Relationship between Some Physiological Characters and Yield of Heat-Tolerant, Non-Tolerant, and Tropical Tomato Cultivars Grown at High Temperature

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Summary

The relationships between physiological characters; photosynthesis (P_r), transpiration (E), stomatal conductance (G_s), and yield of three heat-tolerant tomato (*Lycopersicon esculentum* Mill.) cvs. Shikiaka, Shuki and Ohio 7663, non heat-tolerant cv. Sataan; and two tropical cvs. Owusu-Bioh and Wosowoso, grown at 40°/23°C day/night temperatures were examined.

Physiological characters were measured at air temperatures of 20°, 30°, and 40°C. P_r for heat-tolerant cultivars pooled at the seedling stage (5 ~ 7 leaves) was significantly greater than non heat-tolerant cultivars at 20° and 40°C. P_r , E , and G_s at the flowering and early fruit development stage (13 ~ 15 leaves) were significantly higher in the heat-tolerant cultivars compared to the other cultivars at all temperatures. P_r at the seedling stage did not significantly correlate with yield but P_r , E and G_s were significantly correlated with fruit yield at the flowering and early fruit development stage. A linear relationship between P_r and G_s and between E and G_s revealed a close and significant consequential relationship between E and P_r . Regressions among physiological variables were not homogenous among/between cultivars. Regressions between P_r , E , G_s , and yield were heterogenous among/between cultivars. Heat-tolerant cultivars had greater yields than the other cultivars. The results indicate that yield significantly and positively correlated with P_r , E , and G_s .

Introduction

Physiological characters such as photosynthesis, transpiration and stomatal conductance affect growth and yield in crop plants. Photosynthesis ultimately limits crop productivity, however, its exact relationship with yield is unclear. Correlations between yield and photosynthesis are often inconsistent and not significant (Curtis et al., 1969; Evans, 1976; Gay et al., 1980; Peet et al., 1977). Wong et al. (1979) observed that stomatal conductance correlated with photosynthetic activity. The exact relationship between transpiration or stomatal conductance and yield in heat-tolerant and non heat-tolerant tomatoes are also not well defined.

The effect of high temperature on plant growth and yield through effects on these physiological characters in tomatoes cannot be over-emphasized.

At temperatures of about 30° ~ 35°C, heat-tolerant tomatoes had higher photosynthetic rate than sensitive cultivars (Bar-Tsur et al., 1985a). Transpiration is temperature dependent (Berry and Bjorkman, 1980) and leaf temperature effect on stomatal conductance has been reported for a number of plant species (Schulze et al., 1974).

The cultivation of heat-tolerant tomatoes in many tropical and summer areas is indispensable hence the relationship between photosynthesis, transpiration, stomatal conductance and yield in heat-tolerant tomatoes is deemed important.

The objective of this study was to evaluate the relationships between physiological characters especially photosynthesis, transpiration, stomatal conductance and yield in six tomato cultivars grown at high temperatures.

Materials and Methods

Six cultivars of tomato which differed in sensitivity to high temperature were used (Table 1).

Table 1. Tomato cultivars used in this experiment.

Cultivar	Heat susceptibility	Source
Shikiaka	HT ^z	Known You Seed Company, Taiwan
Shuki	HT	Known You Seed Company, Taiwan
Ohio 7663	HT	Agric. Res. and Devpt. Center, Ohio, USA
Owusu-Bioh	NT ^y	Crop Science Dept., Univ. of Ghana, Ghana
Wosowoso	NT	Crop Science Dept., Univ. of Ghana, Ghana
Sataan	NT	Takii Seed Company, Japan

^z HT indicates heat-tolerant^y NT indicates non heat-tolerant**Table 2.** Yield and yield attributes of six tomato cultivars.

