Effect of Water Stress on Growth, Yield and Eco-Physiological Responses of Four Tomato (*Lycopersicon esculentum* Mill.) Cultivars

S.M. Lutfor Rahman, Eiji Nawata and Tetsuo Sakuratani

Division of Environmental Science and Technology, Kyoto University,

Kitashirakawa, Oiwake-cho, Sakyo-ku, Kyoto 606-8502

Summary

The effect of water stress on the growth, yield, and various morphological characteristics related to yield and eco-physiological responses of tomato was studied in two drought-tolerant cultivars, 'TM 0126' (TM) and 'VF-134-1-2' (VF) and two drought-sensitive ones, 'Kyokko' (KK) and 'Ratan' (RT). Water stress decreased yield, flower number, fruit set percentage and dry matter production in all cultivars, but the reduction was greater in drought-sensitive cultivars than in tolerant ones. Photosynthetic rate (Pr), transpiration rate (Tr), leaf water potential (Ψ_w), and water use efficiency (WUE) were reduced, and leaf temperature (Tl) and stomatal resistance (r_s) were increased by water stress in all cultivars. The reduction of Pr , Tr , Ψ_w and WUE , however, was less pronounced in tolerant cultivars than in sensitive ones, whereas the increase of Tl and r_s was more conspicuous in tolerant cultivars than in sensitive ones. After re-watering, all these eco-physiological responses returned to near normal state, but the recovery was more rapid and complete in tolerant cultivars than in sensitive ones. The better performances of tolerant cultivars under water stress and recovery after re-watering are attributed to the ability of plants to maintain a better water status and minimize the reduction of photosynthesis.

Key Words: drought tolerance, photosynthesis, tomato, water relation, yield.

Introduction

Tomato (*Lycopersicon esculentum* Mill.) is one of the most economically important vegetables in the world: in Asia, approximately 25 million metric tons are produced every year on about 1 million hectares (Anonymous, 1995). Tomato production in the tropical and subtropical Asia tends to be seasonal. Peak production occurs in the early dry season, when slightly lower temperatures and moderate rainfall favor tomato growth in the lowlands (<200m above sea level). Most tomato production shifts to the highlands (>700m above sea level) in summer, when hot and dry conditions prevail in the lowlands. Declining tomato supply to markets in summer results in drastic price increases. Promoting lowland summer tomato production may help to reduce tomato prices and alleviate pressure to open highland areas for the production of vegetables including tomato. For this purpose, cultivars tolerant to drought and heat are expected to be developed in tropical Asia, including Bangladesh.

A shortage of water limits plant growth and crop productivity most seriously in arid and semi-arid regions (Boyer, 1982). Water deficit reduces photosynthesis by inhibiting leaf growth, closing stomata and decreasing the efficiency of carbon fixation (Kramer,

1983). A reduction in the rate of photosynthesis in drought-stressed plants has usually been attributed chiefly to closure of stomata, but drought stress severe enough to cause stomatal closure simultaneously causes inhibition of CO_2 fixation by injuring the photosynthetic machinery (Farquhar and Sharkey, 1982; Keck and Boyer, 1974). Genetic improvement of drought-tolerant cultivars could establish a tomato culture in these areas during summer. An understanding of the mechanism involved in drought tolerance may contribute to efficient breeding for drought tolerant cultivars in tomato (Pillay and Beyl, 1990).

We reported previously that water stress significantly reduced tomato growth and yield, from which study we selected some tolerant cultivars that could stabilize yield under water stress conditions (Rahman et al., 1997). This study was conducted to investigate the effect of water stress on growth, yield, and eco-physiological responses in four tomato cultivars and to compare the mechanism of water stress tolerance between tolerant and intolerant cultivars.

