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Quantitative analysis of relative growth rate based on leaf growth characteristics and evapotranspiration of eggplant and tomato under periodic water deficit at reproductive stage

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Abstract

A quantitative growth analysis was performed using instantaneous leaf growth parameters for eggplant and tomato under soil water deficit conditions. A conventional approach was applied for quantifying the relative growth rate (RGR) calculation and was compared with directly measured RGR. Relative leaf growth rate (R_{LA}) was also measured in relation to leaf area (L_A). Total plant dry weight (W) was significantly reduced under stress for both the crops and hence RGR. Total Leaf area (L_A) and leaf weight (L_{dw}) was higher in tomato than that of eggplant and adversely affected by periodic water deficit at reproductive stage. Water deficit lowered the leaf growth in terms of L_A and L_{dw} in eggplant by 34% and 31% and in tomato by 25% and 25%, respectively. Tomato plants showed higher CET (Cumulative evapotranspiration) by increasing water use at reproductive stages than eggplant but both plants lowered the CET under water deficit. Among the leaf growth characteristics, leaf area ratio (LAR), specific leaf area (SLA), leaf weight ratio (LWR) and unit leaf rate (ULR) were quantified and used as important parameters for RGR analysis. The index LAR was very sensitive and had great influence on simulated RGR although it fluctuated during all growth stages. Higher SLA at reproductive stage representing lower thickness of leaf was the characteristics of eggplant. But tomato showed lower SLA that was attributed to accumulate photosynthates in leaves during reproductive stage. ULR varied during the experiment but exhibited more efficiency in tomato. In general, higher RGR at vegetative and early reproductive stages was common for both crops followed by lower RGR. The measured and calculated RGR were not constant at all at any growth stage. The calculated RGR based on leaf growth characteristics were, in general, well agreed with measured RGR for both cases indicating leaf growth characteristics credibly provides useful information for crop growth behavior. The present findings also suggest that LAR along with ULR had positive influence on RGR of eggplants and tomato at any growth stage.

Key words: Eggplant, leaf area ratio, leaf weight ratio, relative growth rate, specific leaf area, tomato, unit leaf rate

Introduction

Relative growth rate (RGR) represents the efficiency of a plant as a producer of new materials and gives a measure of the plant's economy in working (Hunt, 1978). RGR provides a convenient integration of the combined performances of the various parts of the plant. It is especially useful when the need arises to compare species and treatment differences on a uniform basis.

Eggplant and tomato are the important vegetable crops widely cultivated in tropical and temperate regions of the world (Kashyap *et al.,* 2003). They require large amount of water for their growth and development. Water deficit is the major constraint for leaf growth, water use efficiency and fruit production of these crops. Substantial evidence indicated that water stress decreased the leaf growth, water use efficiency, and ultimately the yield of many crops (Pandey *et al.,* 1984; Saha and Hara, 1998; Rosenthal *et al.,* 1987). There are a number of findings on the agronomic responses to water stress. But a little information on growth behavior in relation to leaf growth development of eggplant and tomato, and their quantitative analysis under periodic water deficit are available. The objective of the present study is the quantitative analysis of relative growth rate based on leaf growth characteristics for eggplant and tomato under periodic water stress at reproductive stage. The present study also focuses the inter-species differences in relative growth rate during their different growth stages. Such study provides an opportunity to explore more fundamental aspects of the link between the dry matter partitioning in the leaf and leaf area growth characteristics, which are more important for solar energy capture to prepare carbohydrate in the green leaves by using soil water in presence of sunlight.

