strain B'	7.97 B	9.05 ab	8.28 BC	9.97 abc	6.07 AB	7.57 bc
'Maverick F_1'	10.03 A	10.14 a	9.24 AB	9.67 bc	6.14 AB	9.26 abc
'UC 82-B'	7.60 B	8.20 bc	5.67 D	8.29 cd	4.18 D	4.61 d
'Drd 85F_1'	8.67 AB	9.53 ab	10.08 AB	10.10 abc	5.65 ABC	9.89 ab
'Kervic F_1'	7.93 B	9.40 ab	10.35 A	10.99 ab	5.69 ABC	11.50 ab
'Omdurman'	7.52 B	7.70 c	6.70 CD	9.06 cd	5.35 BCD	7.72 bc
'Summerset'	9.93 A	10.04 a	10.29 A	12.02 a	6.85 A	11.99 a
Mean	8.39	9.19	8.32	9.69	5.56	8.61
Significance						
Temperature (T)	*, **, ***		*, **, ***		*, **, ***	
Cultivar (C)	*, **, ***		*, **, ***		*, **, ***	
Interaction TxC	NS		NS		*,**	

	Transpiration rate (E) [mmol H_2O m^{-2} s^{-1}]					
Growth stage	Vegetative		Flowering		Late fruiting	
Temperature (°C)	37/27	37/22	37/27	37/22	37/27	37/22
Cultivar						
'Peto 86'	7.38 B	4.37d	9.82 A	8.40 a	7.11 BC	3.31 b
'Strain B'	8.56 AB	4.04 d	8.83 ABC	7.91 a	7.51 BC	7.25 a
'Maverick F_1'	5.94 C	5.45 c	7.78 BCD	7.56 ab	6.46 BCD	5.18 b
'UC 82-B'	8.18 AB	6.72 ab	9.07 AB	6.07 bc	6.29 CD	5.16 b
'Drd 85F_1'	8.15 AB	7.54 a	9.64 A	7.26 ab	6.51 BCD	3.48 b
'Kervic F_1'	9.46 A	5.98 bc	6.94 D	4.32 d	5.08 D	4.19 b
'Omdurman'	8.36 AB	6.63 ab	7.49 CD	5.98 bc	8.46 AB	4.13 b
'Summerset'	8.41 AB	6.25 bc	7.03 D	4.85 cd	9.87 A	5.21 b
Mean	8.05	5.87	8.32	6.54	7.16	4.74
Significance						
Temperature (T)	*, **, ***		*, **, ***		*, **, ***	
Cultivar (C)	*, **, ***		*, **, ***		*, **, ***	
Interaction TxC	*, **, ***		NS		*,**	

†Means followed by the same letter(s) within each column are not significantly different at P≤0.05, according to Duncan's multiple range test for a given temperature regime. n = 5 plants
*, **, ***: Significant at P<0.05, 0.01, and 0.001, respectively

82-B' the lowest value of A at 37/27 °C regime. While, under high day/intermediate night temperatures (37/22 °C), 'Summerset' showed the highest values and 'UC 82-B' and 'Peto 86' the lowest values of A (Table 1).

The pooled transpiration rate (E) of the different cultivars showed only minor changes as a function of temperature at vegetative and flowering stages (Table 1). The different cultivars used in this experiment were slightly inconsistent in their E at the different growth stages at both temperature regimes. The interaction (temperature x cultivar) was significant at both vegetative and late fruiting stages, but not significant at flowering stage, while the effects of the two main factors were highly significant at three growth stages studied (Table 1).

Table 2. Stomatal conductance (gCO_2) and leaf internal CO_2 concentration (C_i) of tomatoes at different growth stages grown under two temperature regimes.

