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Comparison of Response of Two C3 Species to Leaf Water Relation, Proline Synthesis, Gas Exchange and Water Use under Periodic Water Stress

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Water relations, proline content and gas exchange of leaf were investigated under periodic water stress for two C3 plants (eggplant and tomato) in a greenhouse to study comparative adaptive responses. Although both species showed reduced water content of leaf and increased osmolality and proline content under low soil water potential, the recovery capacity after the stress was better in eggplant than tomato. Both species over-accumulated proline under low soil water potential and returned to its initial concentration during the recovery, indicating that proline may act as an osmoprotectant during drought. Proline was directly corresponding with osmolality during stress, and dehydration stress reduced the gas exchange parameters such as transpiration rate (ET), stomatal conductance (GS), and photosynthesis rate (Pn). At the final stage of the experiment both species showed 2.6 and 3.3 times lower Pn and 27 and 19 times lower GS for eggplant and tomato, respectively, as compared to control. But after stress was relieved by rewatering, both plants increased GS for 2 to 3 times and Pn for 4.5 times. Eggplant showed better water use efficiency (WUE) in relation to fruit production under the stress than tomato. Higher biomass allocation at root and fruit parts in eggplant indicated more efficient recovery than that of tomato. These findings inferred that both C3 plants developed internal complementary drought survival mechanism by lowering relative water content, increasing proline, and decreasing stomatal conductance but eggplants withstood the periodic droughting better than tomato, mainly due to its ability to recover from a water stress condition.

Keywords: biomass, eggplant, gas exchange, osmolality, proline, tomato, water relation

Eggplant and tomato, both from the Solanaceae family grouped as C3 species, are important vegetable crops all over the world. Both plants require considerable amount of water during growth, however, water stress is quite frequent especially in the developing countries.

The effect of water deficit on crop growth and yield depends very much upon the timing and duration of drought. Plants are at their most susceptible during flowering and fertilization. At their critical times relatively brief periods of water shortage may seriously reduce yield (Briggs and Courtney, 1989). Water stress likely influences most to physiological processes. It changes the stomatal conductance, transpiration rate and photosynthesis rate (Sánchez-Blanco et al., 2002), and accumulation of osmolytes, especially proline and glycine betaine under water stress is well established (Pilon-Smits et al., 1995; Holmstroöm et al., 1996; Hayashi et al., 1997; Maggio et al., 2002).

Crop plants have developed morphological and physiological adaptation mechanisms such as leaf shading, stomatal closure, osmotic adjustment and overproduction of osmolytes that permit the plants to survive during water stress (Kavi Kishor et al., 1995; Monneveaux and Belhassen, 1996). However, the degree of adaptation to stress appears to vary considerably within the genera and also within the species (Torrecillas et al., 1996).

There may have been a number of findings on the agronomic responses to limited water but not much has been done on eggplant and tomato. Therefore, we have designed to investigate the relationship between leaf water relations, osmolyte content, physiological responses and water use efficiency of the two C3 plants under periodic drought stresses and recovery. This finding might be useful for studying the plant and soil water relation and water management practices in the horticulture industry for crop selection in arid and semi-arid regions as well as in areas where soil water shortage is in common.

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MATERIALS AND METHODS

Plant Culture and Stress Imposition

Each of the selected seedlings of 18 to 20 cm in height with 4 to 5 leaves of eggplants (*Solanum melongena* L. cv. Senryo No. 2) and tomato (*Lycopersicum esculentum* Mill. cv. Momotaro T-93) was transplanted in each pot on May 22, 2002, in a glasshouse at the Iwate University Campus, Morioka (North-eastern Japan). The pot was 50 cm in height and 25 cm in inner diameter, in which 22.5 L alluvial soil was used to fill the pot up to 45 cm height. The soil was previously mixed with granular fertilizer of 1:1:1 for N, P, and K at 50 g/20 L as maintenance dose along with 10 g lime/20 L. The experiment was continued up to 64 days after transplanting (DAT). A completely randomized block design composing two treatments with three replications was followed. The stress treatment was imposed as watering the pot at 15-day intervals, while the controls were watered at the capacity level at three-day intervals up to 36 DAT, two-day intervals from 37 to 45 DAT and followed by daily watering.. E1 and E2 represent control and stress for eggplant while T1 and T2 for tomato.

