Subtropical Plant Science, 54: 16-22.2002

Superoxide Dismutase Activity, Leaf Water Potential, Relative Water Content, Growth and Yield of a Drought-Tolerant and a Drought-Sensitive Tomato (*Lycopersicon esculentum* Mill.) Cultivars

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ABSTRACT

The generation of oxygen radicals can be exacerbated during environmental stresses. Superoxide dismutases (SODs) are metal-containing enzymes that catalyze the dismutation of superoxide radicals to oxygen and hydrogen peroxide. We hypothesized that SOD is an indicator of stress tolerance in plants. In order to support this theory, water deficit effects on SOD activities, fruit yield, yield components, vegetative growth, relative water content (RWC), superoxide dismutase (SOD) activities, and leaf water potential (ψ_l) at different plant ages were examined in two tomato (*Lycopersicon esculentum* Mill.) cultivars, the drought-tolerant 'TM-0126' (TM) and the drought-sensitive 'King Fukuju' (KF). Water stress significantly decreased yield, yield components and dry matter production in both cultivars, but the reductions were more pronounced in the drought sensitive cultivar (KF) compared to the tolerant cultivar (TM). In TM, the fruit yield reduction was 31% compared to the drought sensitive KF (67%). The cultivar TM tolerated water stress for longer periods (14.8 days) than KF (11.2 days). Water stress decreased leaf water potential (ψ_l) at all stages, but reduction of ψ_l was more rapid and pronounced in KF than TM at all "days after seeding" (DAS). After re-watering stressed plants of TM had an increased ψ_l equivalent to the unstressed plants in all seedling ages but in KF, ψ_l of stressed plants were significantly lower than that of control plants. The effects of water stress on relative water content (RWC) of leaves in seedlings 26 DAS were very similar to those of ψ_l. The SOD activities in both cultivars increased in stressed plants at all DAS, but the increase of SOD activity was larger in TM than in KF. This pattern was observed at all DAS. Our results suggest that SOD activities play an important role in drought tolerance of tomato at various plant ages, and suggest that SOD activities could be used as a criterion for selecting drought tolerance in tomato cultivars.

RESUMEN

La formación de radicales de oxígeno puede aumentarse durante situaciones de estrés ambiental. Las dismutasas de superóxido (SODs) son enzimas que contienen metales que catalizan la dismutación de los radicales superóxido a oxígeno y peróxido de hidrógeno. Nosotros hipotetizamos que la presencia de SOD es una indicación de tolerancia al estrés en las plantas. Para apoyar esta teoría, se examinaron en dos cultivares de tomate (*Lycopersicon esculentum* Mill.), la variedad tolerante a la sequía 'TM-0126' (TM) y la sensible a la sequía 'King Fukuju' (KF), los efectos del déficit hídrico sobre la actividad de la SOD, el rendimiento de la cosecha de fruta, los componentes del rendimiento, el crecimiento vegetativo, el contenido relativo de agua (RWC), las actividades de la dismutasa de superóxido y el potencial de agua de la hoja (ψ_l) en diferentes edades de la planta. El estrés hídrico produjo una disminución significativa de la cosecha, los componentes de la cosecha y la producción de la materia seca en ambos cultivares, pero las reducciones fueron mas pronunciadas en el cultivar sensible a la sequía (KF) en comparación con el cultivar tolerante (TM). En TM, la reducción de la cosecha de fruta fue 31% en comparación con el cultivar sensible a la cosecha KF en el que fue 67%. El cultivar TM toleró el estrés hídrico por periodos más largos (14.8 días) que el KF (11.2 días). El estrés hídrico causó disminución del potencial hídrico de la hoja (ψ_l) en todos los estadíos, pero la reducción de ψ_l fue mas rápida y pronunciada en KF que en TM durante todos los días después de la siembra (DDS). Después de regar de nuevo las plantas estresadas, las plantas de TM tuvieron un ψ_l