	Stomatal conductance (gCO_2) [mmol CO_2 m^{-2} s^{-1}]					
Growth stage	Vegetative		Flowering		Late fruiting	
Temperature [day/night (°C)]	37/27	37/22	37/27	37/22	37/27	37/22
Cultivar						
'Peto 86'	111.63 BC †	115.14 d	318.09 A	323.25 ab	214.47 A	219.03 ab
'Strain B'	94.13 C	304.09 a	287.05 AB	388.92 a	74.18 CD	250.10 a
'Maverick F_1'	135.18 B	138.07 cd	255.12 B	278.94 b	104.72 C	215.34 ab
'UC 82-B'	204.73 A	217.96 bc	233.31 B	388.43 a	100.06 C	205.78 ab
'Drd 85F_1'	181.64 A	231.46 ab	282.65 B	383.72 a	81.19 CD	163.40 b
'Kervic F_1'	195.77 A	201.64 bc	127.16 C	150.96 c	51.74 D	253.29 a
'Omdurman'	175.97 A	181.25bcd	277.78 B	306.13 ab	159.90 B	204.70 ab
'Summerset'	133.79 B	137.39 cd	244.41 B	251.74 b	204.45 A	270.58 a
Mean	154.13	190.88	253.20	309.01	123.84	222.78
Significance						
Temperature (T)	*,**,***		*,**,***		*,**, ***	
Cultivar (C)	*,**,***		*,**,***		*,**	
Interaction TxC	*, **, ***		NS		*	

	Leaf internal CO_2 concentration (C_i) [ppm]					
Growth stage	Vegetative		Flowering		Late fruiting	
Temperature (°C)	37/27	37/22	37/27	37/22	37/27	37/22
Cultivar						
'Peto 86'	263.60 B	244.62 b	323.70 A	296.04 a	318.32 A	301.24 a
'Strain B'	250.53 B	232.28 b	307.21 BC	262.48 a	284.19 B	282.20 b
'Maverick F_1'	259.60 B	227.86 b	302.73 BC	261.96 a	276.39 B	271.18 cd
'UC 82-B'	291.12 A	280.21 a	309.48 ABC	274.95 a	271.30 B	264.48 d
'Drd 85F_1'	295.00 A	281.63 a	313.41 AB	272.60 a	282.48 B	276.72 bc
'Kervic F_1'	292.67 A	272.19 a	266.88 D	210.28 b	226.11 C	220.20 e
'Omdurman'	301.71 A	280.59 a	323.08 A	292.95 a	315.00 A	300.46 a
'Summerset'	264.08 B	245.59 b	298.00 C	293.48 a	315.57 A	277.14 bc
Mean	277.22	258.12	305.56	270.59	286.17	274.21
Significance						
Temperature (T)	*,**,***		*,**,***		*,**,***	
Cultivar (C)	*,**,***		*,**,***		*,**	
Interaction TxC	NS		NS		NS	

†Means followed by the same letter(s) within each column are not significantly different at P≤0.05, according to Duncan's multiple range test for a given temperature regime. n = 5 plants
*, **, ***: Significant at P<0.05, 0.01, and 0.001, respectively

Stomatal conductance (gCO_2) means of the different cultivars at the two temperature regimes are illustrated in Table 2. The highest Stomatal conductance (gCO_2) means were observed at the flowering stage at both temperatures regimes. The different cultivars used in this experiment were slightly inconsistent in their stomatal conductance (gCO_2) means at the different growth stages at both temperature regimes. There was a significant interaction (temperature x cultivar) effect on gCO_2 at the vegetative and late fruiting stages (Table 2).

There was a significant difference in the leaf internal CO_2 concentration (C_i) among the different cultivars used at the different growth stages. Most of the heat

Table 3. Vegetative growth of tomatoes grown under two temperature regimes.