Microclimatic Variables and Soil Water Potential

Microclimatic variables in the glasshouse including solar radiation with pyranometer (Li-COR Pyranometer, USA), air temperature and air humidity (% RH) by measuring dry-bulb and wet-bulb temperature were collected through a data logging system at 30-min intervals. Four pots of eggplants and tomato plants were used for volumetric water content measurement with Time Domain Reflectrometry (TDR) sensor for each treatment. The data were collected through data logger CR10X with Multiplexer AM416 (Campbell Scientific Inc., USA). Soil water potential was obtained from the relationship between soil water suction and volumetric water content following the equation by van Ganuchten (1980) and the parameters, m, n and α, were estimated from the retention curve with a pressure plate apparatus using undisturbed core samples from the tested pots.

Relative Water Content and Proline

Relative water content of the upper most 4th leaf was determined gravimetrically. The one third part of the leaf was considered for relative water content measurement. The excised leaf was weighed immediately for fresh weight. The leaves were dipped in distilled water for 12 h at room temperature and blotted carefully and measured for turgid weight, and finally dried in an oven for 90 h at 60°C to have dry weight. Relative water content was calculated using the formula: Relative water content = 100 × (Fresh weight-Dry weight)/(Turgid weight-Dry weight). Leaf sample of about 100 mg from the other one third part of the leaf was used for osmolality estimation. It was measured with a microosmometer (VAPRO- vapor pressure osmometer, Wescor, USA). Fresh leaf sample of about 80 mg from the same leaf that was previously used for relative water content and osmolality measurements was collected in an eppendorf tube for the determination of proline. Then proline content was estimated colorimetrically by the acid ninhydrin method following Bates et al. (1973).

Leaf Gas Exchange Parameters

ET, GS and Pn were monitored in the pot plant for single leaf using a portable porometer and environmentally controlled leaf cuvette (CIRAS-1, PP System, Koito, Japan). All the measurements with porometer were performed during day time in between 10 am to 1 pm, and data were taken from the fully expanded upper most 4th leaf. The leaf was allowed to acclimate to the leaf cuvette for 5 min, and then the average ET, GS, and Pn over the next 5 min were accumulated for the analysis and interpretation.

Biomass and Water Use Efficiency

Three seedlings were separately used for initial biomass weight (0 DAT) prior to transplant other seedlings to the experimental pot. Three replicated plants from each treatment were harvested at 15-day intervals, and collected data were represented as 0, 15, 30, 45 and 60 DAT. Stems, leaves and roots (carefully washed and blotted) were separated and dried in an oven at 60°C for 4 days, and fruits were dried for 6 days. Total plant dry weight was recorded and averaged for biomass yield. WUE has been defined as the ratio of economic yield (fruit yield) to total water use or ET. It was calculated periodically from the measured cumulative ET (CET) and fruit yield on dry basis at different times of growing period.

Statistical Analysis

The $LSD_{(P<0.05)}$ test for eggplants and tomato was performed separately to investigate the treatment difference for biomass allocation in different plant parts. Multiple correlation regression analysis was done for determining the relationship among the soil water potential, leaf water relation, proline content and gas exchange parameters.

RESULTS

Microclimatic Variables and Volumetric Water Content

Microclimatic variables measured in the glasshouse have been depicted in Fig. 1. The weather was warm and humid. Air temperature increased gradually during the experiment with small fluctuations. Daily solar radiation fluctuated widely due to frequent overcast and rainy days, and high relative humidity (RH) also represented the general feature which was the typical for the area.