equivalente a las plantas no estresadas en todos los estadíos de las plántulas pero en KF, el ψ_l de las plantas estresadas fue significativamente menor que las de las plantas testigo. Los efectos del estrés hídrico sobre el contenido relativo de agua (RWC) de las hojas en las plántulas 26 DDS fue muy similar a aquellos de ψ_l. Las actividades de la SOD en ambos cultivares se incrementaron en las plantas estresadas en todos los DDS, pero el incremento de la actividad de la SOD fue mayor en las TM que en KF. Este patrón se observo todos los DDS. Nuestros resultados sugieren que las actividades de la SOD tienen un papel importante en la tolerancia del tomate a la sequía en varios estadíos de la planta y sugieren que las actividades de la SOD podrían ser usadas como un criterio para seleccionar tolerancia a sequía en cultivares de tomate.

Additional index words: water, water stress, stress-tolerant, cultivars, shoot-root ratio

Reactive oxygen species (ROS) are generated in all aerobic organisms as components or byproducts of different biological processes. In plant cells, the major source of ROS are the chloroplasts, where light driven electron transport and oxygen evolution lead to the formation of singlet oxygen and superoxide radicals (Salin, 1987). In order to prevent damage to cellular components, ROS levels are controlled by the combined action of enzymatic and non-enzymatic detoxifying agents. Superoxide dismutases (SODs, EC 1.15.1.1) are key elements of this protective system, since they catalyze the dismutation of superoxide radicals to O_2 and H_2O_2, a reaction that constitutes the first cellular defense against oxidative stress (Bowler et al., 1994; Casano et al., 1994).

The production of ROS in plant cells increases under many stress conditions. Most of the injury to plants caused by these situations is associated with oxidative damage at the cellular level. In addition, stress exposure frequently results in increased activities of antioxidative enzymes (Bowler et al., 1992; Foyer et al., 1994). This has lead to the conclusion that the stress-defense capability of plants could be directly related to the efficiency of their antioxidative systems (Foyer et al., 1997). The analysis of plants overproducing ROS scavenging enzymes in chloroplasts has provided evidence supporting this hypothesis; in most cases, significant changes in oxidative stress tolerance have been reported (Holmberg and Bulow, 1998).

Superoxide dismutase is considered essential for the survival and function of aerobic organisms. These metaloenzymes scavenge the toxic super oxide radicals that are formed as by-products of aerobic metabolism. Antioxidant defense systems are a prominent element in plant responses to environment stresses. Many condition such water deficit, waterlogging, treatment with paraquat or infection by *Phytophthora infestans* may give rise to activated oxygen species in plants. The enzyme of superoxide dismutase (SOD) constitutes the first line of cellular defense against oxidative stress by scavenging quickly the superoxide radical and converted it to hydrogen peroxide. In plants, the photosynthetic process produces high intra-cellular concentrations of active oxygen species and reduced compounds such as NADPH (Asada and Takahashi 1987). Oxyradicals are also formed in cellular compartments other than the chloroplast (Elstner, 1982; Halliwell, 1984).

SODs are considered to be important components of the plant defense mechanisms. In the presence of metal ions such as iron, O_2 and hydrogen peroxide can react in a Haber-Weiss reaction to form hydroxyl radicals:

$$H_2O_2 + O_2^{\cdot} \xrightarrow{Fe^{2+},\ Fe^{3+}} OH^- + O_2 + OH\bullet \qquad \text{(Haber-Weiss reaction)} \qquad [1]$$

$$2O_2^{\cdot} + 2H^+ \longrightarrow H_2O_2 + O_2 \qquad \text{(SOD)} \qquad [2]$$

In plants, this SOD enzyme is unique in that its activity determines the concentrations of $O_2^{\cdot}$ and H_2O_2, the two Haber-Weiss reaction substrates, and it is therefore very likely to play an essential role in preventing plant stress injury. A plant response to drought stress is a complex phenomenon that appears to involve the synthesis of polyamines and a newly discovered set of proteins whose function is largely unknown (Caplan et al., 1990). Drought also triggers stomata closure and in extreme cases reduces the availability of CO_2 for photosynthesis, which can lead to the formation of reactive oxygen species as a result of excess excitation energy. Hence, mechanisms that reduce oxidative stress may play a secondary role in drought tolerance (Bowler et al., 1992).