Cultivar	Growth habit	Yield t. ha ⁻¹	Yield components		
			Fruit set (%)	Fruit no. no./plant	Fruit size g/fruit
Shikiaka	D ^y	20.33 d ^z	56.3 c	90.1 c	11.2 a
Shuki	I	12.83 c	33.3 b	42.6 b	15.1 ab
Ohio 7663	D	5.97 b	22.9 ab	5.6 a	53.6 bc
Sataan	I	2.30 a	7.4 a	2.0 a	60.0 c
Owusu-Bioh	I	0.64 a	3.0 a	1.1 a	26.5 abc
Wosowoso	I	1.07 a	2.7 a	1.7 a	28.9 abc

^z Mean separation within columns by Duncan's new multiple range test; 5% level.^y I=Indeterminate; D=Determinate

Seeds of these cultivars were sown on 4 May, 1990. Seedlings were grown in plastic pots (500 cm³) containing garden soil.

Seedlings were transplanted into soil in the greenhouse five weeks after seeds were sown. Plants were grown under natural daylight (14 ~ 15 hrs) at 40° ± 1°C maximum temperature and 23° ± 1°C night temperature. Plants were exposed to maximum day temperature during 10:00 am to 3:00 pm. On sunny days, photosynthetic active radiation (PAR) increased from 750 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ at 8.30am to about 1200 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ around noon before it gradually decreased to about 470 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ at 16:30pm. A fertilizer rate of 15 : 25 : 15kg/1,000 m² (N : P : K) and 80kg/1,000 m² CaCO₃ was applied to the soil. A randomized complete block design with three replications was used. Each experimental plot consisted of seven plants per cultivar with a spacing of 110 cm × 45 cm per plant. The inner five plants per treatment per plot were used for data collection hence 15 plants per variable were measured.

At the 5~7 leaf stage, five weeks after sowing, photosynthetic rate was measured in an assimila-

tion chamber using an infra-red gas analyzer (Shimadzu, URAS-2) as described by Ito (1971). Four plants/cultivar were used for each temperature treatment. Temperatures used for measurements in the chamber were 20°, 30°, and 40°C. Air flow rate was controlled at 7 liters · min⁻¹. Light source was high pressure sodium lamps of 420 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ photosynthetic photon flux density.

Leaf photosynthesis, transpiration, and stomatal conductance during flowering and early fruit development stage (13~15 leaves) were measured in the greenhouse with the use of a portable porometer (Kip-8510 Ver. 2.03, Koito Industries). A fully expanded, matured, and attached second or third leaf from the apex was used for measurement. Temperatures used for physiological measurements were the same as those used in growth chamber.

Pollination was carried out by means of wire vibration and no plant growth regulator was used for fruit set. Fruit number and fruit weight (kg) per plant per cultivar were calculated, at each harvest. Harvesting lasted for three months. Plants were topped at the seventh truss where the determinate cultivars terminated flowering.

Fig. 1. Effect of temperature on photosynthesis ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$) of six tomato cultivars at the seedling stage. Same letters within each measured temperature among cultivars are not significantly different by Duncan's new multiple range test, $P=0.05$.

Fig. 2. Effect of temperature on photosynthesis ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$) of six tomato cultivars at the flowering and early fruit development stage. Same letters within each measured temperature among cultivars are not significantly different by Duncan's new multiple range test, $P=0.05$.

The data were analyzed using analysis of variance procedure and means were separated at $P = 0.05$ by Duncan's new multiple range and the paired T-tests. The relationship between yield and physiological characters (P_r , E , G_s) were described

with linear regression analysis. Homogeneity of regressions to compare slopes between physiological variables and yield among cultivars were evaluated using a technique outlined by Gomez and Gomez (1984). Since slopes between the tropical

and non heat-tolerant were homogeneous, they were classified as conventional cultivars.

Results

Yield and yield components

Results in Table 2 indicate that, 'Shikiaka' had the highest yield, fruit set, and number followed by 'Shuki' and 'Ohio 7663'. The heat-tolerant cultivars, 'Shikiaka', 'Shuki' and 'Ohio 7663' differed significantly from the conventional cultivars in terms of yield and percent fruit set.

Photosynthesis, transpiration, and stomatal conductance response to temperature

Photosynthetic rate (P_r) at the seedling stage (5 ~ 7 leaves) decreased from 20° to 40°C (Fig. 1 and Table 3). Heat-tolerant cultivars showed higher P_r at 20° and 40°C. P_r varied significantly among the cultivars. 'Ohio 7663' had the highest P_r at all temperatures and 'Sataan' had the lowest at 20° and 30°C, and 'Wosowoso' the lowest at 40°C.