Parameters	Leaf area [cm²]		Leaf fresh weight [g]		Leaf dry weight [g]	
Temperature [day/night (°C)]	37/27	37/22	37/27	37/22	37/27	37/22
Cultivar						
'Peto 86'	4530.28 CDE†	9024.73 b	216.59 D	416.39 bc	36.39 DE	50.77 b
'Strain B'	4263.65 DE	4379.15 d	244.87 D	288.68 cd	31.43 EF	32.97 cd
'Maverick F_1'	4312.33 DE	5519.08 cd	305.70 BC	437.98 b	44.38 BC	51.83 b
'UC 82-B'	3598.87 E	3859.15 d	111.64 E	198.44 d	25.67 F	26.64 d
'Drd 85 F_1'	4881.15 CD	4851.83 cd	336.84 B	418.98 bc	48.96 B	53.93 b
'Kervic F_1'	6443.31 AB	11915.00 a	395.98 A	649.09 a	64.60 A	81.98 a
'Omdurman'	5679.19 BC	7309.32 bc	268.71 CD	356.65 bc	33.88 DE	45.66 bc
'Summerset'	7056.67 A	8946.53 b	315.39 BC	439.13 b	39.72 CD	50.60 b
Mean	5095.68	6975.60	274.47	400.42	40.63	49.30
Significance						
Temperature (T)	*, **, ***		*, **, ***		*, **, ***	
Cultivar (C)	*, **, ***		*, **, ***		*, **, ***	
Interaction TxC	*, **, ***		NS		NS	

Parameters	Stem fresh weight [g]		Stem dry weight [g]	
Temperature (°C)	37/27	37/22	37/27	37/22
Cultivar				
'Peto 86'	130.19 B	143.67 d	25.35 B	31.06 cd
'Strain B'	151.81 B	199.00 bc	24.53 B	29.99 cd
'Maverick F_1'	135.98 B	137.27 d	39.66 A	41.07 b
'UC 82-B'	86.98 C	88.56 e	21.17 B	24.22 d
'Drd 85 F_1'	219.07 A	246.23 ab	42.38 A	53.34 a
'Kervic F_1'	232.65 A	285.47 a	43.18 A	54.79 a
'Omdurman'	75.59 C	140.50 d	9.67 D	27.67 cd
'Summerset'	101.91 C	168.73 cd	16.05 C	34.62 bc
Mean	141.77	176.18	27.75	37.10
Significance				
Temperature (T)	*, **, ***		*, **, ***	
Cultivar (C)	*, **, ***		*, **, ***	
Interaction TxC	NS		*, **, ***	

†Means followed by the same letter(s) within each column are not significantly different at P≤0.05, according to Duncan's multiple range test for a given temperature regime. n = 5 plants
*, **, ***: Significant at P<0.05, 0.01, and 0.001, respectively

tolerant cultivars showed low values of C_i at both temperature regimes during the vegetative and flowering growth stages. No interaction between the temperature and cultivar was detected (Table 2).

Vegetative growth

Growth under different night temperatures caused differences in the vegetative growth of the different tomato cultivars used in this study.

Heat stress markedly reduced the total leaf area in all eight cultivars tested. Moreover, 'Summerset' and 'Kervic F_1' had the highest leaf area and 'Peto 86', 'UC 82-B', 'Maverick F_1', 'Strain B' and 'Drd 85 F_1' had the lowest values. There were significant effects of cultivar, temperature, and their interaction on leaf area (Table 3).

Under heat stress conditions 'Kervic F_1' had significantly highest leaf fresh and dry weight, while, 'Strain B', 'Peto 86' and 'UC 82-B' had the lowest values. 'Drd 85 F_1' 'Summerset', 'Maverick F_1' were intermediate. Leaf fresh

Table 4. Generative development of tomatoes grown under two temperature regimes.

Parameters	Number of pollen grains flower^{-1}		Fruit set percentage [%]		Fruit fresh weight [g plant^{-1}]	
Temperature [day/night (°C)]	37/27	37/22	37/27	37/22	37/27	37/22
Cultivar						
'Peto 86'	2420 C †	3340 c	3.29 CD	5.55 bc	27.43 C	49.85 bc
'Strain B'	3800 B	3880 bc	8.08 BC	11.9 b	66.53 C	102.86 bc
'Maverick F_1'	3490 B	3800 bc	4.49 CD	6.39 bc	51.85 C	70.81 bc
'UC 82-B'	2310 C	2460 d	1.27 D	3.39 c	11.02 C	24.55 c
'Drd 85F_1'	3510 B	4340 b	9.51 B	33.56 a	276.80 A	316.84 a
'Kervic F_1'	3270 B	3950 bc	5.23 BCD	7.42 bc	74.68 C	132.69 b
'Omdurman'	3260 B	3850 bc	6.07 BCD	10.86 b	46.18 C	63.32 bc
'Summerset'	5550 A	6110 a	23.50 A	38.86 a	182.50 B	231.04 a
Mean	3451.25	3966.25	7.68	14.74	92.12	123.99
Significance						
Temperature (T)	*, **, ***		*, **, ***		*, **, ***	
Cultivar (C)	*, **, ***		*, **, ***		*	
Interaction TxC	NS		*, **, ***		NS	