Previous studies have shown that glutathione reductase activity increased in drought-stressed wheat, *Triticum aestivum*, (Burke et al., 1985) and cotton *Gossypium hirsutum*, (Gamble and Burke, 1984), and it was proposed that in addition to removing H_2O_2, this increase may produce NADP that can in turn electrons from ferredoxin to an available form, and thereby minimize superoxide formation. In drought-tolerant *Hordeum* species, levels of glutathione reductase and ascorbate peroxidase increased in response to water stress, but SOD activity was not examined (Smirnoff and Colombe, 1988). Drought-stressed cotton was found to be resistant to a subsequent challenge of paraquat treatment (Burke et al., 1985), which may also indicate the existence of a common protective mechanism against photo-oxidation. We also have observed that increases in superoxide dismutase activity have been reported to play a role in tolerance to cold in potatoes, *Solanum tuberosum* L., (Spychalla and Desborough, 1990) and maize, *Zea mays* L., to paraquat in ryegrass, *Lolium perenne* L., (Harper and Harvey, 1978), to salt in chick pea, *Cicer arietinum* L., (Hernandez et al., 1994) and resistance but no SOD studies have been conducted in tomato in relation to drought stress tolerance.

It was hypothesized that SOD activity would be greater in drought tolerant than sensitive tomato and by characterizing plant physiological water relations, growth, and yield under stressed or unstressed conditions, SOD activity could be evaluated as a drought tolerance screening tool. Our overall objective was to determine the relationships between leaf water potential, relative water content, growth, yield, and SOD activities in two different tomato cultivars, the drought-sensitive 'King Fukuju' (KF) and the drought tolerant 'TM-0126' (TM).

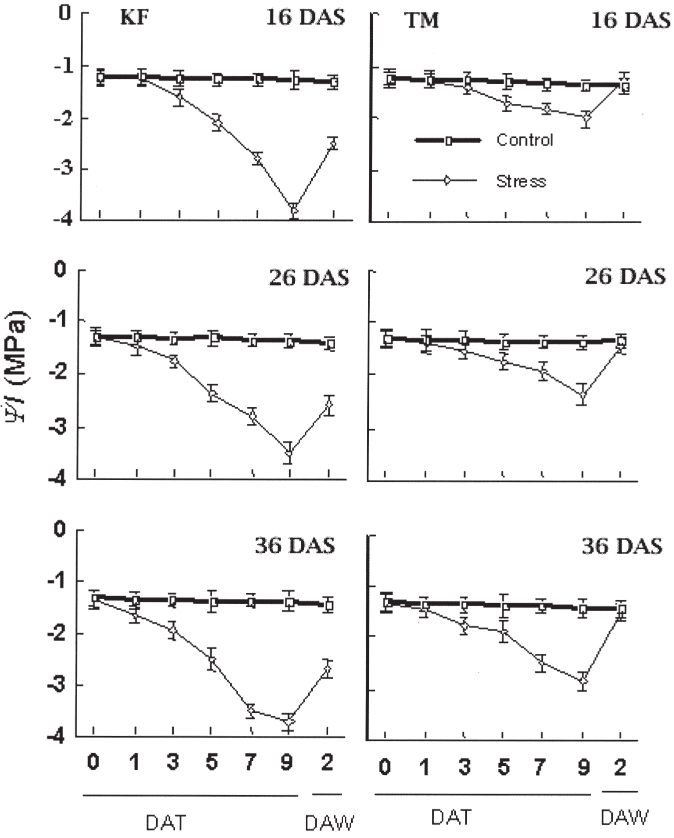

Fig. 1. Effects of water stress on leaf water-potential (ψ_l) of tomato at various days after seeding(DAS). DAT and DAW: Days after treatment and days after re-watering, respectively. Error bars indicate standard error (±SE). n=24. KF = King Fukuzu; TM = TM0126.