At the flowering and early fruit development stage (13 ~ 15 leaves), P_r in all cultivars increased from 20° to 30°C and declined at 40°C (Fig. 2 and Table 3). Transpiration rate (E) increased as temperature was increased from 20° to 40°C (Fig. 3 and Table 3) while stomatal conductance (G_s) decreased at 40°C (Fig. 4 and Table 3). Results in

Table 3. Effect of temperature on photosynthesis (P_r), transpiration (E), and stomatal conductance (G_s) of tomatoes.

Cultivar	Temperature (°C)		
	20	30	40
P_r ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$) at seedling stage			
Heat-tolerant	8.30	6.84	3.09
Conventional	7.39	5.99	2.60
Paired T-test ^z	*	NS	*
P_r ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$) at flowering and early fruiting stage			
Heat-tolerant	11.65	17.73	13.12
Conventional	9.26	13.91	11.00
Paired T-test ^z	***	***	***
E ($\text{mmol} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$) at flowering and early fruiting stage			
Heat-tolerant	0.79	2.91	3.95
Conventional	0.64	2.41	3.29
Paired T-test ^z	**	*	*
G_s ($\text{cm} \cdot \text{sec}^{-1}$) at flowering and early fruiting stage			
Heat-tolerant	0.15	0.35	0.30
Conventional	0.13	0.30	0.20
Paired T-test ^z	*	**	**

^z NS, *, **, ***: Nonsignificant or significant at $P = 0.05$, 0.01 and 0.001, respectively

Fig. 3. Effect of temperature on transpiration ($\text{mmol} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$) of six tomato cultivars at the flowering and early fruit development stage. Same letters within each measured temperature among cultivars are not significantly different by Duncan's new multiple range test, $P=0.05$.

Fig. 4. Effect of temperature on stomatal conductance ($\text{cm}^2 \cdot \text{sec}^{-1}$) of six tomato cultivars at the flowering and early fruit development stage. Same letters within each measured temperature among cultivars are not significantly different by Duncan's new multiple range test, $P=0.05$.

Figure 2 indicate that, at the flowering and initial fruit development stage, P_r of 'Shikiaka', 'Shuki', and 'Ohio 7663' were greater than that of the conventional cultivars at 20° and 30°C. At 40°C 'Ohio 7663' did not differ from 'Wosowoso' and 'Sataan' although its P_r value was numerically higher.

Cultivar and temperature effects on E and G_s measured at the flowering and early fruit development stage differed among cultivars (Figs. 3 and 4). At 20 °C, E for 'Owusu-Bioh' did not differ from the heat-tolerant lines while at 30°C and 40°C, E was greater in all the heat-tolerant cultivars compared to 'Owusu-Bioh' and 'Sataan' (Fig. 3). G_s at 20°C was greater for two of the heat-tolerant cultivars, 'Shikiaka' and 'Ohio 7663'. At 30°C, G_s was greater in all the heat-tolerant cultivars compared to the other cultivars, but at 40°C, 'Wosowoso' did not differ from two of the heat-tolerant lines, 'Shikiaka' and 'Shuki' (Fig. 4).

When physiological characters for all heat-tolerant cultivars were pooled and compared to the conventional cultivars (Table 3), P_r of the former was significantly higher than the latter at 20°C and 40 °C at the seedling stage. At the flowering and fruit development stage, P_r , E , and G_s of the heat-tolerant cultivars were higher than the conventional cultivars at all temperatures.

Relationship between physiological characters and Yield

Correlations of P_r , E , and G_s on yield at the flowering and early fruit development stage were significant at all three temperature levels but only results at 40°C are presented (Table 4). Correlations for P_r on yield at the seedling stage was non-significant (data not shown). Yield correlated significantly with photosynthesis at the flowering and early fruit development stage (Table 4). There was a significant positive relationship between yield and E as well as with G_s among cultivars (Table 4).

Results in Table 4 also indicate that, G_s (X) and P_r (Y), and G_s (X) and E (Y) were correlated among cultivars. The correlation between G_s and P_r or E resulted in a consequential close and significant relationship between E (X) and P_r (Y).

