Effects of Temperature and Water Stress on Growth, Yield and Physiological Characteristics of Heat-tolerant Tomato

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

Graduate School of Agriculture, Kyoto University, Oiwake-cho, Kitashirakawa, Sakyo-ku, Kyoto, 606-8502 Japan

Abstract The effects of temperature and water stress on agronomic and physiological characteristics were studied in heat-tolerant tomato cultivar TM 0126. Water stress significantly reduced yield, flower number, fruit weight, fruit number, pollen germination percentage, and shoot and root dry weight. High temperature (HT, 30/25°C day/night) significantly reduced yield, pollen germination percentage, shoot and root dry weight. No statistical interaction between the effect of water stress and temperature regimes was observed for yield, yield components, pollen germination percentage, shoot and root dry weight. A more pronounced decrease in the photosynthetic rate (Pr) by the water stress treatment was detected under HT than under MT (moderate temperature regime, 23/18°C day/night), but after re-watering a more rapid increase of Pr was observed under HT than under MT. A similar tendency was found in the effect of water stress on the transpiration rate (Tr). Stomatal resistance (Rs) was significantly higher under HT than under MT, but the increase by water stress was more remarkable under MT than under HT. Leaf water potential (Ψ) was significantly reduced by the water stress treatment under both temperature regimes. The absence of interaction between water stress and temperature for some agronomic characteristics of this cultivar may be caused by the rapid recovery of physiological characteristics after re-watering. Mechanism of drought and high temperature tolerance of TM 0126 was discussed.

Key words Photosynthesis, Pollen germination, Stomatal resistance, Tomato, Transpiration, Water stress

Introduction

In the tropics, it is generally recognized that water stress, irrespective of duration, adversely affects growth and yield of tomato. Rudich and Luchinsky reported that water plays an important role in determining the yield of tomato (Lycopersicon esculentum Mill.). High temperature also limits field production of tomatoes. Hot ambient conditions are known to retard flower initiation, reduce pollen viability and induce malformation of flower organs, resulting in poor fruit setting and low yield. High temperature also decreases photosynthetic rates by damaging the photosynthetic apparatus, leading to low productivity. In the lowlands of the tropics, both water stress and high temperature are one of the major limiting factors for tomato production. In Bangladesh, breeding of tomato cultivars tolerant to these stresses is an urgent problem.

Although a large number of studies have been carried out on the effects of water...
stress and high temperature on tomato growth, yield and several physiological characteristics\(^6,7,11,18\), the interaction of these factors has been seldom examined. The effect of short-term or long-term water stress on tomato growth and yield is considered to be affected by the ambient temperature and should be investigated, in order to analyze the responses of tomato plants to drought and heat, and to elucidate the mechanisms of tolerance to these stresses.

In the previous study\(^14\), we evaluated several tomato cultivars for drought tolerance and TM 0126 showed a superior tolerance to water stress during the seedling stage. This cultivar is known to be heat tolerant, too (MONOWAR, 1995, personal communication). In the present study, using this cultivar, we aimed at determining how the effect of water stress on tomato growth, yield and several physiological characteristics is affected by the ambient temperature and discussing the mechanism of the tolerance of this cultivar to drought and high temperature.

**Materials and Methods**

Tomato cultivar TM 0126 (collected from AVRDC, Taiwan) was used as a material. The experiment was carried out from September 6, 1995 to January 30, 1996 in a phytotron (natural sunlight conditions) at Kyoto University, Japan. Seeds were sown in plastic beds filled with vermiculite, after sterilization with Benlate, a commercial fungicide (Dupont Ltd., France). During the initial 20 day period, the seedlings were grown under a 30/25°C day/night temperature regime. The seedlings were then transplanted into 9 cm plastic pots filled with vermiculite and grown under the same conditions. Twenty days after the first transplanting (October 16, 1995), they were re-transplanted to 40 cm plastic pots filled with a soil mixture of perlite, sand and organic matter in a ratio of 1 : 2 : 1. Plants were then divided into two groups. One group was kept under a 23/18°C day/night temperature regime (moderate temperature treatment, MT). The other group was kept under a 30/25°C day/night temperature regime (high temperature treatment, HT). Fifteen grams of slow release fertilizer (a 100 days type), containing 14% N, 12% P\(_2\)O\(_5\), and 14% K\(_2\)O was applied to each pot. Plants were irrigated three times a week with half strength of “Enshi” (for macro nutrients\(^20\)) and “ARNON” (for micro nutrients\(^2\)) solution except for the treatment period. During the treatment period, the slow release granular fertilizer described above was used.