MATERIALS AND METHODS

Plant Materials and Growth Conditions. This study was conducted at Kyoto University, Japan using two tomato cultivars, a drought tolerant 'TM-0126' (TM) and drought sensitive 'King Fukuju' (KF). Before starting the treatment, soils were saturated with 500 mL of water per pot in order to create equal soil moisture conditions in all the pots. After that, water was withheld until visible severe wilting symptoms persisted throughout the night in the stressed pots. Water stress effects were examined 16, 26 and 36 "days after seeding" (DAS). For the 16, 26 and 36 DAS treatments, seeds were sown on 4 August, 26 August, and 12 September 1997, respectively. In all cases, seeds were sown in a plastic tray filled with vermiculite and placed at a phytotron under 30/25ºC day/night temperature regime. The growth chamber (phytotron) provided high irradiance at 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPFD at the top of the plant canopy, 70% relative humidity (RH), 30/25ºC day/night fixed temperature, an ambient CO_2 concentration of 400 $\mu L \cdot L^{-1}$ and a 12 HR photoperiod (0600-1800 hours). Six days after sowing, germinated plants at the two-leaf cotyledonary stage were transplanted to 2-liter plastic pots (9 cm in diameter; 12 cm high). For the individual plant ages of 16, 26 and 36 days, the water stress treatments were started on August 15, September 22 and October 18, 1997, respectively. The plants were separated into 2 groups; each group consisted of 8 individual plants per cultivar. One group was watered as needed (500 mL of H_2O per pot) while water was withheld to the second group (-1.0 to -1.5 megapascals, MPa). Two half-strength nutrients solution, Enshi (Yamasaki, 1982) which contains 94.5 $g \cdot L^{-1}$ $Ca(NO_3)_2 . 4H_2O$, 49.3 $g \cdot L^{-1}$ $MgSO_4 . 7H_2O$, 80.9 $g \cdot L^{-1}$ KNO_3 and 15.3 $g \cdot L^{-1}$ $NH_4H_2PO_4$ and Arnon (Arnon and Hoagland, 1940) which contains 11 $g \cdot L^{-1}$ $Na_2B_4O_7 . 10H_2O$, 0.55 $g \cdot L^{-1}$ $ZnSO_4 . 7H_2O$, 5 $g \cdot L^{-1}$ $MnSO_4 . 4H_2O$, 0.125 $g \cdot L^{-1}$ $CuSO_4 . 5H_2O$, 0.05 $g \cdot L^{-1}$ Na_2MoO_4, and 60 $g \cdot L^{-1}$ Fe-EDTA were applied. Two different nutrient solutions were used to supply both macro (Enshi solution) and micro elements (Arnon solution). During the water stress treatment, no nutrient solution was applied. At the beginning of the water stress treatment, 100 mL of water was applied to each plant to obtain uniform water content. Data were collected 0, 1, 3, 5, 7 and 9 days after initiating treatments (DAT) and 2 days after re-watering (DAW). Wilting and recovery symptoms were evaluated visually as well as by measuring leaf water potentials. To obtain yield and yield component data, twenty six (26) DAS plants were repotted into 18-liter plastic pots (40 cm in diameter; 40 cm high) filled with a mixture of perlite, sand, and peat at a ratio of 1:2:1, and 15 g of slow release fertilizer containing 14% N, 12% P_2O_5 and 12% K_2O were applied to each pot. These plants were used for first truss yield, yield components, root and shoot dry weight. Plants were harvested between 80 to 90 DAS for first truss yield.

Superoxide Dismutase and Protein Analysis. For SOD analysis, fully emerged leaves, third or fourth leaves from the apex were excised. At least two leaves per plant were used for SOD analysis. The used plants were than discarded. The leaves were rapidly weighed (about 0.5 g fresh weight), and ground with a pestle in a mixture of 1 mL of 50 mM potassium phosphate and 1 mM EDTA (pH 7.5) buffer. The homogenates were collected and centrifuged at 4ºC for 15 min at 43000xg. The supernatants were used for the assays of enzymatic activities and protein concentrations.

SOD activities were determined according to the method of Beyer and Fridovich (1987). One enzyme unit of SOD was defined as the amount of enzyme required to cause 50% inhibition of the rate of NBT (Nitroblue tetrazolium) reduction measured spectrometrically at 560 nm (Hitachi model U- 2000).