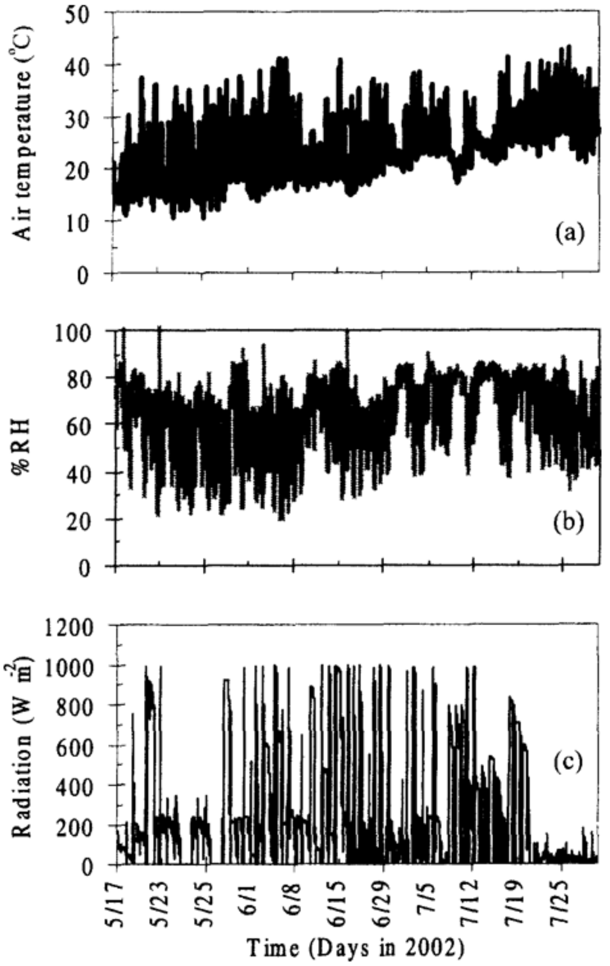

Figure 1. Air temperature (a) and relative humidity (b) in the glasshouse, and solar radiation (c) at outside of the glasshouse.

Soil water potential of different pot during growing period was presented in Fig. 2. Fig. 2a and b represented changing pattern of soil water potential of pot soil with plant growth and development. The initial soil water potential of experimental pots was about –0.002 MPa. After water extraction in response of evapotranspiration it gradually decreased. Both eggplant and tomato subjected to water stress showed gradually decreasing soil water potential during drying period. The relative soil water potential at which leaf wilting was first visualized was about -0.15 MPa. The relative changes of soil water status in both plants were different due to different amount of requirement and extraction capability of water during their development.

Relative Water Content, Osmolality and Proline Synthesis of Leaf

Relative water content in the leaf at the cellular level was shown in Fig. 3. Initial relative water content was not distinctly different. However, during the 3rd and 4th irrigation-drying cycles, a wide variation was

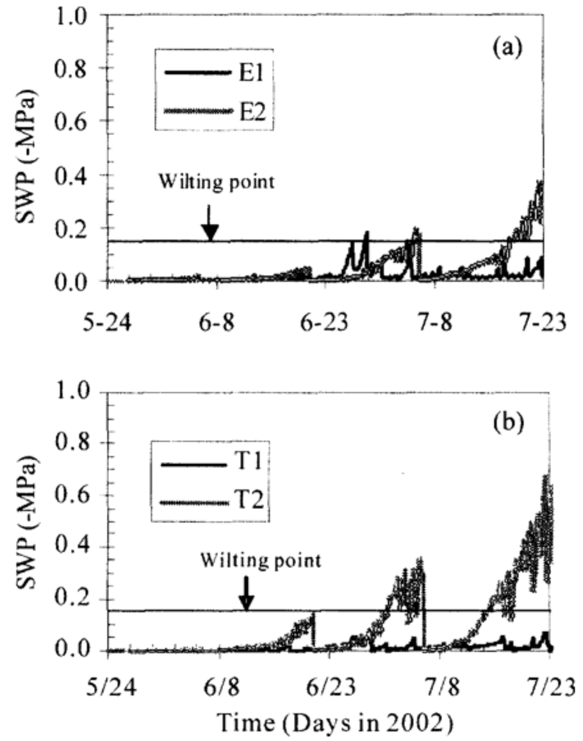

Figure 2. Soil water potentials of pot soil for eggplant (a) and tomato (b). E1 and E2 represent control and stress treatment for eggplants while T1 and T2 were for tomato plants.