Materials and Methods

Four tomato cultivars which differed in sensitivity to water stress were used. 'Kyokko' (KK) was obtained from Musashi Plant Breeding Corp., Japan, 'TM 0126' (TM) from Asian Vegetable Research and Development Center (AVRDC) in Taiwan, 'VF-134-1-2' (VF) from

the USA (through Khon Kaen University in Thailand), and 'Ratan' (RT) from Bangladesh (developed by Bangladesh Agricultural Research Institute, Gazipur). KK and RT are considered to be sensitive to water stress, whereas TM and VF are tolerant (Anonymous, 1995; Rahman et al., 1997).

Seeds were sown in vermiculite on March 3, 1996, in a phytotron under natural daylight and 30/25 °C (day/night) temperature regime. On March 18, seedlings were transferred to 23/18 °C (day/night) temperature regime. On March 21, they were transplanted to plastic pots, 9cm in diameter, containing soil mixture of organic matter, sand and perlite (1:2:1, v/v/v); they were grown in a plastic greenhouse. On April 10, they were re-transplanted to 30cm plastic pots filled with the same soil mixture and 10g slow-release granular fertilizer containing 14 %N, 12 % P₂O₅, and 12 % K₂O. The pots were well-watered until plants were subjected to water stress. Ambient temperatures fluctuated between 15 and 35 °C during the experiment.

A half strength of "Enshi" solution (Yamasaki, 1982) for macro elements and "Arnon" solution (Arnon and Hoagland, 1940) for micro elements were applied three times a week after transplanting to 30 cm pots except for the treatment period. Five grams of the above slow-release granular fertilizer were applied at the start of the treatment. All plants were spaced 75cm apart in rows and 60 cm between rows. Plants were not topped and supported by plastic poles.

On 51st day after sowing (April 23, 1996), when the plants were flowering and at the early fruit development stage of the first truss, each pot was brought to field capacity with 500 ml of water. Then the plants were divided into two groups; in one group they were water-stressed by withholding irrigation completely, whereas the other group was watered adequately as needed and served as control. Water-stressed plants were re-watered when severe wilting symptoms persisted throughout the night. Days of water withholding period (*DWW*) were recorded for each cultivar. After re-watering, the recovery from the damage caused by water stress was carefully observed.

Photosynthetic rate (*Pr*), transpiration rate (*Tr*), stomatal resistance (*r_s*), and leaf temperature (*TL*) on the

4th or 5th fully developed leaf from the apex were measured with a portable photosynthesis apparatus (model LI-6200, LICOR inc., USA). The data were collected from 11.00 to 13.00 under full sun (more than 800 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (400 to 700nm)). Water use efficiency (*WUE*) was calculated by dividing *Pr* by *Tr* (Nobel, 1991). Leaf water potential (Ψ_w) was measured immediately after determining *Pr*, *Tr*, *r_s*, and *TL*, using the same leaves by a pressure-bomb technique (Tyree and Hammel, 1972).

Fruit number, the setting percentage, average fruit weight, and yield of the first truss were measured between June 3 and 20, 1996 (40 to 57 days after the onset of the treatment). Flower number (first truss) per plant was also recorded. When the yield determination of the first truss was terminated, the plants were dried in an oven at 80 °C for 96 hours, and the shoots and roots weighed separately. The top to root ratio (*T/R*) was calculated by dividing shoot dry weight by that of the root.

To compare the relative performance between cultivars, the following statistic was calculated for all characteristics related to yield and vegetative growth.

Relative performance (RP)

$$= \frac{\text{Performance under stress}}{\text{Performance under control condition}} \times 100$$

Plants were arranged in a factorial design with six replications, a single plant representing one replication. Data were analyzed by the analysis of variance and the means were separated by Student's *t*-test. Arc-sine transformation was made for the percentage data such as fruit set, according to Steel and Torrie (1960).

Results

DWW of VF and TM were significantly longer than that of RT and KK (Table 1). Tip burn-like symptoms and shrinkage of the leaves in water-stressed plants were observed during the treatment period. When the water-stressed plants were re-watered, plants recovered rapidly from wilting and leaf shrinkage. Recovery took only a few hours in TM and VF, but longer in KK and RT.