Soluble protein content was determined according to Bradford (1976) using bovine serum albumin (BSA) as a standard. Protein concentration was measured to calculate SOD activity only.

Leaf Water Potential and Relative Water Content Measurement. Leaf water potential (ψ_l) was measured by the pressure-bomb technique (Tyree and Hammel, 1972) using third or fourth leaves from the apex. The relative water content (RWC) of leaf discs were calculated as follows (Barrs and Weatherley, 1962):

$$RWC(\%) = \frac{Freshweight - dryweight}{Trugidweight - dryweight} \times 100 \qquad [3]$$

After sampling and weighing (fresh wt.), leaves were

Table 1. Effects of water stress on fruit yield, flower number, fruit number, fruit set percentage and fruit weight of 1st truss in drought-sensitive and drought-tolerant tomato cultivars.

Cultivar	Treatment	Fruit yield per plant	Flowers per plant	Fruits per plant	Fruit Set per plant	Fruit Wt. per plant
		g	#	#	%	g
'King Fukuju'	Unstressed	864.2Aa[z]	10.0Ba	6.0Ba	60.3Aa	154.8Aa
(KF)	Stressed	288.2Bb	6.1Bb	3.2Bb	50.3Ab	95.1ab
	Reduction %	67	39	47	16	39
	RP(%)[y]	33	61	53	84	61
'TM-0126'	Unstressed	643.2Ba	15.0Aa	9.0Aa	60.3Aa	71.5Ba
(TM)	Stressed	445.1Ab	13.0Aa	7.3Aa	57.3Aa	60.2Bb
	Reduction %	31	13	19	5	16
	RP(%)	69	87	81	95	84

[z] Different letters indicate statistical significance different at p=0.05. Lower case letters indicate differences between no stress and stress treatment. Upper case letters indicate differences between cultivars.

[y] RP= Relative Performance (%).

Table 2. Effects of water stress on root dry weight shoot dry weight, shoot-root ratio and days of water withholding period (DWW).

Cultivar	Treatment	Root Dry Wt. per plant	Shoot Dry Wt. per plant	Shoot-Root Ratio	DWW[x]
		g	g		
'King Fukuju'	Unstressed	9.9Ba[y]	16.9Aa	1.71Ab	11.2B
(KF)	Stressed	6.2Ba	12.0Bb	1.92Aa	
	Reduction %	37	29		
	RP (%)[z]	63	71		
'TM-0126'	Not Stressed	11.2Aa	16.2Aa	1.45Bb	14.8A
(TM)	Stressed	8.8Ab	13.5Ab	1.53Ba	
	Reduction %	21	16		
	RP(%)	79	84		

[z] RP= Relative Performance (%).

[y] Different letters significantly varies at p=0.05. Lower case letters indicate differences between no stress and stress treatment. Upper case letters indicate differences between cultivars.

[x] DWW: Days of water withholding period.

floated for 20 hours on distilled water, then blotted and weighed to obtain the turgid weight. For dry weight determination leaves were dried overnight in an oven at 80ºC. RWC was measured only in the 26 DAS plants.

Relative Performance Calculation and Stress Tolerance Measurement. The following equation was used to calculate the measured parameters of yield, flower number, fruit number, and fruit set percentage, fruit weight, dry weight of root and shoot to compare the relative performance between cultivars:

$$\text{Re}\textit{lative performance} = \frac{\textit{Performance under stress}}{\textit{Performance under no stress}} \times 100 \quad [4]$$

Plants were then re-watered and day of water withholding period (DWW) was recorded for each cultivar. After re-watering the recovery of the cultivars was carefully observed. Yield, flower number, fruit number, fruit set percentage and fruit weight, dry matter of root and shoot were determined only from 26 DAS plants.

Yield Determination. Flower numbers, fruit number, percentage fruit set, average fruit weight and the yield of the first truss were determined (first truss) per plant were also recorded. After the complete development of the first truss, the plants were terminated and root and shoot dry weight were determined by drying the plant in an oven (Eyela Windy Oven WFO 600ND, Tokyo Rikakikai Co. Ltd.) at 80ºC for 96 HR. The shoot-root ratio was calculated by dividing shoot dry weight by root dry weight.