Materials and methods

The selected seedlings of 18 to 20 cm height with 5 to 6 leaves of eggplant (*Solanum melongena* L. cv. Senryo No. 2) and tomato plant (*Lycopersicum esculentum* Mill. cv. Momotaro T-93) were transplanted (one seedling 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 up to 45 cm height. The soil was previously incorporated with mixed granular fertilizer of 1:1:1 for N, P, and K @ 50 g/20 l soil as maintenance dose along with 10 g lime/20 l soil. The experiment was continued up to 60 days after transplanting (DAT). A complete randomized block design composing two treatments with three replications was followed for this purpose. The irrigation treatments were designed as T1 (Control)- watering the pot at its field capacity level every three days interval up to 36 DAT, two days interval from 37 to 45 DAT and followed by daily watering; T2: (Short-term stress)- watering the pot at every 15 days interval. ET1 and ET2 represented for control and short-term stress for eggplant while TT1 and TT2 for tomato plant. To satisfy the ET loss at every wetting and drying cycle, pot capacity condition was considered as the pot was irrigated to raise its soil moisture status up to its capacity level just replenishing the total amount of water lost by ET after each wetting and drying cycles. Growth of both test plants can be divided in to three stages and are separated by vertical bars (Fig 1). Stage I is characterized by vegetative period, Stage II is the beginning of flowering *i.e.*, early reproductive stage, and Stage III represents the flowering, fruiting and harvesting stage *i.e.*, peak of reproductive stages.

Growth analysis: The classical approach of RGR by Blackman (1919) for crop growth analysis was used. From a mathematical point of view, RGR was noted as an instantaneous value, expressed as:

$$\mathrm{R} = \frac{1}{W}\frac{\mathrm{d}W}{\mathrm{d}T} \qquad [1]$$

Where W and T are the total dry weight and harvesting time, respectively. The above expression for instantaneous relative growth rate is the increase in plant weight per unit of plant weight per unit of time and it is equivalent to

$$\mathrm{R} = \frac{\mathrm{d}(\log W)}{\mathrm{d}T} \qquad [2]$$

Equation [2] shows the instantaneous relative growth rate, **R**, is the slop of the plot of natural logarithms of W against T, which is free to change with different values of T. Further, the overall growth indices, RGR, is split into three components of leaf growth characteristics as

$$\mathrm{RGR} = \mathrm{ULR} \times \mathrm{SLA} \times \mathrm{LWR}, \ (\mathrm{SLA} \times \mathrm{LWR} = \mathrm{LAR}) \qquad [3]$$

Where ULR is the unit leaf rate *i.e.*, a meaningful index of productive efficiency of plants in relation to some clearly identifiable component. SLA is the mean area of leaf displayed per unit leaf weight (in a sense a measure of leaf density or relative thickness) and LWR is an index of the leafiness of plant on a dry weight basis. Equation [3] can be rearranged as:

$$\mathrm{R} = \left(\frac{1}{L_A}\frac{\mathrm{d}W}{\mathrm{d}T}\right) \times \frac{L_A}{L_{dw}} \times \frac{L_{dw}}{W} \qquad [4]$$

Where L_A indicates for total leaf area and L_{dw} for total leaf dry weight. It is integrated using the equation [1] and [3]

$$\frac{1}{W} \times \frac{\mathrm{d}W}{\mathrm{d}T} = \left(\frac{1}{L_A}\frac{\mathrm{d}W}{\mathrm{d}T}\right) \times \frac{L_A}{L_W} \times \frac{L_W}{W} \qquad [5]$$

We can also obtain relative leaf growth rate ($\mathbf{R}_{LA}$) in terms of L_A which is analogous to **R** of Equation [1] and derived as

$$\mathrm{R}_{LA} = \frac{1}{L_A}\frac{\mathrm{d}L_A}{\mathrm{d}T} \qquad [6]$$

Plant parameters and statistical analysis: Three seedlings were separately used for initial plant data for leaf weight, area and biomass (0 DAT) prior to transplanting other seedlings to the experimental pot. Three replicated plants from each treatment were harvested at every 15 days interval, and collected data was represented as 0, 15, 30, 45 and 60 DAT, respectively. The plant parts such as stems, leaves and roots were separated and dried in an oven at 60 ^{0}C for 4 days but fruits for 6 days. Total plant dry weight was recorded and averaged for future analysis and interpretation. Among plant components, plant height, number of photosynthetically active leaves, leaf surface area, fresh and dry biomass for each plant were monitored separately. Plant height was determined by meter scale, and number of leaves was counted on three days interval. Leaf surface area (L_A) for whole plant was measured by leaf area meter (Atomic area meter, Model: AAM-7, Hayashi Denkoh Co. Ltd., Japan) after separating the leaves from the plant. Evapotranspiration (ET) was measured daily by weighing the experimental pot thrice a day through out the growing period. The daily pot weight decreased by soil evaporation and transpiration loss by plant was considered for this daily ET value. The daily ET values obtained were integrated to calculate cumulative evapotranspiration (CET) or total water use for any particular plant during the 60 day growing period. Data of total plant dry matter were analyzed for treatment differences using LSD test at $P<0.05$. Linear correlation regression was performed among the leaf growth parameters: L_{dw}, L_A, SLA, ULR and LAR, and RGR of eggplant and tomato. A regression analysis was also made to compare between measured and calculated RGR.

