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Physiological and morphological responses of rice (*Oryza sativa* L.) to varying water stress management strategies

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Abstract

Sustainability of rice production under limited water conditions is threatened by increasing irrigation water scarcity. Therefore, physiological and morphological responses of rice to varying water stress management strategies should be determined. The physiological and morphological responses of a semi dwarf rice (Hashemi cultivar) to water stress intensities (mild and severe, i.e., short-duration of stress with early recovery and long-duration stress with late recovery, respectively) and timing (mid-tillering, booting and 50% of flowering) were studied in a pot experiment. The severe water stress at mid-tillering significantly ($P<0.05$) decreased plant height and the number of panicle per hill and delayed flowering. The severe water stress at different growth stages caused substantial yield losses by large percentage of unfilled grains. Root weight was highest under mild water stress at 50% of flowering followed by severe water stress at mid-tillering. Relative transpiration (RT) was not lowered until the thresholds of the fraction of transpirable soil water (FTSW), plant available water (PAW) and soil water tension (h) reached to 0.46 (-), 0.9 (-) and 78.0 kPa, respectively. These values were approximately close to those obtained for the relative leaf development rate (RL), as 0.44 (-), 0.91 (-) and 74.6 kPa, respectively. These results indicated that transpiration and leaf development rates have the same sensitivity to water deficits. However, in the mid-tillering, RL was more sensitive to water deficit than RT. The results of thresholds for RT indicated that booting stage is more sensitive than other stages. It is concluded that water tension of 1500 kPa as considered for permanent wilting point is not suitable for rice. Therefore, PAW can not be a suitable soil-water criteria for rice plants that are sensitive to water deficit. Furthermore, It is concluded that Hashemi cultivar is very sensitive to mild and severe drought stress during reproductive stage.

Keywords: Guilan province; Iran; Leaf development; Leaf rolling; Rice; Transpiration; Water stress

Introduction

About 75% of total rice production over the world comes from irrigated lowlands (Guerra et al., 1998). Hashemi cultivar is a semi dwarf rice (*Oryza sativa*) and generally is cultivated in irrigated lowland paddy fields under continuous ponded condition in Guilan province in Islamic Republic (I.R.) of Iran during the period of May to August. The irrigation water requirements of these fields are relatively high due to high seepage and percolation losses. Therefore, sustainability of rice production in this condition is threatened by increasing irrigation water scarcity. The main reasons for irrigation water scarcity are population growth, increasing urban and industrial demand for water, water pollution, water resource depletion (Bouman and Tuong, 2001), climate change due to increasing carbon dioxide concentration in the atmosphere (i.e., global warming) and finally changes in precipitation and solar radiation distribution pattern (Soltani et al., 2001).

Drought may delay the phenological development of the rice plant (Inthapan and Fukai, 1988) and affect physiological processes like transpiration, photosynthesis, respiration and translocation of assimilates to the grain (Turner, 1986). Plant processes that depend on cell volume enhancement are particularly sensitive to water deficit. Leaf expansion and leaf gas exchange rates are two such sensitive processes. At the plant level, reduced leaf area is probably the obvious mechanism by which plants and crops restrict their water loss in response to drought (Sadras and Milory, 1996).

Quantification of physiological and morphological responses of rice to water stress is essential to predict the impact of soil and weather conditions on rice production using process-based crop simulation models. Modeling plant responses to water deficit requires not only an understanding but also quantitative relationships for the effects of water deficits on leaf growth expansion and gas exchange rates (Sadras and Milory, 1996).

Modeling plant responses to water stress requires the proper definition of variables to describe plant and soil water status. The use of soil water content to quantify plant responses to water deficits has a two-fold quality, i.e., it is simple to monitor and it reflects some apparent physiological mechanism. One of the frequently used variables is PAW, the amount of soil water that is currently available for the plant, expressed as a proportion of the maximum amount of plant available water that a soil can hold (Ritchie, 1981). Another variable is the fraction of transpirable soil water (FTSW) defined by Sinclair and Ludlow (1986). Wopereis et al., (1996) evaluated rice physiological and morphological responses to water stress by soil water tension, h (kPa). The advantage of expressing water stress responses as a function of soil-water tension is that it can be employed for any soil type (Bouman et al., 2001). Plants react, in principle, to soil-water tension since the uptake of water by the roots is governed by the difference in water potential in the roots and that in the soil surrounding the roots. Wopereis et al., (1996) showed a decline of relative transpiration (RT) of rice, if the soil water tension dropped below-200 kPa.

Much of the experimental evidence for a number of plants species and experimental conditions have shown the consistent pattern of leaf gas exchange response to extractable soil water (Rosenthal et al., 1987; Muchow and Sinclair, 1991) with exceptions in sandy soils (Gollan et al., 1986; Rosenthal et al., 1987; Soltani et al., 2000). In this pattern, the decrease in leaf gas exchange occurs at around 0.25 of the extractable soil water depletion. Ritchie (1981) proposed that plant gas exchange is unaffected by soil dehydration until the soil dries to less than 0.3 of the FTSW.