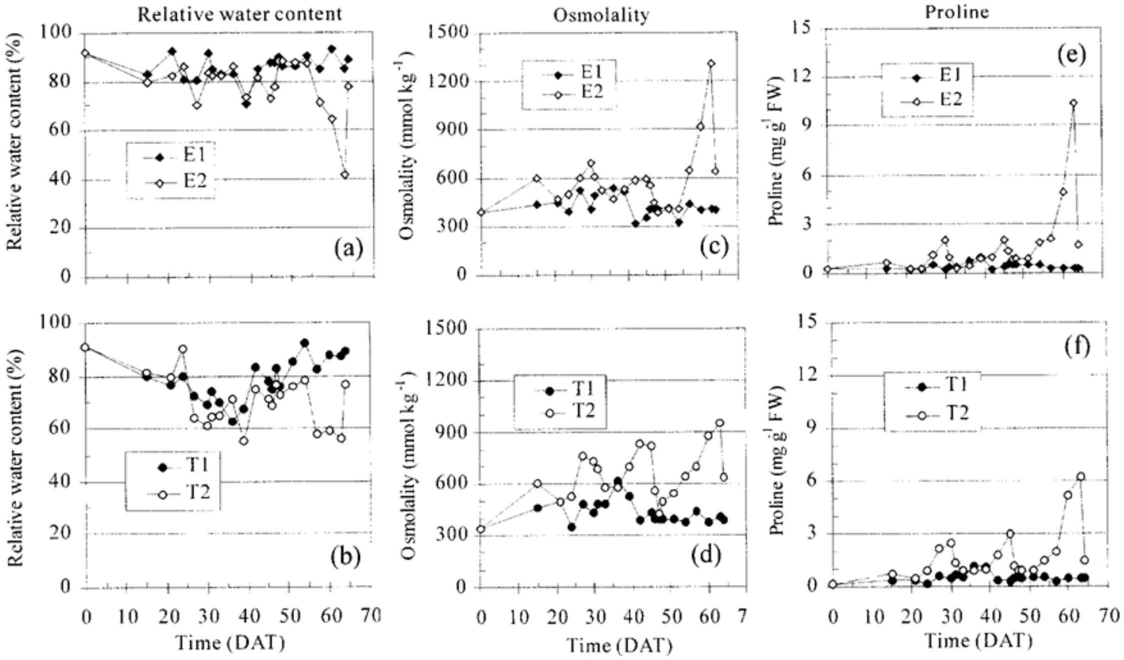

Figure 3. Relative water content, osmolality and proline content of leaf.

visualized between stressed and control plants. E2 and T2 showed 50% and 35% lesser amount of relative water content than those of their corresponding counterparts. When watering was reinitiated, E2 recovered to 86% while T2 recovered only to 36% of relative water content. At the same stage, osmolality of cell sap increased under stress in all the plants tested. After the final stress, treatment osmolality of E2 and T2 reached 3.2 and 2.4 greater than those of the controls. By rewatering, osmolarity was recovered to was 75% and 60% levels for E2 and T2, respectively.

Proline synthesis was greatly enhanced under low soil water potential in stressed plants (Fig. 3). Initially, proline content was as low as 0.27 and 0.16 mg g^{-1} FW in eggplant and tomato, respectively. Irrespective of test species, the plant under stress produced excess proline. After the imposition of stress, E2 and T2 synthesized proline as much as 10.35 and 6.18 mg g^{-1} FW, 32 and 15 times greater than those of controls. Proline was also accumulated 3 and 7 times more in E1 and T1 at 39 DAT probably due to lack of enough moisture supply. Fig. 3e and f showed that both C3 species synthesized proline exponentially under severe stress. However, the stress recovery for proline was 83 and 76% for E2 and T2, respectively.

Leaf Gas Exchange Parameters

Leaf gas exchange parameters of the two C3 plants were presented in Fig. 4. In Fig. 4a and b, E2 and T2 plants showed lower ET rates than E1 and T1, respectively. Plants with frequent irrigation showed higher ET rates. After rewatering both stressed species increased their ET rates. Like ET, eggplant and tomato showed similar pattern for stomatal conductance. E2 and T2 plants showed lower conductance than controls. In Fig. 4c and d, GS of E1 was comparatively higher than that of T1. In the 3rd and 4th drying periods all species showed declined GS. Pn of eggplant and tomato was also presented in Fig. 4e and f. In general GS and Pn had higher values in eggplant (E1) than in tomato (T1). E2 and T2 showed igher Pn after stress recovery but gradually declined again due to subsequent moisture stress. After the final stress, E2 and T2 showed 27 and 19 times lower GS than those of the controls. Corresponding Pn was decreased by2.6 and 3.3 times. The rate of GS in E2 and T2 increased 2 to 3 times and Pn increased 5 times after stress recovery.