Shoot and root dry weight were significantly de-

Table 1. Effects of water stress on growth, top / root ratio and days of water withholding period (*DWW*) in four tomato cultivars.

Cultivars ^z	Shoot dry weight (g)			Root dry weight (g)			T / R ratio		<i>DWW</i> (days)
	Cont.	Stress	RP ^y (%)	Cont.	Stress	Rp (%)	Cont.	Stress	
KK	16.9Aa ^x	12.0Bb	71.1	9.9Ba	6.2Bb	63.1	1.71Ab	1.92Aa	11.2B
RT	9.9Ca	5.7Cb	58.2	6.1Da	2.9Cb	49.2	1.65Ab	1.97Aa	9.3C
TM	16.2Aa	13.5Ab	83.8	11.2Ab	8.8Ab	79.1	1.45Bb	1.53Ba	12.8A
VF	14.7Ba	11.6Bb	79.1	9.1Ca	6.5Bb	70.8	1.81Aa	1.62Ab	13.3A

^z KK: 'Kyokko', RT: 'Ratan', TM: 'TM0126' and VF: 'VF-134-1-2'.

^y RP: Relative performance, performance under stress / performance under control condition x 100.

^x Means with different capital and small letters are significantly different among cultivars and between treatments respectively at *p*=0.05.

Table 2. Effects of water stress on yield and various characteristics related to yield on the first truss in four tomato cultivars.

Cultivars ²	Yield (g)			Flower No.			Fruit No.		
	Cont.	Stress	RP ^y (%)	Cont.	Stress	RP (%)	Cont.	Stress	RP (%)
KK	864.2Aa ^x	288.2Bb	33.4	10.0Ba	6.1Bb	61.0	6.0Ba	3.2Bb	52.8
RT	344.7Ca	89.3Db	25.9	8.0Ca	4.0Cb	50.0	5.0Ba	2.1Bb	42.4
TM	643.2Ba	445.1Ab	69.2	15.0Aa	13.0Aa	86.6	9.0Aa	7.3Aa	81.1
VF	346.8Ca	227.8Cb	65.7	15.0Aa	12.0Ab	80.0	7.7Ba	6.1Ab	79.9

Cultivars ²	Fruit Set %			Fruit weight (g)		
	Cont.	Stress	RP (%)	Cont.	Stress	RP (%)
KK	60.3Aa	50.3Ab	83.5	154.8Aa	95.1Ab	61.4
RT	62.5Aa	52.2Ab	83.6	69.2Ba	42.1Cb	60.6
TM	62.5Aa	52.2Ab	94.9	71.5Ba	60.2Bb	84.3
VF	53.3Aa	52.1Aa	97.6	43.2Ca	36.2Db	83.8

² KK : 'Kyokko', Rt : 'Ratan', TM : 'TM0126' and VF : 'VF-134-1-2'.

^y RP : Relative performance, performance under stress / performance under control condition x 100.

^x Means with different capital and small letters are significantly different among cultivars and between treatments respectively at p=0.05.

creased by the water stress treatment, with the exception of root dry weight of TM (Table 1). TM and VF had relatively small growth reduction in comparison to that of KK and RT. T/R ratio was increased by water stress except for VF (Table 1); it was significantly lower in TM under both soil moisture conditions than the other cultivars. There was a tendency for T/R ratio of TM and VF grown under water stress to be lower than that of KK and RT.

Water stress significantly reduced yield in the first truss of all cultivars (Table 2), but the extent of the reduction was different among them. In TM and VF, yield reduction was small as compared with that in KK and RT. The total number of flowers, fruit formed, and fruit set percentage were reduced slightly or unaffected by the water stress treatment in TM and VF, whereas they were markedly reduced in KK and RT (Table 2). Flower bud abscission occurred in stressed plants in all cultivars. The reduction in fruit weight by water stress was also less appreciable in TM and VF than it was in KK and RT (Table 2).