In addition to the temperature treatments, water stress treatments were imposed. Control plants were watered as and when necessary. Water stress was induced by withholding water completely. When severe wilting symptoms persisted throughout the night, plants were re-watered. Days of water withholding period (DWW) were recorded. Water stress treatment was started on November 4, 1995, when plants were flowering and at the early fruit development stage of the first truss. Six plants in each of 4 experimental plots (2 temperature and 2 watering treatments) were used for determining yield, yield components and dry matter production. Four plants were selected for analyzing physiological characteristics in 6 plants of each experimental plot. The plants were allowed to grow under natural day length conditions.

The leaves which had matured most recently, i.e. third or fourth leaves from the apex were used for the analysis of the physiological characteristics. Photosynthetic rate (Pr), transpiration rate (Tr), stomatal resistance (Rs) and leaf temperature (Tl) were measured with a portable photosynthesis system (model LI-6200, LICOR Inc., USA) from 11.00 to 13.00 at 2, 4, 6, 8, 12, 14, 16 days after the water stress treatment (DAT) and 4, 10, 14, 17, 24 days after re-watering (DAW). Leaf water potential (ψl) was measured at noon at 6, 7, 8, 9, 10 DAT based on a pressure-bomb technique\(^19\), using three to four youngest fully expanded leaves.

For the determination of pollen germination, anthers were collected from naturally fertilized flowers, put on the pollen germination medium of ABDALLA and VERKERK\(^1\) and kept in a constant-temperature room (25±2°C). Pollen from the first flower in each plant was used for the test. Counts of total pollen grains and grains with pollen tubes were
made in 2 non-overlapping fields in each cup under a binocular microscope, 4 hours after sampling. The results were expressed as percentage of germination.

Number of flowers and fruits in each of the first truss was determined. Fruits of the first truss were picked at maturity and weighed individually. The number of fruits, yield and average fruit weight were also determined. Shoot and root dry weights were determined after oven-drying for 96 hours at 80°C.

Data were processed by analysis of variance. Arc-sine transformation was made for percent data like fruit setting percentage and pollen germination percentage, according to Steel and Torrie17).

**Results**

No statistical interaction between the effect of water stress and temperature regime was observed for yield, yield components, pollen germination percentage, shoot and root dry weight (Table 1). Thus the average value of each factor (each stress treatment and temperature regime) is shown in Table 2.

The yield of tomato TM 0126 decreased significantly by the water stress treatment (Table 2). Yield was slightly but significantly higher under a MT regime than under a HT regime. Number of flowers was significantly reduced by the water stress treatment (Table 2). No significant differences were observed

Table 1. F value calculated by analysis of variance for yield, flower number, fruit number, fruit weight, fruit setting percentage, pollen germination percentage, and shoot and root dry weight.

<table>
<thead>
<tr>
<th>Factors</th>
<th>Yield</th>
<th>Fl. No.a</th>
<th>Fr. No.</th>
<th>Fr. Wt.</th>
<th>Fr. %</th>
<th>Pl. %</th>
<th>St. DW</th>
<th>Rt. DW</th>
</tr>
</thead>
<tbody>
<tr>
<td>W.S. b</td>
<td>610.52** c</td>
<td>39.60**</td>
<td>23.00**</td>
<td>84.78**</td>
<td>1.39ns</td>
<td>524.30**</td>
<td>14.60**</td>
<td>18.56**</td>
</tr>
<tr>
<td>Temp.</td>
<td>17.35**</td>
<td>1.69ns</td>
<td>0.10ns</td>
<td>1.87ns</td>
<td>0.81ns</td>
<td>347.41**</td>
<td>10.34**</td>
<td>10.44**</td>
</tr>
<tr>
<td>Int.</td>
<td>0.41ns</td>
<td>0.59ns</td>
<td>0.12ns</td>
<td>0.12ns</td>
<td>0.02ns</td>
<td>1.91ns</td>
<td>0.05ns</td>
<td>0.15ns</td>
</tr>
</tbody>
</table>

a Fl. No.; flower number, Fr. No.; fruit number, Fr. Wt.; fruit weight, Fr. %; fruit setting percentage, Pl. %; pollen germination percentage, St. DW; shoot dry weight and Rt. DW; root dry weight.
b W.S.; water stress treatment, Temp.; temperature regime and Int.; interaction between the two factors.
c ** statistically significant at P<0.01 and ns not significant.

Table 2. Effects of water stress and temperature on agronomic characteristics and days of water withholding period (DWW) in tomato.