Relationship Among the Measured Variables

Results of multiple correlation regression analyses were presented in Table 1. Under well watered condition, soil water potential showed no relationship with ET, GS, Pn and relative water content while soil water potential was significantly negatively correlated with osmolality and proline. In both species, soil water potential positively correlated with ET GS, Pn and relative water

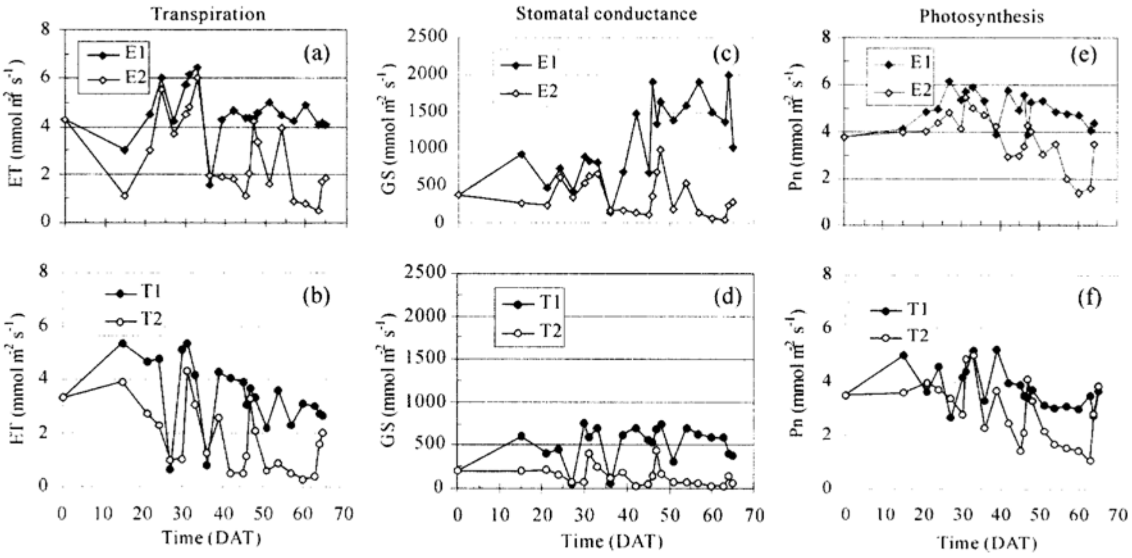

Figure 4. Transpiration rate, stomatal conductance and photosynthesis rate of eggplant and tomato.

Table 1. Correlation matrix for the relationship among soil water potential (SWP), leaf gas exchange, relative water content (RWC), osmolality and proline content of two C3 plants.

Treatment	SWP	ET	GS	Pn	RWC	O smolality	SWP	ET	GS	Pn	RWC	O smolality
Control			E1						T1			
ET	0.381						0.214					
GS	0.102	0.112					−0.079	0.654**				
Pn	0.344	0.344	−0.059				0.301	0.732**	0.425			
RWC	0.429	0.092	0.253	−0.079			−0.273	−0.003	0.109	−0.462*		
O smolality	−0.542*	−0.290	−0.401	0.119	−0.482*		0.094	−0.166	−0.283	0.260	−0.800**	
Proline	−0.700**	−0.406	−0.181	−0.049	−0.603**	0.662**	−0.103	−0.336	−0.240	0.086	−0.616**	0.791**
Stress			E2						T2			
ET	0.539*						0.507*					
GS	0.497*	0.792**					0.449*	0.886**				
Pn	0.791**	0.740**	0.615**				0.566**	0.878**	0.819**			
RWC	0.814**	0.572**	0.559**	0.604**			0.484*	0.457*	0.323	0.310		
O smolality	−0.827**	−0.464*	−0.471*	−0.597**	−0.927**		−0.640*	−0.600**	−0.589**	−0.536*	−0.688**	
Proline	−0.891**	−0.480*	−0.401	−0.695**	−0.880**	0.929**	−0.826*	−0.596**	−0.528*	−0.631**	−0.592*	0.835**

Significant values of r = 0.433 for $P<0.05$ and 0.549 for $P < 0.01$, * and ** indicate significance at 5% and 1% level, respectively.

content and negatively correlated with proline under stress. Leaf gas exchange parameters had a highly significant relationship among each other.