Pr was reduced markedly by the water stress treatment during the first 3 days and gradually thereafter in all cultivars (Fig. 1a); that of KK and RT was lower than TM and VF. After re-watering, it increased rapidly to the value of control plants within 2 to 4 days in TM and VF, but it stayed far below the control value in KK and RT even after 4 days.

A significant reduction of *Tr* by the water stress treatment occurred in all cultivars (Fig. 1b). In KK and RT, the initial reduction of *Tr* was more pronounced than that in TM and VF. After re-watering, it rapidly increased in all cultivars; in VF and TM the increase was more rapid than it was in KK and RT. Four days after re-watering, stressed plants of TM and VF reached

the control value, while those in RT and KK did not.

r_s of leaves as affected by water stress was also different between drought-tolerant and -sensitive cultivars (Fig. 1c). r_s increased sharply during the initial 3 days of the water stress treatment in all cultivars and then became almost constant in the sensitive-cultivars (KK and RT), whereas in tolerant cultivars (TM and VF), r_s continued to increase until the end of the treatment. Consequently, the maximum r_s of water-stressed leaves was much larger in the latter than in the former. Upon re-watering, r_s was reduced to the control value in TM and VF, whereas it was still larger than the control value in KK and RT plants even 4 days later.

The *tl* in control plants of TM and VF was higher than that of KK and RT during the experimental period (Fig. 1d). *tl* in stressed plants of all cultivars was increased by the water stress treatment; it was more pronounced in TM and VF than it was in KK and RT. After re-watering, *tl* decreased to the control value in all cultivars.

WUE was reduced by water stress in all cultivars, but it rapidly returned to the control level or became higher than the control after re-watering (Fig. 2a). Stressed plants of TM and VF showed higher average *WUE* during the water withholding period (TM: 2.81, VF: 2.56 mg CO₂/gH₂O) than did those of KK and RT (KK: 2.02, RT: 2.26 mgCO₂/gH₂O).

Significant reduction of Ψ_w was induced by the water stress treatment in the four cultivars (Fig. 2b). Ψ_w was decreased more sharply in KK and RT than it did in TM and VF. The lowest Ψ_w was higher in TM and VF than in KK and RT. Ψ_w in stressed plants of TM and VF returned to near control values 2 days after re-watering, while Ψ_w in KK and RT was still below the control value even 4 days after re-watering.

Fig. 1. Effect of water stress on a) photosynthetic rate (Pr), b) transpiration rate (Tr), c) stomatal resistance (r_s), and d) leaf temperature (WUE) in four tomato cultivars. DAT and DAW represent days after treatment and days after re-watering, respectively. KK, RT, TM and VF represent 'Kyokko', 'Ratan', 'TM 0126' and 'VF-134-1-2', respectively. Bar indicates the standard error.

Discussion

Tolerance to drought stress is an important characteristic for tomatoes grown in tropical regions, where they are subjected occasionally to a limitation of water (Boyer, 1982). In this study, four tomato cultivars were examined for their tolerance to drought, by comparing

the changes in eco-physiological responses during and shortly after short-term water stress and those in growth and yield after the stress. Drought-tolerant TM and VF, responded by exhibiting better growth and yield than the less tolerant KK and RT. Reduction of plant growth and yield by water stress was much smaller in TM and VF than it was in KK and RT. The results agree well with

Fig. 2. Effect of water stress on a) water use efficiency (WUE) and b) leaf water potential (Ψ_w) in four tomato cultivars. DAT and DAW, and KK, RT, TM and VF: same as in Fig. 1. Bar represents the standard error.

our previous study (Rahman et al., 1997).

TM and VF tolerated water stress for a longer period (DWW in Table 1) and exhibited a slower reduction of Ψ_w , but recovered faster after water stress than did KK and RT (Fig. 2b). These results indicate that drought-tolerant cultivars performed better with respect to growth and yield, which we attribute to the better maintenance of water status during the stress period and a more rapid recovery to normal water status after re-watering. These characteristics are considered to be very important for drought-tolerant cultivars, as shown in maize (Saneoka et al., 1996), rice (Fukai and Cooper, 1995), soybean (Hida et al., 1995) and chilli pepper (Techawongstien et al., 1992).