Experimental Design and Data Analysis. The experiment was laid out in a randomized complete block with a split-plot arrangement with four replicates. Main plots were water treatment (stressed and unstressed) and subplots were cultivars (TM and KF). Data were analyzed by analyses of variance (ANOVA). The format of the analysis of variance was that of a split-plot design with four blocks, two main-plot treatments (water level), and two subplot treatments (cultivar) patterned after Gomez and Gomez (1984). Following the analysis of variance, standard error of the mean difference for each of two types of pair comparison with a split-plot design was calculated. Parameters of the equations were compared by *t* tests. The tomato fruit yield, flower number, fruit number, and fruit weight, root and shoot dry weight, shoot root ratio were statistically analyzed for a randomized split-plot complete block design where water stress treatments were main factor and cultivars were sub factor. The arcsine percentage transformation was calculated according to Steel and Torrie (1980) on fruit set percentage data only.

RESULT AND DISCUSSIONS

Effect of water stress on the yield of the first truss of two tomato cultivars is shown in Table 1. Water stress significantly reduced fruit yield of both cultivars, but was more pronounced in the drought-sensitive KF cultivar than KF. In TM, the tomato fruit yield reduction due to water deficit was 67%, whereas the reduction was 31% in KF. First truss flower numbers were reduced (39%) significantly by water stress in KF but were not reduced (13%) in TM. A similar trend was observed for fruit numbers per plant. Fruit set percentage was reduced (16%) by water stress in KF but lower in TM (5%). Tomato fruit weight per plant was reduced by water stress in both cultivars, but this reduction was greater in KF (39%) compared to TM (16%). In unstressed plants, tomato fruit yield per plant was significantly higher (26%) in KF compared to TM.

Root dry weights were reduced by water deficit in TM and KF by 21 and 37%, respectively (Table 2). Shoot dry weights were reduced by water deficit in TM and KF by 16 and 29%, respectively. Shoot/root ratio was increased by water stress in both cultivars. TM had a lower Shoot/Root ratio under both stressed and non-stressed conditions than the cultivar KF. The Shoot/Root ratio of TM under water stress conditions was lower than that of KF.

As water was withheld, the cultivar TM tolerated water stress for up to 14.8 days compared to 11.2 days for KF (Table 2). After the completion of the water stress treatment, rapid recovery from wilting was observed in TM but not in KF (Table 2 and Fig. 2). In TM, wilting symptoms disappeared within two to three hours after re-watering, while four to five hours were required for KF (data not shown). Water stress decreased the leaf water potential (more negative), ψ_l, of both cultivars (Fig.1). The reduction of leaf ψ_l was more rapid and pronounced in KF than TM in all DAS. After re-watering, the stressed TM plants, the ψ_l increased to control levels in all stages, but for KF, ψ_l of stressed plants were much lower than those of unstressed plants.

Relative water content (RWC) of stressed plants was decreased significantly and to a greater degree in KF than in TM compared to unstressed plants (Fig. 2). Wilting symptoms appeared two days earlier in KF than TM in all DAS (data not shown). Yet even the most affected plants of TM (about 52% RWC) recovered rapidly and regained turgor in 2 days after re-watering (DAW). In stressed KF plants, RWC was about 42% and leaves did not regain their turgor within 2 DAW.

The SOD activities in both cultivars were significantly increased ($p<0.05$) by water stress treatment at all seedling stages (Fig. 3). The SOD activities of TM were on average 30-35% higher than those of KF. After re-watering, SOD activities reached those of unstressed plants in both cultivars at all DAS except for KF at 10 DAS, whose SOD activities were still higher than that of unstressed plants.

Drought stress tolerance is an important trait for tomatoes when they are frequently subjected to water limitations (Boyer, 1982). In this study, two tomato cultivars were examined for their drought tolerance, agronomic and eco-physiological characteristics during and after short-term water stress. Reduction in fruit yield, various yield components and plant growth in TM was less affected by water stress.