<table>
<thead>
<tr>
<th>Characters</th>
<th>Control</th>
<th>Water Stress</th>
<th>HT y</th>
<th>MY y</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yield (g)</td>
<td>532.7 A 1</td>
<td>352.6 B</td>
<td>427.4 a</td>
<td>457.8 a</td>
</tr>
<tr>
<td>Flower No.</td>
<td>15.0 A</td>
<td>10.2 B</td>
<td>12.1 a</td>
<td>13.1 a</td>
</tr>
<tr>
<td>Fruit No.</td>
<td>8.7 A</td>
<td>5.6 B</td>
<td>7.0 a</td>
<td>7.3 a</td>
</tr>
<tr>
<td>Fruit wt. (g)</td>
<td>61.2 A</td>
<td>63.6 A</td>
<td>61.0 a</td>
<td>62.7 a</td>
</tr>
<tr>
<td>Fruit set (%)</td>
<td>58.1 A</td>
<td>54.4 A</td>
<td>57.6 a</td>
<td>55.8 a</td>
</tr>
<tr>
<td>Pollen germ. (%)</td>
<td>47.0 A</td>
<td>32.0 B</td>
<td>34.0 b</td>
<td>45.0 a</td>
</tr>
<tr>
<td>SDW x (g)</td>
<td>20.6 A</td>
<td>16.0 B</td>
<td>16.4 b</td>
<td>20.2 a</td>
</tr>
<tr>
<td>RDW w (g)</td>
<td>11.0 A</td>
<td>8.0 B</td>
<td>8.3 b</td>
<td>10.6 a</td>
</tr>
<tr>
<td>DWW v</td>
<td>—</td>
<td>—</td>
<td>12.0 b</td>
<td>16.0 a</td>
</tr>
</tbody>
</table>

1 Different letters indicate significant difference at p<0.05
y high temperature
y Moderate temperature
x Shoot dry weight
w Root dry weight
v Days of water withholding period
between the two temperature regimes. Water stress treatment significantly reduced the fruit number (Table 2). Temperatures had no effect on this parameter. Effect of temperature and water stress on fruit weight is also shown in Table 2. Both the water stress and temperature treatments did not affect the fruit weight.

No significant effects of the treatments on the fruit setting percentage were observed (Table 2). Pollen germination percentage was significantly reduced by the water stress treatment (Table 2). Pollen germination percentage was significantly higher under MT than HT.

Shoot dry weight was reduced by the water stress treatment (Table 2). MT application led to a significantly higher shoot dry weight than HT. Root dry weight was significantly reduced by the water stress treatment (Table 2). Root dry weight was significantly smaller under HT than MT. Under MT, DWW significantly increased compared with HT (Table 2).

Plants showed generally a higher Pr under HT than MT and the rate was markedly reduced by the water stress treatment (Fig. 1). Under HT, after the onset of the treatment, Pr decreased more rapidly than under MT. Just before re-watering, Pr in both tem-

Fig. 1. Effect of water stress and temperature regimes on photosynthesis. DAT stands for days after start of the treatment and DAW, days after re-watering. Vertical bar indicates the standard error (SE).

Fig. 2. Effect of water stress and temperature regimes on transpiration rates. DAW stands for days after start of the treatment and DAW, days after re-watering, respectively. Vertical bar indicates the standard error (SE).
perature regimes reached the lowest value. After re-watering, a more rapid increase was observed under HT than MT. Only at 4 DAW, did Pr under HT reach a value of about 10 μmol CO₂m⁻²s⁻¹, while under MT the value was about 7 μmol CO₂m⁻²s⁻¹ at 12 DAW.

Without stress, Tr was higher under HT than MT during the experiment (Fig. 2). Tr decreased more abruptly under HT than MT by the water stress treatment. Under MT, Tr decreased by the treatment more gradually, but eventually reached a similar level to that under HT just before re-watering. After re-watering, Tr under both temperature regimes increased, and reached values comparable to those of controls at 24 DAW. Rs increased by the water stress treatment under both HT and MT (Fig. 3). It was higher in general under HT than under MT. After re-watering, Rs decreased more rapidly under MT than HT.

Fig. 3. Effect of water stress and temperature regimes on stomatal resistance. DAT stands for days after start of the treatment and DAW, days after re-watering. Vertical bar indicates the standard error (SE).