The stomata of stressed drought-tolerant plants closed, responding a small decrease in water potential and they exhibited a higher r_s during the stress period (Fig. 1c). This closure suppresses excess water loss by transpiration from the plant and may have helped stressed plants of tolerant cultivars to maintain higher Ψ_w . The ability to keep a better water status in tolerant cultivars is likely to: 1) prolong normal metabolism under stress conditions (Kramer, 1983); 2) lead to smaller reduction of Pr ; 3) rapid recovery after re-watering and 4) cause a smaller reduction of growth and yield thereafter.

In addition to Pr , Tr was also higher in stressed plants of tolerant cultivars than it was in sensitive ones during the stress period (Fig. 1b), which seems to be incon-

sistent with the fact that r_s in stressed plants of tolerant cultivars remained larger than that in sensitive ones (Fig. 1c). Leaf temperatures in both control and stressed plants of tolerant cultivars were usually higher than those in sensitive ones during the experimental period (Fig. 1d). The higher leaf temperatures may have resulted in a higher saturation deficit between the leaves and the surrounding air, thus promoting higher Tr . It is known that high leaf temperature induces the rise of transpiration, even though r_s is high (Jones, 1992). Although Tr in stressed plants of tolerant cultivars was higher than that in sensitive ones, Ψ_w remained higher. This may occur partly because the tolerant cultivars maintain a higher activity in root water uptake than the sensitive ones, as indicated by their low T/R ratio (Table. 1) (Tanaka and Arima, 1996). Further studies on the role of root function in drought tolerant cultivars are required.

In all cultivars, Pr in stressed plants rapidly recovered after re-watering (Fig. 1a) and the value of WUE also returned rapidly to the control level (Fig. 2a). These results suggest that photosynthetic machinery of the cultivars was not adversely affected by the degree of water stress imposed. The slow Pr recovery in stressed plants of sensitive cultivars after re-watering is attributed to the time required for complete recovery of plant water status.

WUE during water withholding period in stressed plants of tolerant cultivars was higher than that in

sensitive cultivars (Fig. 2a) which may be an important characteristic for drought-tolerant plants to maintain photosynthetic activity to some extent under water stress conditions.

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トマト4品種の生育、収量および生理生態的特性に及ぼす水ストレスの影響

S. M. Lutfor Rahman・縄田栄治・桜谷哲夫

京都大学農学研究科 606-8502 京都市左京区北白川追分町

摘 要

トマトの収量、収量構成要素、栄養生長および生理生態的特性に及ぼす水ストレスの影響を調査した。耐乾性の大きい TM0126 (TM) と VF-134-1-2 (VF) および耐乾性の小さい 旭光 (KK) と Ratan (RT) の4品種を供試した。収量、収量構成要素および乾物生産は断水処理によって与えた水ストレスにより低下したが、耐乾性品種では低下の程度がより小さかった。光合成速度 (Pr)、蒸散速度 (Tr)、葉の水ポテンシャル (Ψ_w) および水利用効率 (WUE) も水ストレスにより低下した。葉温 (TI) ならびに気孔抵抗 (r_s) は水ストレスにより上昇した。以上の水ストレスに対する生理生態的特性の反応のう

ち、 Pr , Tr , Ψ_w および WUE の水ストレスによる低下は耐乾性品種の方が小さかったが、水ストレスによる TI ならびに r_s の上昇は耐乾性品種の方が大きかった。また、再灌水後これらの生理生態的特性はすみやかに回復へ向かったが、耐乾性品種の方が回復が早く、回復の程度も大きかった。耐乾性品種において水ストレスによる生育・収量の低下が小さかったのは、水ストレス下で比較的良好な水分状態を維持し、光合成の低下を抑え、再灌水後に速やかに生育を回復させる能力をもっているためと考えられる。