†Means followed by the same letter(s) within each column are not significantly different at P = 0.05, according to Duncan's multiple range test for a given temperature regime. n = 5 plants
*, **, ***: Significant at P<0.05, 0.01, and 0.001, respective

and dry weights were significantly affected by temperature and cultivar, but not by the interaction (Table 3).

Reproductive development

For tomato plants grown under high day/high night temperatures (37/27 °C), for prolonged period, the number of pollen grains produced and released was markedly reduced irrespective of the cultivar. 'Summerset' produced the highest number of pollen grains. 'UC 82-B' and 'Peto 86' had the lowest ones, while the other cultivars were intermediate (Table 4).

With regard to fruit set percentage, 'Summerset' had the highest fruit set percentage at both temperatures regimes and 'UC 82-B' had the lowest percentage, the other cultivars were in between (Table 4).

In line with the previous results of fruit set percentage of the different tomato cultivars, fruit fresh weight showed the same trend (Table 4). Heat stress and cultivar had a significant effect on the number of pollen grains per flower, fruit set percentage and fruit fresh weight, respectively. For the interaction the differences were only significant on fruit set percentage (Table 4).

A positive correlation was observed between A and fruit set at the different growth stages for plants grown under both temperature regimes (r = 0.375–0.512, P<0.05; P<0.01) with the exception of the vegetative stage at 37/22 °C regime. Moreover, there was a significant and positive correlation between E and g CO_2 at the flowering and late fruiting stages at both temperature regimes (r = 0.489–0.680, P<0.01). A similar association between g CO_2 and C_i was observed (r = 0.466–0.813, P<0.01) (data not shown).

Discussion

Leaf gas exchange rate

Photosynthesis is known to be one of the most heat-sensitive processes and it can be completely inhibited by high temperature before other symptoms of the stress are detected (Berry and Björkman 1980).

The higher rate of CO_2 assimilation rate observed in the heat tolerant cultivars compared to the heat sensitive ones under heat stress conditions was attributable to their efficient photosynthetic apparatus, which contributes to their tolerance to heat stress. This is in agreement with earlier reports (Nkansah and Ito 1994, 1995; Camejo et al. 2005). According to Salvucci and Crafts-Brandner (2004a, b) the reason behind the inhibition of the net photosynthetic CO_2 assimilation rate by high temperature primarily originates from a reduction of the Rubisco activation state or an inhibition of electron transport.

Nkansah and Ito (1994, 1995) reported that the high A at the flowering stage for the different cultivars might be due to a more efficient physiological mechanism at this stage. This strengthening the results found in the present study. The decline in the A from flowering to late fruiting stage at both temperature regimes may be attributed to whole plant senescence and less assimilate demand as already fruits were matured (Nkansah and Ito 1995).

Decline in A in the present study under high temperature conditions might be attributed mainly to the reductions in the stomatal conductance.

There was an increase in E of the different cultivars used in this experiment at the different growth stages un-

der high temperature conditions. This agrees with the findings of BERRY and BJÖRKMAN (1980) who reported that transpiration is temperature-dependent. Also, in agreement with, NKANSAH and ITO (1994, 1995) who observed an increase in transpiration rate up to 39/40 °C in studies with different tomato genotypes. Differences between cultivars in transpiration may be due to their differences in leaf area development.