Results and discussion

Plant growth characteristics: Plant growth for the test plants closely monitored during growing period by rate of increase in main stem or plant height is presented in Fig. 1A. Plant growth rate of both plants was adversely affected by water deficit at reproductive stages. Fig. 1A shows that the rate was higher in tomato plant than that of eggplant under stress treatments and it was observed during the whole growing period. Water deficit in reproductive stage also brought about lower rate of increase in plant height, distinctly visualized in ET2 and TT2, as compared to control. The rate started to differ from the growth *Stage II* for both plants and it continued to *Stage III*. Water deficit reduced the total plant dry matter production for both plants (Table 1) and the reduction was pronounced at growth *Stage II* and *III*. Significant difference were also observed in between two treatments throughout the growing period and also for all the test plants. At *Stage III*, eggplant under stress showed 29% lower dry matter than that of control, while 26% lower in tomato.

Leaf growth characteristics: Leaf growth is examined in terms of leaf numbers, leaf area expansion and leaf dry weight increase. The number of total photosynthetically active leaves has been plotted against three days interval in Fig. 1B. Both the plants distinctly produced lower number of leaves from the *Stage I* under water deficit conditions and had the consistent feature with plant height characteristics. L_A expansion was highly influenced by moisture deficit (Fig. 2A). Curve describing changes in the L_A growth in tomato was higher than eggplants regardless their soil water conditions. Both stressed plants showed linear growth pattern while control plants followed typical sigmoid shape growth pattern. Fig. 2B shows a remarkable difference in L_{dw} between tomato and eggplants from the *Stage II*, and it registered more than double at *Stage III*. Water deficit significantly reduced leaf growth by lowering biomass allocation in the leaves. L_{dw} under stress started to decrease from the *Stage II* which might be affected by lower L_A and hence lower photosynthesizing area. Both plants under stress demonstrated 34% and 25% lower L_A,

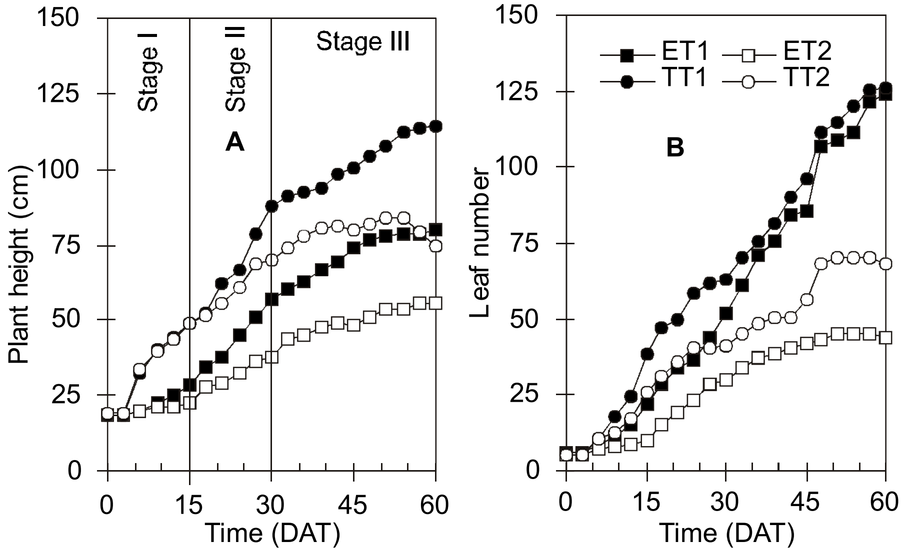

Fig.1. Periodic plant height (A) and leaf number (B) increase in eggplant and tomato under periodic water deficit.

and 31% and 25% lower L_{dw}, than in control condition. The ratio of L_{dw} and L_A describes the linear relationship during *Stage I* and *II* followed by exponential at *Stage III* (Fig. 2C). This indicated that the rate of L_{dw} increase was higher than the rate of leaf expansion at *Stage III* and tomato plant showed higher efficiency in accumulating assimilates in leaves than eggplant irrespective to their soil water stress.