Fig. 4. Effect of water stress and temperature regimes on leaf temperature. DAT stands for days after start of the treatment and DAW, days after re-watering. Vertical bar indicates the standard error (SE).
Tl was significantly higher under HT than MT (Fig. 4). Tl increased by the water stress treatment under both temperature regimes. Increases by the water stress treatment were larger under HT than MT. After re-watering, there was a decrease in both temperature regimes.

$j_1$ was significantly reduced by the water stress treatments under both the temperature regimes (Fig. 5). A significantly lower $j_1$ was observed under HT than MT. Declining tendency was observed in all the experimental plots.

Discussion

As stated previously, TM 0126, used in this study, is known to be a heat tolerant cultivar and also shows a superior drought tolerance. No statistical interaction between the effects of temperature and water stress was detected for most of the yield related characters, reproductive growth and dry matter production in this cultivar (Tables 1, 2), suggesting that the effect of water stress was not affected by the ambient temperature in these characters. Generally, water loss from plants is larger under high ambient temperature than under low ambient temperature, due to the higher transpiration demand under hot conditions\textsuperscript{10}. Therefore, it is likely that the effect of water stress is more pronounced under high temperature conditions. The results on yield and yield components, reproductive growth and dry matter production in this study did not agree with this assumption. On the other hand, the effects of water stress were clearly more pronounced under high temperature for various physiological and ecological characteristics, as expected. The reduction of $Pr$, $Tr$ and $j_1$ by water stress was more rapid and pronounced under HT than under MT (Fig. 1, 2 and 5). Water withholding period, the period during which water stress is tolerated, was shorter under HT than under MT (Table 2, DWW). The effect of water stress on Rs was less conspicuous under HT than under MT (Fig. 3), as discussed later. Although the adverse effects of water stress on the physiological characteristics were generally more pronounced under HT, the plants recovered after re-watering from the damage caused by water stress under high temperature, as evidenced by the rapid increase of $Pr$ and $Tr$ after re-watering. These effects may compensate for the damage associated with water stress under high temperature to some extent, in most of the yield-related characters, and vegetative and reproductive growth, leading to the absence of interaction between the effects of water stress and temperature for these characters. Drought tolerance of TM 0126 under high temperature conditions may be related to such a superior recovery ability.

The effect of water stress on Rs was affected by the temperature regime rather differently. More pronounced increase of Rs was found under MT than HT during the water stress treatment (Fig. 3). Rs of control plants under HT was higher than that of stressed plants under MT until 12 DAT. As stated above, transpiration demand is larger under high temperature than under low temperature, which may account for the high Rs value of the control plants under HT. Therefore, it is conceivable that Rs did not increase appreciably by water stress under high temperature. Under HT, stomata had been already closed partially even in plants with appropriate watering. Thus, water stress treatment may not have induced a

![Image of Fig. 5. Effects of water stress and temperature regimes on midday leaf water potential during water withholding period. DAT stands for days after start of the treatment period. Vertical bar indicates the standard error (SE).](image)
rapid rise of Rs. Conversely, stomata of well-watered plants under MT may have responded to water stress and closed promptly, leading to a rapid rise of Rs.

Even though Rs was higher under HT than MT, Tr was higher under HT than MT during the experimental period, presumably due to the higher leaf temperature under HT than MT (Fig. 4), which is known to increase transpiration.

The fact that control plants under HT maintained a high Rs value suggests that under hot conditions even well-watered plants usually experience mild water stress conditions. It is possible that a heat-tolerant cultivar generally displays drought tolerance to some extent. Even though TM 0126 closed stomata partially, Pr was higher under HT than MT. This phenomenon appears to be an important characteristic for heat- and drought-tolerant cultivars. In contrast, under water stress conditions, leaf temperature usually increases due to partial stomatal closure, as shown in Fig. 4, indicating that plant drought tolerance requires heat tolerance as well, under high temperature conditions.

In most of the tomato cultivars, daytime temperature under HT, i.e. 30°C in this study, did not seem to be high enough to induce serious physiological problems. Conversely, nighttime temperature under HT, i.e. 25°C, is very high for the growth of ordinary tomato cultivars. Many studies indicated that a high nighttime temperature adversely affected flower bud initiation, pollen production and final fruit set, while the flower number and fruit setting percentage were not affected by high nighttime temperature in this study. These results also indicate that TM 0126 exhibits a tolerance to high temperature.

Both water stress and HT reduced the pollen germination percentage, while the final fruit setting percentage was not affected by both factors, suggesting that TM 0126 displays a specific ability to tolerate a low pollen viability and set fruits. The high temperature tolerance of this cultivar may contribute partly to these characteristics which require further studies.

References