According to our knowledge, the effect of water stress on the physiological and morphological responses of Hashemi cultivar has not been studied. The objectives of this study were to determine the effects of varying water stress management strategies on water extraction pattern, soil water content of root zone and growth, yield and yield components of pot-grown rice and their importance evaluation on rice crop performance under limited water conditions.

Materials and Methods

Description of the plant establishment

This experiment was conducted in pots under shelter condition, since imposing water stress in field-grown crops is difficult because of unpredictability of rainfall and possibility of seepage from adjoining plots. This research was carried out in Rice Research Institute located in Rasht, Guilan province, I.R. of Iran, during May-August, 2007.

Rice (Hashemi cultivar) was grown in polyvinyl chloride (PVC) pots with 20 cm diameter and 25 cm height. Three 21-day old seedlings were planted in the center of each pot. All pots were filled with saturated puddled clay soil with the following characteristics on average: sand=12%, silt=42%, clay=46%, θs=0.59 cm^3 cm^{-3}, field capacity=0.51 cm^3 cm^{-3} and permanent wilting point=0.22 cm^3 cm^{-3}. The soil samples were taken from a submerged field at the study area that was plowed and harrowed 8 days before use. Daily weather data (temperature, relative humidity and solar radiation) were recorded at a synoptic weather station located 80 meter distance from the experimental site.

A basal application equivalent to 150 kg N ha^{-1}, 60 kg P ha^{-1} and 50 kg K ha^{-1}, was applied to each pot one day before transplanting (on August 20, 2007) in pots. Additional 50 kg N ha^{-1} and 25 kg K ha^{-1} were added at mid-tillering and panicle initiation stages.

During the experiments, occasional spraying of insecticides and fungicides against rice pest (striped stem borer) and blast disease was carried out to avoid damages.

Intensity and timing of water stress

Water stress treatments were imposed by withholding water application at mid-tillering, booting and 50% flowering stages as treatments A, B and S, respectively. For comparison, a well-watered treatment (WW) was also included in the experiment as control treatment. The experiment was laid out in completely randomized design (CRD), where each treatment replicated 16 times.

Leaf rolling was occurred due to water stress implication. Leaf water status is usually monitored by measuring the leaf water potential (Cabuslay et al., 2002). However, it is slow and is not applicable for mass screening of cultivars. Leaf rolling score, LR, is considered as an alternative way to show leaf water status. It is simply determined visually on the base of the degree of leaf rolling and was found to be highly correlated with maintenance of leaf water potential (O'Toole and Moya, 1987). Leaf rolling reduced canopy photosynthesis, and it is also used to simulate the effect of drought stress on spikelet fertility (Bouman et al., 2001).

The degree of leaf rolling from 0 to 5 was monitored as a stress intensity indicator. It was determined based on a standard chart presented by O'Toole and Cruz (1980). Leaf rolling factor of 1 indicates a first sign of leaf rolling, whereas score 5 means leaf has rolled completely.

The duration of stress was also varied in order to investigate responses and ability of the rice plant to recover from different degrees of stress. In the short-duration treatments of water stress (or mild stressed, early recovery: ER), stressed plants were recovered when plants reached leaf rolling score 5. In the long–duration treatment (or severe stressed, late recovery: LR) plants were recovered when they were close to dying, i.e., leaf rolling score of 5 and roughly 50% dead leaves. However, plant recovery was achieved by re-irrigating the pots to bring the dried soil to saturation. After onset of the recovery period, plants were kept well watered until maturity.

Experiment layout

Pots of the same treatment were concentrated in one block. Four blocks were used in total. In each block, pots were placed side by side on a wooden tray of 10 cm height, with no space in between, to prepare a 20×20 cm planting density. To avoid any influence of pot arrangement on plant growth, pots were rotated daily within the blocks. Each block was surrounded by one row of border pots to make the experimental design similar to what is obtained under field conditions. Border pots received the same treatment as the center pots within a block, but they were not used for any measurement. A large number of replication, i.e., 16, was used in each experiment to allow for periodic destructive sampling from plant.

Plant and soil sampling

Plants from the well-watered treatments were sampled every two weeks. Plants from the stressed treatments were sampled at the start of the recovery and at final harvest. Four pots per treatment were removed for each sampling. Plant components (i.e., green and dead leaves, stems, roots, panicles and grains) were detached and oven-dried for 72 hours at 70˚C. Green leaf area was determined immediately after sampling, using a leaf area meter. Leaf Area Index (LAI) was calculated based on 20×20 cm spacing (Pirmoradian et al., 2004). At harvest (August 21, 2007), yield component analysis was accomplished based on four pots (four replications) per treatment. Plant height was determined from the ground level to the tip of the tallest leaf; and for mature plants it was measured from ground level to the tip of the tallest panicle by using a measuring stick. Height measurements were made daily during the early stage of growth and weekly at the later stage. For all treatments, the actual number of flowering panicles per pot was recorded daily. A visual estimate of the degree of leaf rolling was made daily at midday based on a standard chart presented O'Toole and Cruz (1980). Leaf rolling is usually associated with soil water deficits as an effective mechanism to reduce transpiration losses.