Table 1. Total plant weight of tomato and eggplant at different stages of growing period

DAT	Total plant weight (W, dry basis)		
	ET1	ET2	$LSD_{0.05}$
0	2.24 (+0.20)	2.24 (+0.20)	-
15	8.38 (+1.41)	5.42 (+0.33)	2.14
30	37.39 (+4.11)	14.15 (+1.15)	6.33
45	107.96 (+6.11)	44.82 (+8.83)	15.93
60	202.76 (+17.28)	59.54 (+8.84)	28.79
	TT1	TT2	$LSD_{0.05}$
0	1.63 (+0.13)	1.63 (+0.13)	-
15	12.01 (+0.24)	8.65 (+0.13)	0.46
30	64.76 (+2.29)	24.00 (+1.53)	4.08
45	159.54 (+7.14)	56.01 (+2.44)	11.20
60	290.68 (+5.07)	74.48 (+3.78)	9.38

LAR is an important leaf growth characteristics known as physiological index, determines what proportion of the new materials are translocated to the portions of new developing leaves. LAR at any growing time represents an integration of the effects of different sets of mechanism that occur after arrival of assimilates in the young leaves which is responsible for controlling leaf area expansion (Evans, 1972). Fig. 3A depicts a much more fluctuating phenomenon of LAR during each growth stage. Although it starts from higher instantaneous values followed by gradual decrease, but eventually converged to a value lower than initial. SLA, a component of LAR, also fluctuated during different growth stages as shown in Fig. 3B. SLA is an important determinant for relative growth analysis. It is seen that higher SLA was at *Stage I* for tomato than eggplant but eggplant maintained higher SLA during *Stage II* and *III*. In the present study, increased SLA in eggplant implies thinner leaves during its reproductive stage, probably transmitting more light and with less photosynthesizing materials. This is also well in agreement with the findings of Goudriaan and Monteith (1990). In contrast, LWR which is another splitting component of LAR commonly characterized for leafiness of plant, shows almost linear pattern during its growing period. Between two test plants, tomato had almost constant LWR while eggplant showed gradual decrease (Fig. 3C). Presently, leafiness of both plants differed and tomato showed higher leafy nature and is hardly affected by soil moisture deficit. This was also well supported by the results of leaf number and leaf area documented earlier, *i.e.*, leaf number and area of leaves of tomato plants were remarkably greater than eggplant. ULR, the net gain in weight per unit of leaf area (average rate of assimilation) is another meaningful index of plant growth (Hunt, 1978). Fig. 3D shows that ULR of both plants varied considerably during its different growth stages. Eggplant maintained almost constant ULR under well watered condition but under stress showed comparatively higher at reproductive stages. In the present study, tomato plant evidently found to be more efficient with respect to ULR at the vegetative stage (*Stage I*) and early reproductive stage (*Stage II*).

Table 2. Correlation matrix among different leaf growth parameters and RGR for eggplant and tomato