Biomass and Water Use Efficiency

Table 2 summarized the comparative biomass partitioning in stem, leaf, fruit, and root for two C3 species. A remarkable difference in biomass production was observed between the test species. Total biomass production of tomato plants either under stress or control condition was evidently higher than that of eggplants. Both species showed higher biomass partitioning in the stem and leaf. Furthermore, eggplants allocated more biomass in the root and fruit than tomato plants. We observed that the total biomass yield in per cent gradually decreased in stressed plants either in eggplants or tomato. Biomass production of stressed plants was 64.68, 37.84, 41.52 and 29.36% of the control for eggplant while tomato registered 72.02, 37.85, 35.11 and 25.62% of the control plants at 15, 30, 45 and 60 DAT, respectively. The $LSD_{(P<0.05)}$ analysis for both species showed that stressed plants had significantly less biomass in all parts. A statistically significant difference between the control and the stressed plants was evidently observed throughout the growing period. The calculated WUE for both species was shown in Fig. 5. Higher WUE in different times was demonstrated by eggplants as compared with tomato. In the present study, stressed plants showed higher efficiency for using water. Furthermore, at the early period, i.e. in vegetative stage, both species showed low WUE. As the plant growth and development proceeded, the WUE of both species gradually increased.

Table 2. Relative distribution of biomass in different parts of eggplant and tomato plants at different times of experiment. Inclined numbers are the percentage of total.

Time	Treatment	Eggplant						Tomato plant					
DAT		Root	Stem	Leaf	Fruit	Total	Percent	Root	Stem	Leaf	Fruit	Total	Percent
		g plant^{-1}						g plant^{-1}					
0		0.59	0.49	1.16	0.00	2.24		0.30	0.51	0.82	0.00	1.63	
		26.34	*21.88*	*51.79*	*0.00*	*100.00*		*18.40*	*31.29*	*50.31*	*0.00*	*100.00*	
15	Control	2.24	1.36	4.78	0.00	8.38	100.00	2.69	2.08	7.24	0.00	12.01	100.00
		26.73	*16.23*	*57.04*	*0.00*	*100.00*		*22.40*	*17.32*	*60.28*	*0.00*	*100.00*	
	Stress	1.82	1.21	2.39	0.00	5.42	64.68	1.40	2.77	4.48	0.00	8.65	72.02
		33.58	*22.32*	*44.10*	*0.00*	*100.00*		*16.18*	*32.02*	*51.79*	*0.00*	*100.00*	
LSD$_{(P<0.05)}$		1.02	1.41	0.33		2.14		0.41	0.60	0.74		0.40	
30	Control	10.16	11.33	15.90	0.00	37.39	100.00	7.82	22.23	34.71	0.00	64.76	100.00
		27.17	*30.30*	*45.52*	*0.00*	*100.00*		*12.08*	*34.33*	*53.60*	*0.00*	*100.00*	
	Stress	4.47	3.78	5.90	0.00	14.15	37.84	4.20	8.79	11.52	0.00	24.51	37.85
		31.59	*26.71*	*41.70*	*0.00*	*100.00*		*17.14*	*35.86*	*47.00*	*0.00*	*100.00*	
LSD$_{(P<0.05)}$		3.46	1.49	3.37		6.33		0.49	1.51	3.34		4.08	
40	Control	24.48	32.20	33.47	17.81	107.96	100.00	13.22	59.83	81.10	5.39	159.54	100.00
		22.68	*29.83*	*31.00*	*16.50*	*100.00*		*8.29*	*37.50*	*50.83*	*3.38*	*100.00*	
	Stress	10.28	16.90	11.11	6.53	44.82	41.52	6.22	22.77	25.18	1.84	56.01	35.11
		22.94	*37.71*	*24.79*	*14.57*	*100.00*		*11.11*	*40.65*	*44.96*	*3.29*	*100.00*	
LSD$_{(P<0.05)}$		8.91	7.45	6.26	10.23	15.93		2.32	10.96	2.89	1.81	11.20	
60	Control	38.68	43.20	44.53	76.35	202.76	100.00	13.67	103.19	116.30	57.52	290.68	100.00
		19.08	*21.31*	*21.96*	*37.66*	*100.00*		*4.70*	*35.50*	*40.01*	*19.79*	*100.00*	
	Stress	10.85	12.67	13.99	22.03	59.54	29.36	9.17	20.21	29.52	15.58	74.48	25.62
		18.22	*21.28*	*23.50*	*37.00*	*100.00*		*12.31*	*27.13*	*39.63*	*20.92*	*100.00*	
LSD$_{(P<0.05)}$		12.35	7.37	14.24	6.34	28.79		1.45	6.04	2.79	10.24	9.38	