Heterogeneity in regression coefficients was observed between the heat-tolerant and conventional cultivars except E on yield at 40°C. The increase in yield due to P_r and G_s was greater in the former than in the latter cultivar (Table 5).

Regressions among P_r , E , and G_s were heterogeneous between heat-tolerant and conventional cultivars at the measured temperatures (Table 5). Slopes were greater in the former than the latter

at 20° and 30°C but, at 40°C, G_s on P_r or E was greater for the conventional cultivars (Table 5).

Discussion

Photosynthesis, transpiration, and stomatal conductance were affected by high temperature. The decrease in photosynthesis at 40°C may be due to enzyme inhibition and increased resistance to CO_2 diffusion from the outside air to the chloroplast as a result of partial stomatal closure.

The lower photosynthetic activity in young tomato plants (5~7 leaves) may be attributed to a

photosynthetic system that may not yet be completely developed, high rates of dark respiration (Valanne et al., 1981) and low stomatal and intracellular conductances for CO_2 transfer.

The higher rate of photosynthetic activity of leaves at the flowering and early fruit development stage (13~15 leaves) compared to those of leaves at the seedling stage indicate that, the presence of flowers and fruits positively stimulates the photosynthetic activity of leaves, probably by enhancing the rate at which the products of photosynthesis are translocated from the production sites. This agrees with the works of Maggs (1963) and Hall and Brady (1977) who observed that the presence of fruits enhances the photosynthetic activity of leaves.

The higher photosynthetic rate for the heat-tolerant cultivars compared to the conventional cultivars at the seedling and the flowering and early fruit development stages (Table 3) may be due to their different physiological trait such as an efficient photosynthetic apparatus and wider stomatal opening which contribute to their tolerance especially at high temperatures. Bar-Tsur et al. (1985a) reported higher photosynthetic activity for heat-tolerant cultivars than for sensitive ones.

The lower transpiration rates at 20°C indicated the possibility of increased resistance to water flow into and through the plant (Fig. 3). The data also indicate that temperature may reduce photosynthesis while stomata are still open. Thus an increase in transpiration but a decrease in photo-

Table 4. Regression equations and correlations between yield and photosynthesis (P_r), transpiration (E), stomatal conductance (G_s), and fruit set (FS) and the relations among physiological characters measured at 40°C at the flowering and early fruit development stage of six tomato cultivars.

Variable	Equation	R	R ²
Pr on Yield	$Y = -57.66 + 5.39 X$	0.95*** ^z	0.90
E on Yield	$Y = -40.49 + 13.05 X$	0.69***	0.48
G_s on Yield	$Y = -19.65 + 97.64 X$	0.48***	0.23
FS on Yield	$Y = -0.51 + 0.37 X$	0.95***	0.90
Relationship among physiological variables			
G_s on Pr	$Y = 6.33 + 20.76 X$	0.49***	0.24
G_s on E	$Y = 0.93 + 9.90 X$	0.72***	0.51
E on Pr	$Y = 2.76 + 2.54 X$	0.63***	0.41

^z *** Significant at $P=0.001$

Table 5. Regression coefficients between yield (Yd) and physiological characters and among physiological characters of tomato cultivars at the flowering and early fruit development stage. Slopes were evaluated using a technique outlined by Gomez and Gomez (1984).

Temperature (°C)	Cultivar	Yd and Pr	Yd and E	Yd and G_s	E and Pr ($\times 10^{-2}$)	G_s and Pr ($\times 10^{-2}$)	G_s and E ($\times 10^{-2}$)
20	HT ^y	1.96	19.25	78.34	10.20	2.51	24.60
	CC ^x	0.94	11.72	47.50	8.10	1.97	24.50
Significance ^z		**	**	**	**	**	**
30	HT ^z	2.66	5.37	53.15	50.00	5.00	10.10
	CC ^y	1.21	2.31	34.04	54.60	3.70	6.90
Significance		**	**	**	ns	**	**
40	HT ^z	1.97	4.04	53.45	48.70	3.70	7.60
	CC ^y	0.98	4.89	23.13	20.00	4.30	21.40
Significance		**	NS	**	**	**	**

^z **, NS : Significant at 1% and nonsignificant respectively according to t-test with 26 df.