Treatment Leaf		Eggplant						Tomato					
parameters RGR		L_{dw}	ULR	SLA	LWR	L_A	RGR	L_{dw}	ULR	SLA	LWR	L_A	
Control	L_{dw}	-0.853						0.979*					
	ULR	-0.282	0.740					0.763	-0.847				
	SLA	0.843	-0.441	0.277				0.989*	-0.948	0.658			
	LWR	0.771	0.990*	-0.828	0.309			0.938	0.961*	0.700	0.938		
	L_A	-0.711	0.970*	0.873	-0.222	0.992**		0.988*	0.967*	-0.819	0.959*	-0.882	
	LAR	0.975*	-0.948	-0.489	0.702	0.893	-0.85	0.987*	-0.948	0.652	0.999**	0.945	0.953*
Stress	L_{dw}	-0.668						-0.918					
	ULR	0.469	0.257					0.707	-0.534				
	SLA	-0.096	-0.645	-0.902				0.949	0.950*	0.456			
	LWR	0.604	0.965*	-0.408	0.735			0.960*	0.956*	0.758	0.898		
	L_A	-0.802	0.963*	-0.007	-0.424	-0.876		-0.946	0.996**	-0.553	0.970*	0.962*	
	LAR	0.427	-0.937	-0.57	0.858	0.977*	-0.809	0.966*	0.957*	0.511	0.998**	0.922	0.977*

* and ** represent significant at $p<0.05$ and $p<0.01$ level of significance, respectively.

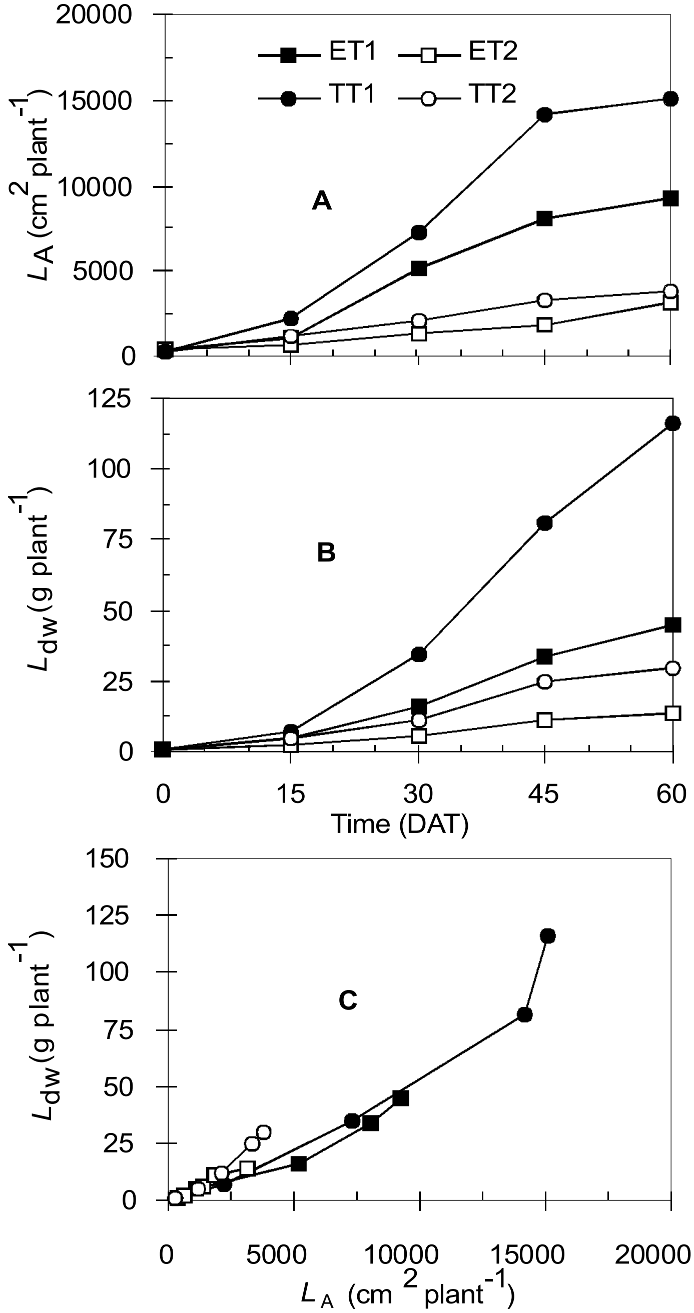

Fig. 2. Leaf area, leaf dry matter of eggplant and tomato, and their relationship under periodic water deficit during different growth stages