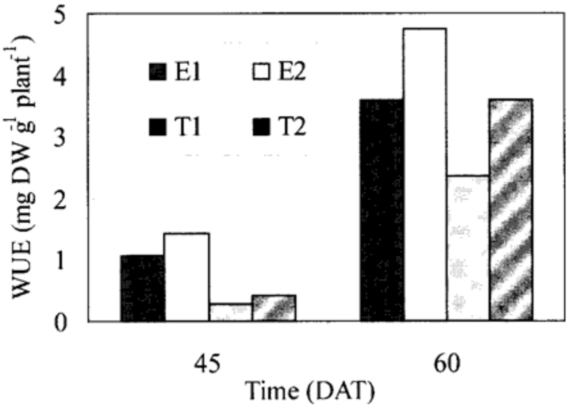

Figure 5. Water use efficiency of eggplant and tomato.

DISCUSSION

It is evident that soil water potential of the pot is different according to plant species, age and their water extraction capability by root systems. Both eggplant and tomato plants showed the lower leaf relative water content in cellular level under stress, i.e. low soil water potential, and it returned to the initial level after rewatering. Severe reduction of relative water content at the end of drying period and sharp recovery just after replenishment with water was observed (Fig. 3). On the other hand, osmolality started to increase as the stress intensity increased (Fig. 3). Osmolality of both species returned its initial level after recovery from stress. It might be due to stress effect on leaf cellular relative water content and higher accumulation of solute concentration. The concentrations of a variety of organic compounds are known to increase in plant tissues subjected to water stress (Hsiao, 1973). Eggplant adjusted more efficiently under stress by increasing osmotic concentration than tomato did and anticipated 51% recovery while tomato plant showed 33% recovery. The maintenance of higher relative water content has been considered as an indicator of mechanism for drought resistance in plants and genotypic variability under soil drying (Kramer, 1983). The regain of high relative water content just after rewatering the stressed plant might indicate survival mechanism during water stress, which is in well agreement with Kramer (1983). Eggplants maintained higher relative water content and adapted well under periodic drought than tomato plants. As regards to osmolality, eggplant showed higher capability to resist drought by producing more solute during severe stress and rapid return to normal level after stress removal.

Proline accumulation was remarkably high in both species during stress at low soil water potential and it sharply returned to the initial level after irrigation. Similar observations have been reported that overproduction of proline in crop plants occurs under water stress (Yoshiba et al., 1997; Sánchez et al., 1998). This phenomenon supports a hypothesis that over-accumulation of proline is a part of physiological response to an intense stress (Hare et al., 1998). Recently, Maggio et al. (2002) proposed that proline and other osmolytes may act as signaling/regulatory molecules to activate multiple responses that are part of the adaptation process. In the present study, after the recovery of stress, both species reversibly decreased the synthesis of proline and retuned to the original concentration, indicating the ability to survive during the drought. The assumption behind this approach has been that overproduction of this osmolyte may help plants to tolerate stress by improving their ability to adjust osmotically (Kavi Kishore et al., 1995; Pilon-Smits et al., 1995; Holmström et al., 1996; Hayashi et al., 1997). Considering the comparative response of proline synthesis, we found that eggplant evidently showed higher adaptive response during drought than that of tomato plant.