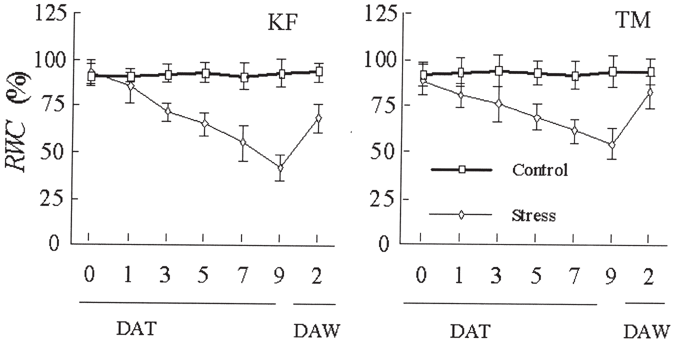

Fig. 2. Effects of water stress on related water content (RWC, %) of two tomato cultivars. DAT and DAW: same as Fig. 1. Error bars indicate standard error (± SE). n=24. KF and TM: same as Fig. 1.

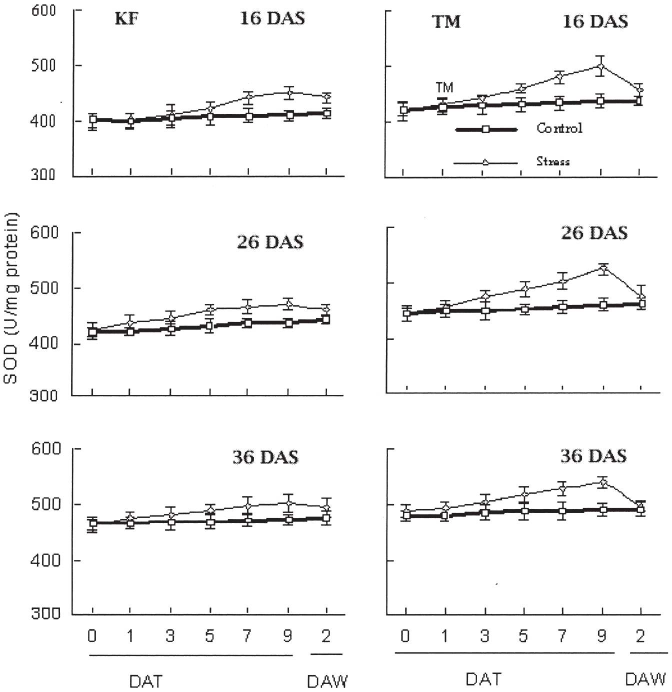

Fig. 3. Effects of water stress on leaf superoxide dismutase (SOD) activity on tomato at various days after seeding (DAS). DAT and DAW: same as Fig. 1. Error bars indicate standard error (± SE). n=24. KF and TM: same as Fig. 1.

Leaf water potential was reduced after initiating water stress in both tolerant (TM) and susceptible (KF) cultivars (Fig. 1). RWC also showed a similar trend (Fig. 2). The reduction of ψ_l by water stress was more rapid and pronounced as plant maturation increased. This may be due to large plant size, at later DAS and more rapid removal of soil water at this stage of development.

SOD activities were increased by water stress in both cultivars regardless of seedling age (Fig. 3). The increased SOD activities were also observed early in plant development, even in 5-day old seedlings. This suggests that the defense system against superoxide radicals becomes active at a very young growth stage in tomato. The increase in SOD activities in response to water stress was greater in TM than in KF at all the DAS, suggesting that cultivar differences are independent of plant age. This may enable the screening procedure for SOD to be initiated at earlier stages of plant development, which will save time, space and labor during an initial screening program for drought tolerance.

The cultivar TM can tolerate water stress for a longer period than the sensitive cultivar KF (DWW in Table 2). Based on our studies, this cultivar is a good potential candidate for a tomato line breeding and as a genotype for studying the mechanism and inheritance of water stress tolerance.

Based on our studies, we have found that the drought-tolerant cultivar (TM) has the following distinguishing characteristics, which are all related to increase water stress tolerance.