Evapotranspiration: The CET of eggplant and tomato plant during 60 days growing period is shown in Fig. 4A. The CET increased with the progression of growth irrespective of water deficit. However, it is important to note that from 7 DAT, both plants started to differ their CET under water deficit. The higher CET was registered by tomato plants than eggplant comparing both soil water conditions. Under deficit condition, CET by both plants was about a quarter of total water use with respect to control. Fig. 4B shows the periodic CET (15-day period) at different growth stages for both plants. Both plants used large amount of water during reproductive stages except water deficit. Eggplant showed the highest CET at *Stage I*, *i.e.*, vegetative stage while tomato plant showed the highest at *Stage II* and *III*, *i.e.*, reproductive stages. The higher CET by tomato plant might be correlated with higher leaf area increase during reproductive stages. Lower ET under soil water stress was also reported in tomato (Hara and Saha, 2000), in potato (Khan *et al.,* 1992), and also in sorghum and cotton (Rosenthal *et al.,* 1987). In the present investigation, we observed that reduced CET was due to water deficit although their amount and time of reduction varied by plant species during different growth stages. The reduced ET is expected to be affected on lower RGR of both plants under water deficit.

Correlation studies: The results of linear correlation coefficient analysis among the leaf growth parameters and RGR shows the interdependence characteristics summarized in Table 2. In tomato

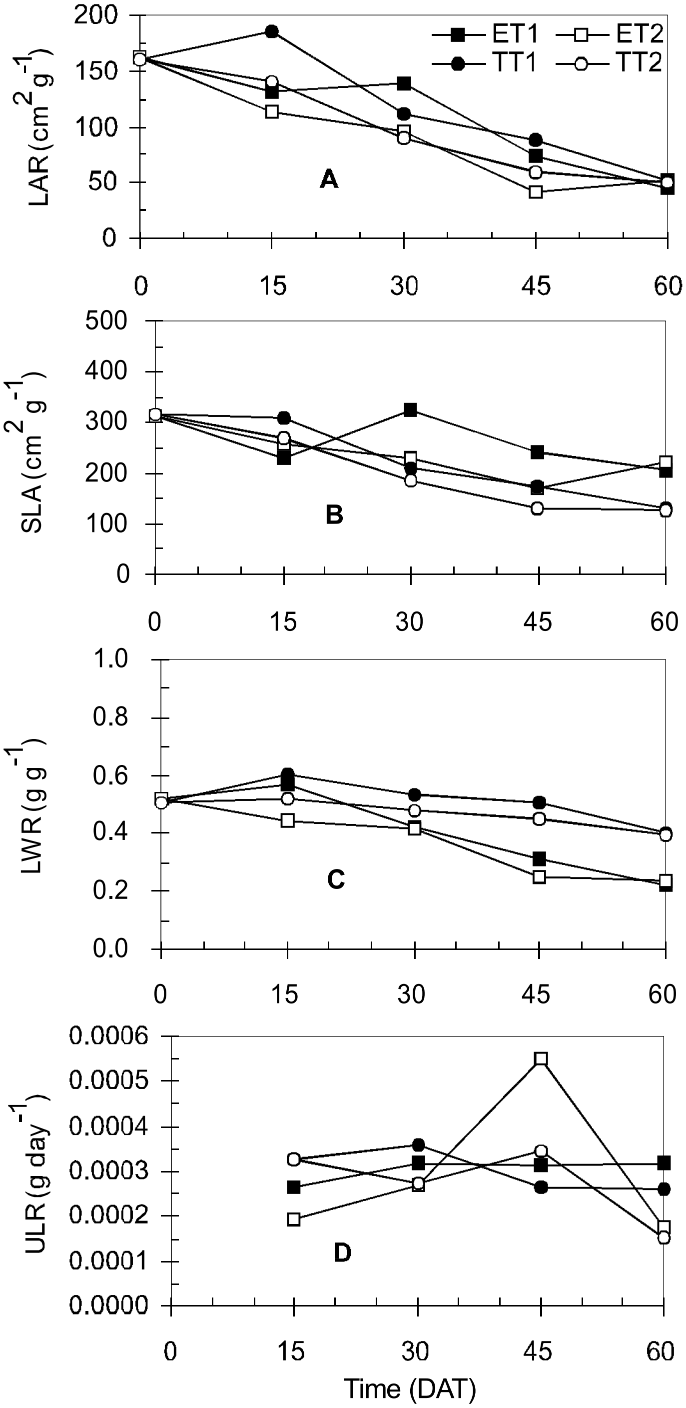

Fig. 3. Leaf growth parameters in terms of LAR, SLA, LWR and ULR of eggplant and tomato, and their relationship under periodic water deficit