Of the daily fluctuation of microclimatic variables, especially incoming solar radiation is the best correlated to transpiration followed by temperature and relative humidity (Gil, 1995). Similarly, GS was also influenced directly by water deficit and daily microclimatic variables. In the present study, we found in the 3rd and 4th drying period that water stress distinctly reduced the GS and sometimes leaf gas exchange parameters showed distinctly lower values. This would explain the decrease in the gas exchange parameters occurred during a decent in irradiance, high temperature and high RH instead of imposed water deficit situation.

Water stress decreased the photosynthetic rates at all stages while frequent irrigation increased the rate in both species. Since ET, GS and Pn are moisture and temperature dependent (Berry and Bjorkman, 1980; Schulze and Hall, 1982), Pn in both species increases with sufficient moisture but it gradually decreases in small extent at latter growing period while daily temperature was above 30°C. Bar-Tsur et al. (1985) reported that photosynthesis seemed to be affected by mesophyll resistance which might be dependent on enzymatic response at temperature higher than 30°C. In the present investigation, microclimatic data showed that temperature gradually increased and exceeded 30°C at latter growing period. Therefore, higher temperature might be associated with lower Pn. In comparison between the two species, eggplant demonstrated higher GS and Pn than tomato. Moorby et al. (1975) reported that decrease in stomatal conductance and relatively large increase in mesophyll resistance during water stress were associated with decrease in photosynthesis rate. Pn depressed under water stress was in well agreement with the findings of Ghosh et al. (2000) and Ohashi et al. (2000). Pn showed almost full recovery after the removal of water stress by rewatering while ET and GS did not. It explained that the periodic stress affected more severely on stomatal opening, hence on ET but not on Pn. Eggplant reduced its GS greater than tomato did but the former showed higher recovery rate. Furthermore, like GS, Pn of E2 was also affected more in eggplant than tomato and maintained higher recovery after rewatering. This also anticipated the higher adaptive capability of eggplant under water stress than tomato.

The correlation studies suggested that the two species showed ET, GS, Pn and the cellular relative water content significantly decreased with decrease in soil water potential under stress. It was also evident that osmolality and proline synthesis of eggplant negatively correlated with soil water potential. The existence of significant relationship between the relative water content, osmolality and proline content under stress indicated a direct association with adaptive mechanism. It is reported that solute content at cellular level has a close relationship with relative water content, which is important for increasing osmolality and proline (Naidu et al., 1992; Iannucci et al., 2000). In the present study, the stress history of both plants had great influence on the osmolality and accumulation of proline. Under stress condition, GS had the pronounce effect on photosynthesis for both species. Many pot experiments have indicated that changes in GS are the main cause of the great decrease of photosynthesis with declining water potential (Boyer, 1976). The results documented here evidently showed that the leaf gas exchange parameters were always in good agreement with soil water potential. The leaf gas exchange might be also well associated with microclimatic variables (Gil, 1995).

Eggplant and tomato that experienced periodic drough showed lower total biomass from all the measurements (Table 2). This is in well agreement with the findings of De Herralde et al. (1998) and Sánchez-Blanco et al. (2002). However, as regards to biomass partition in different plant parts both species behaved differently.

Eggplant allocated comparatively higher biomass in root part, indicating the higher ability to survive during drought, and also in fruit part. Importance of extensive root development in drought tolerance has been reported from some field crops (Smucker et al., 1991; Carrow, 1996; Qian et al., 1997). WUE was higher under periodic stress, which was consistent with the findings of Li et al. (2001) that long term stress increased WUE. Eggplant showed higher efficiency in using water than that of tomato plant. It is apparently due to the ability of better WUE associated with higher photosynthesis and higher biomass production over the growing period which was not markedly pronounced in tomato plants under stress.

Comparing between two C3 plants tested here, eggplant (*S. melongena* L. cv. Senryo No. 2) showed more competent with greater yield stability under periodic drough than that of tomato plant (*L. esculentum* Mill. cv. Momotaro T-93) and exhibited greater drought tolerant ability as evidenced by relative water content, osmolality, proline, stomatal conductance, water use efficiency and biomass allocation in root parts. This study suggested that adequate soil moisture is very important for getting maximum fruit yields, hence biomass yield for C3 vegetable crops like eggplants as well as tomato plants. Nevertheless, higher photosynthesis is an inevitable process that might be considered for higher fruit yield.

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