1. Ability to tolerate a longer water-withholding period.
2. More developed roots (shown in lower shoot-root ratio).
3. Ability to maintain higher water potential during a water stress period.
4. Rapid recovery from stress after re-watering.
5. Higher SOD activities during water stress.

Some of these traits were also found as general characteristics of drought-tolerant cultivars in various other crop species including tomato, moss, peanuts and rice (Nkansah and Ito, 1994; Dhinsa and Motowe, 1981; Bennett et al., 1981, Novero et al., 1985). These traits are all inter-related. For example, the ability to tolerate a longer water withholding period seems to result from an ability to maintain higher water potential during water stress period, and the ability to maintain higher (less negative) water potential may be due to better root development.

The ability to tolerate periods of water deficiency is also supported by several plant eco-physiological characteristics, including both dehydration postponement and dehydration tolerance (Kramer, 1983; Malan et al., 1990). In our study, the cultivar TM maintained higher water potential than drought-sensitive KF. This indicates that TM has improved capability to prevent water loss and to maintain a better water status during water deficiency. Further extensive genetic studies are needed to separate dehydration postponement and dehydration tolerance in tomato.

SOD plays a key role in plant defense systems against adverse effects induced by various superoxide radicals produced under many different kinds of stress conditions and increases its activities responding to the onset of stress (Van-Rensburg and Kruger; 1994; Stajner et al., 1995). In this study, SOD activities were increased by stress in tomato, but the increase in SOD activities in drought-tolerant cultivar was greater than in a drought-sensitive cultivar. Superoxide radicals are considered to be formed in various physiological processes under conditions of water stress. One important process is photosynthesis. Water stress induces the formation of reactive oxygen radicals by misdirecting of electrons in the true photo-systems (Bowler et al., 1992). An increased SOD activity by water stress is considered to antagonize harmful actions of superoxides radicals and this indicates that higher activities of SOD are important for drought tolerance. Our studies with tomato indicate that drought-tolerant cultivars have higher (30-40%) SOD activities under water stress conditions.

Based on our studies we are proposing that SOD activities under short-term water stress may be extremely useful in a breeding program selecting for drought tolerance. Our studies indicated that cultivar difference of the increase in SOD activities by water stress is remarkable and generally independent of plant age and ambient temperatures. Even at the early seedling stages, simple water stress treatment induces cultivar differences. At present, it appears that the SOD analysis can be more economical in terms of both time and space compared to other screening approaches. In addition, the results of our studies also suggest a possibility for using SOD activities for plants grown under normal, non-stress conditions as a criterion for initial screening for tomato drought tolerance. It is not clear that the SOD activity of unstressed plants were similar in both cultivars, a further study should be needed to clarify this. One of the disadvantages in using SOD activities in actual breeding program, especially in developing countries, is the cost and availability of laboratory chemicals and facilities needed for the SOD measurements. However, the procedure is basically non-destructive.

In conclusion, tomato drought-tolerant cultivars used for production under water stress conditions can be expected to have the both ability to tolerate water deficit and to recover rapidly after re-watering. Our study indicates that the drought-tolerant cultivar TM can satisfy this condition and the reduction in final fruit yield is much less than in the drought-sensitive cultivar KF. It also suggested that because of the superior recovering ability in TM to water deficits, any time-dependent effect of water stress might have been reduced.

ACKNOWLEDGEMENTS

This work was supported by the Japanese Ministry of Education, Science, Sports and Culture (MONBUSHO) fellowship to senior author (SMLR). Work was conducted while the senior author was affiliated with the Division of Environmental Science and Technology, Post Graduate School of Agriculture, Faculty of Agriculture, Kyoto University, Kyoto 606-8502, Japan. Our special thanks to Prof. Susumo Yazawa, Vegetables and Ornamental Horticulture Laboratory, Kyoto University, Japan for the opportunity to conduct research in his laboratory. We would like to express our special thanks to Mr. Sean Peas, System Manager of Texas A&M University, Research and Extension Center at Dallas for his kind help during preparation of the manuscript.

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