VON CAEMMERER and FARQUHAR (1981) and CAMEJO et al. (2005) explained that the changes in the net rate of CO_2 assimilation reflect alterations in both stomatal conductance and/or mesophyll capacity for photosynthesis. Furthermore, in this study high temperature reduces stomatal conductance (gCO_2). This reduction might be due to the partial stomata closure, which increased resistance to diffusion of CO_2 from outside air to chloroplast.

Increased C_i in tomato cultivars under heat stress conditions was apart from the partial inhibition of the photosynthetic apparatus (enzymatic activity) (NKANSAH and ITO 1994). This confirms the findings of the present study.

Vegetative growth

Exposure of the different tomato cultivars to heat stress for prolonged periods reduced the vegetative growth in the present study.

Mean values across genotypes were higher at 37/22 °C than at 37/27 °C. This general response indicated a favourable effect of low night temperature on plant growth.

The cultivar 'Summerset' had the highest leaf area at 37/27 °C (day/night), while at 37/22 °C (day/night) regime 'Kervic F_1' and 'Summerset' had the highest leaf area and 'UC 82-B' the lowest values at both temperature regimes. This indicated that the heat tolerant cultivars had greater leaf area when compared to heat sensitive one under high temperature conditions, which are similar to those reported for tomatoes under similar conditions (NKANSAH and ITO 1994; ABDELMAGEED and GRUDA 2009).

In this study most of the heat tolerant cultivars had greater stem fresh and dry weight than the heat sensitive cultivar. This greater increase in stem fresh and dry weight of the heat tolerant cultivars may have resulted from its ability to produce more carbohydrates than the heat sensitive ones (NKANSAH and ITO 1994). Furthermore, the results for the leaf fresh weight and leaf dry weight of the cultivars were similar to that of the stem fresh weight and stem dry weight. These results are in agreement with result reported elsewhere by NKANSAH and ITO (1994).

Reproductive development

GRUDA (2005) reported that fruit vegetables will not remain generative enough during hot summer months. Plant growth become more and more vegetative due to higher temperatures and there is an abortion of flowers and young fruits and a reduction of pollen grains.

The results of the present study showed that continuous exposure of the tomato plants to heat stress markedly reduced the number of pollen grains produced and released by all cultivars tested. 'Summerset' produced the highest number of pollen grains and 'UC 82-B' the lowest one. Many authors reported that the heat tolerant cultivars had the ability to produce significantly higher number of pollen grains under heat stress conditions (SATO et al. 2000, 2006; FIRON et al. 2006; ABDELMAGEED and GRUDA 2007, 2009), this strengthens the results found in the present study.

The heat tolerant cultivar 'Summerset' had the highest fruit set percentage at both temperature regimes and the heat sensitive one 'UC 82-B' had the lowest percentage. Similar findings were reported by SATO et al. (2000, 2006) and was observed in 'UC 82-B' in a previous study (ABDELMAGEED and GRUDA 2007, 2009).

Heat stress markedly decreased the fruit fresh weight and the percentage of fruit set significantly in all eight cultivars. The proportion of parthenocarpic fruit, undeveloped and aborted flowers also increased (data not shown). The primary factor affecting fruit set under high-elevated temperature stress in 'UC 82-B' was considered to be a disruption of male reproductive development (SATO et al. 2000; ABDELMAGEED and GRUDA 2009). These results are in accordance with those of PEET et al. (1997) who showed that a low night time temperature could compensate for a high daytime temperature. Thus tomatoes would be expected to tolerate much higher daytime temperatures/lower night time temperatures than in higher day time/higher night time temperatures. Positive significant correlation between A and fruit set suggested that A might be used as an indicator of heat tolerance of tomatoes under heat stress conditions. In conclusion, the genotypic variations observed at the vegetative growth, generative phase and in the instantaneous gas exchange measurements in this study give some indications of superiority when comparing different tomato cultivars for fruit set under heat stress conditions. These cultivars also provide opportunities as genetic materials for breeding more heat tolerant cultivars adapted to high temperature stress conditions for further increases in productivity and extending the growing season. They may as well be important in physiological studies concerning the physiological basis of heat tolerance.

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