plants, L_{dw} had significantly negative relationship with RGR under control. For both plants, LAR had the direct correspondence with RGR except stressed eggplant. A significant interrelationship among LWR, L_A and L_{dw} was observed in both plants. For tomato plants L_A, LAR and SLA showed close relationship among each other in the present investigation but not for eggplant. SLA also had an influence on RGR for tomato under well watered conditions. Furthermore, significant negative correlation existed in eggplant under control condition and water stressed tomato between leaf growth characteristics *viz.* L_A and LWR. LWR also had a positive influence on LAR only for stressed eggplant.

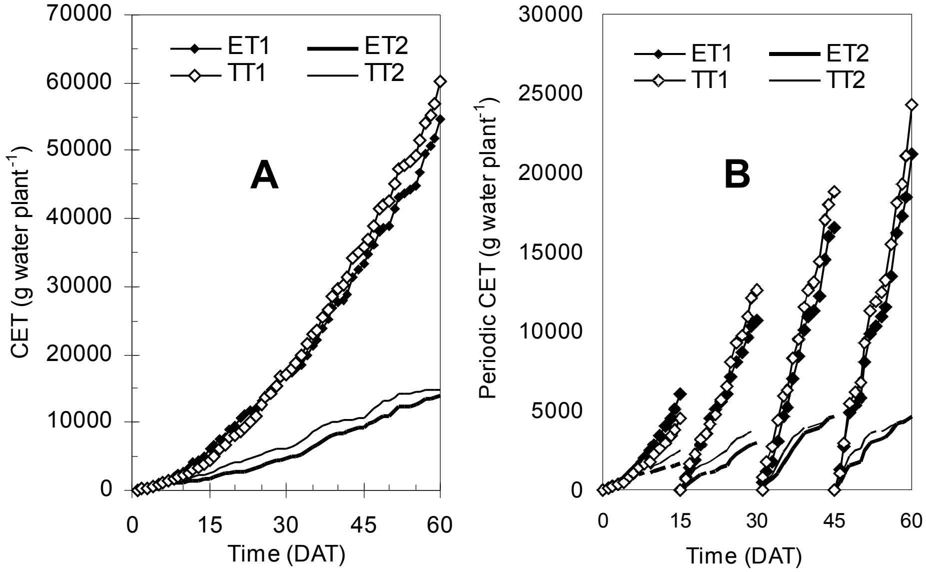

Fig. 4. Cumulative evapotranspiration (CET) and periodic CET at different growth stages of eggplant and tomato under periodic water deficit

Growth analyses: The quantitative RGR analyzed directly based on total plant dry weight following Equation [1] was presented in Fig. 5. A remarkable difference in RGR was observed at different harvest intervals. Initially, the RGR was higher at *Stage I* and *II*, *i.e.*, vegetative stage and early reproductive stage but gradually it decreased. Water deficit was considered an important constraint for RGR. The curves describe the changing RGR at any growth stages which was never constant through out the growing period. Furthermore, RGR analysis based on leaf growth characteristics has been calculated following Equation [3]. The instantaneous values of leaf growth characteristics, *i.e.*, SLA, LWR and ULR, used for the quantitative analysis of RGR have been calculated from directly measured values of L_A, L_{dw} and W following the Equation [4], respectively. The comparative statement of measured RGR and calculated RGR following Equation [1] and [4] has been shown in Fig. 4. Quantitative analysis of RGR based on leaf characteristics fit the data well with measured one. Yet a close inspection of fitted data at different growth stages shows a small discrepancy for both plants. Our calculated results are significantly justified or statistically well agreed in regression analysis ($p < 0.05$), although different leaf growth characteristics of two tested plants appeared differently under water deficit. During the latter part of the growth stage of both, when the plants are large and the absolute growth rates high, LAR makes the major contribution to the fall of RGR (Evans, 1972). The present findings also credibly inform that LAR along with ULR had positive influence on RGR of eggplant and tomato at any growth stage.