^y Pooled heat-tolerant cultivars.

^x Pooled tropical and non-tolerant cultivars.

synthesis at higher temperatures (Table 3). This agrees with Bar-Tsur et al. (1985b) who observed that, photosynthesis decreased while transpiration increased with temperature up to 39°C.

The higher transpiration rates of the heat-tolerant cultivars may have some ecological significance concerning tolerance to hot, humid conditions. An increase in stomatal conductance may confer several adaptive advantages. Open stomata would enhance evaporative cooling at high temperatures (Schulze et al., 1973) and high photosynthesis at optimum air temperatures (Al-Ani et al., 1972).

The lack of correlation between photosynthesis and yield at the seedling stage may be attributed to an incomplete photosynthetic system (Leopold and Kriedemann, 1975; Sams and Flore, 1982).

The significant and positive correlation between photosynthesis and yield at the flowering and early fruit development stage (Table 4) contrasts earlier reports that, correlations between yield and photosynthesis are often inconsistent and not significant (Curtis et al., 1969; Evans, 1976; Gay et al., 1980; Peet et al., 1977). The reason may be attributed to the no significant differences they observed in CO₂ uptake between the high and low yielding soybeans they used. However, we found significant differences in photosynthesis between the heat-tolerant and conventional tomato cultivars (Table 3).

The correlation between stomatal conductance and photosynthesis or transpiration which resulted in a consequential close and significant relationship between transpiration and photosynthesis (Table 4) agrees with other reports (Hamid et al., 1990; Raschke, 1975).

The higher regression coefficients of the heat-tolerant cultivars compared to the conventional ones when photosynthesis was regressed on yield indicates that, higher yields were associated with higher photosynthesis in the former cultivars. Fruit set correlated significantly with yield (Table 4). Yield variation was partly due to percentage fruit set. Fruit set was much better in the heat-tolerant cultivars than in the conventional ones at high temperatures. The evidence that the heat-tolerant cultivars are better adapted to high temperature indicates a possible linkage between fruit set and continued photosynthesis at high temperatures.

In this experiment, we found that yield correlated significantly and positively with photosynthesis, transpiration and stomatal conductance. Higher photosynthetic activity, transpiration, stomatal conductance, fruit set and yield were associated with the heat-tolerant cultivars compared to the conventional ones. In view of these findings, we may recommend these heat-tolerant cultivars for tomato cultivation in the hot humid tropics and areas with high summer temperature 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. They may as well be important in physiological and biochemical studies concerning the molecular basis of heat tolerance.

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高温条件下で生育した耐暑性、非耐暑性ならびに熱帯性トマト品種の生理的特性と収量

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摘 要

耐暑性トマト品種‘四季紅’、‘朱喜’、‘Ohio 7663’、非耐暑性トマト品種‘サターン’、ならびに熱帯性品種‘Owus-Bioh’、‘Wosowoso’を昼温 40°/夜温 23°C で栽培し、光合成速度 (P_r)、蒸散速度 (E)、気孔コンダクタンス (G_s)、水利用効率などの生理的特性と収量との関係を調査した。生理的特性はそれぞれ 20°, 30°, 40°C の条件下で測定した。幼苗期の耐暑性トマト品種における光合成速度は、非耐暑性品種に比べ、20° と 40°C で高かった。開花期および果実肥大初期の P_r 、 E 、 G_s は、耐暑性品種が他の品種より、すべての温度条件で高かった。幼苗期の光合成速度と収量との間には、統計的有意差は認められなかったが、開花期、果

実肥大初期の P_r 、 E 、 G_s のそれぞれと収量との間には、有意な相関関係が認められた。 P_r と E 、ならびに E と G_s との間には直線的な相関関係が認められ、その結果、光合成速度と蒸散速度は高い相関を示した。生理的特性を示す各数値間の回帰式は、品種により異なった。また、 P_r 、 E 、 G_s のそれぞれと収量との間の回帰式も、品種間で一定ではなかった。耐暑性トマト品種は他の品種に比べて高温条件下で高い収量を得ることができた。以上の結果、収量と光合成、蒸散速度、および気孔コンダクタンスの間には、統計的に有意な正の相関関係が存在することが明らかとなった。