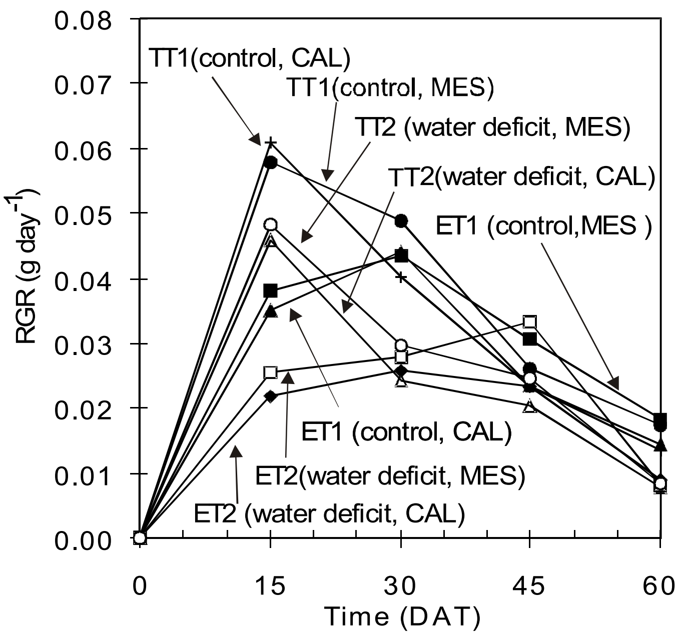

Fig. 5. Calculated (CAL) and measured (MES) RGR of eggplant and tomato at different stages of growing period under periodic water deficit

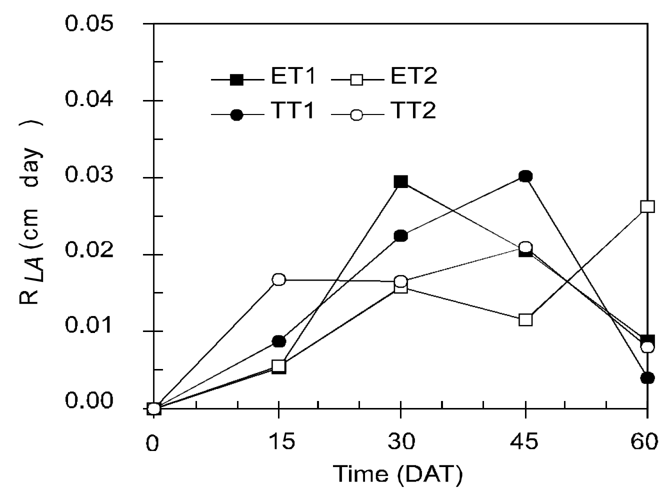

Fig. 6. Relative leaf growth rate (R_{LA}) of eggplant and tomato, and their relationship under periodic water deficit

Fig. 6 represented the calculated R_{LA} using equation [6]. The contrasting characteristics of R_{LA} of eggplant and tomato during different growth stages were observed. In both plants, the rate of R_{LA} in terms of L_A demonstrated a complex growth pattern. Water deficit at reproductive stages inhibited the R_{LA}. Sufficient soil water promoted R_{LA} but finally decreased at latter reproductive stage which was consistent with RGR except stressed eggplant. Eggplant under stress showed higher relative leaf growth rate at late reproductive stages.

From the analysis based on leaf growth characteristics, RGR has been quantified for eggplant and tomato under periodic water deficit at reproductive stages. The Equation [4], although a classical approach, is a useful tool for studying general principles of crop growth and yield ability pattern for plant scientists to apply and interpret their experimental findings. It could conceivably be applied to optimize the supply of water and also nutrient management in the glasshouse and at the field level. Tomato plants demonstrate more competent than eggplant in their water use through ET during reproductive stages. The instantaneous values for leaf growth characteristics, especially leaf thickness characteristics (LAR), evidently showed that tomato plant had more capability for higher RGR than that of eggplant. The present findings suggest that tomato plant efficiently assimilated more carbon and used water through ET than eggplant.

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