Volumetric soil water contents were measured daily by TDR in pots with stressed plants to determine the soil water status of the root-zone. Soil water contents in the well watered pots were considered as saturated water content.

Actual and potential transpiration rates

In each pot, evaporation losses were minimized by polyethylene cover sheets on the soil surface. All pots, both well-watered and stressed plants (except for border pots) were weighed every evening to estimate daily transpiration losses from the difference in pot weight between successive days. Transpiration rate from the well-watered pots was regarded as potential transpiration (Doorenbos and Pruitt, 1977).

Relative transpiration rates (RT) of stressed plants was measured as the ratio between weight loss of stressed pots and that of well-watered pots (Sinclair and Ludlow, 1986).

Evaporative demand of the air

This experiment was conducted in pots which have no hole for drainage. However, the standing water in pots was refreshed by frequent application of water to prevent CO_2 accumulation. Thus, percolation rate is zero and evaporation demand met from the ponded irrigation water and soil water. The evaporation demand of air was estimated from the transpiration rate of the well-watered plants between 40 and 80 days after transplanting (closed canopy condition). Atmospheric demand is a function of the solar radiation, wind, humidity and air temperatures or sensible heat level (Shaw and Newman, 1985). During 40 to 80 days after transplanting, average daily minimum and maximum temperatures were 17.9 and 29^{o}C, respectively. Average daily sun hours, maximum wind speed and relative humidity were 11.1 h, 4.1 ms^{-1} and 79%, respectively, with an average transpiration rate of 9.8 mm day^{-1} during July 1 to August 10, 2007 (standard deviation, SD: 2.8 mm day^{-1}).

Soil water status

Plant responses to water stress were related to soil water content measured in the pots through daily weighting. The stress levels were expressed as a function of soil water content. For each stress treatment, the fraction of transpirable soil water criterion, FTSW, left in the soil on each day was calculated as follows (Soltani et al., 2000):

$$\text{FTSW}=\frac{ATSW}{TTSW}=\frac{W_t-W_f}{W_i-W_f} \qquad [1]$$

Where ATSW is the actual transpirable soil water determined for each pot as pot weight at specific day (W_t) minus final pot weight (W_f), i.e., pot weight when daily transpiration rate decreased to < 0.1 of well-watered plants; and TTSW is the total transpirable soil water calculated for each treatment as the difference between initial and final pot weight (W_i and W_f, respectively). The upper limit of FTSW is one and it declines with time as soil water availability for transpiration declines.

The plant available water, PAW, described as follows (Ritchie, 1981):

$$\text{PAW}=\frac{\theta_a-\theta_{ll}}{\theta_{ul}-\theta_{ll}} \qquad [2]$$

Where θ is volumetric soil water content and subscripts a, ul and ll denote actual, upper limit (i.e., the water retained by saturated soil) and lower limit (i.e., the water retained by soil at -1.5 MPa), respectively. The PAW criterion varies in the range of one to zero.

Relating the plant drought responses to volumetric soil-water content are risky and can not be generalized because of the differences in soil-water retention characteristics between different soil types. To make results more widely applicable, the volumetric soil water contents were converted to soil-water tension, h (kPa), by soil-water retention curve. The soil-water retention characteristic was determined by using the pressure plate extractor (Dane and Hopmans, 2002). To obtain uniform description of all the soil-water retention curve, the volumetric soil water content, θ, in cm^3 cm^{-3} as a function of soil-water materic head, h in kPa, was described with the following equation (van Genuchten, 1980):

$$\theta(h)=\theta_r+\frac{\theta_S-\theta_r}{\left[1+(\infty h)^n\right]^m} \qquad [3]$$

Where subscripts r and s refer to residual and saturated values, and α, n and m are curve shape parameters. The values of α, n and m (dimensionless) are 0.001 kPa^{-1}, 2.485 (-) and 4.596 (-), respectively.

The plant response expressed as relative transpiration (RT) and relative leaf expansion (RL) to soil water status, FTSW, PAW and h (kPa). They were evaluated using linear spline models. The example application of this model for FTSW is shown as follow (Soltani et al., 2000):

$$\text{RL or RT}=\begin{cases}1 & if\ FTSW_i \geq C_T\\ 1-((FTSW_i-C_T)/(A-C_T)) & if\ FTSW_i \langle C_T\end{cases} \qquad [4]$$

Where FTSWi is the fraction of transpirable soil water on a specific day (i), A is the FTSW when RL or RT reached to zero, C_T is the critical threshold of FTSW demarcating the two stages of the two-piece linear-spline model. In addition, CT can be accounted as the upper limit of soil water criteria or the threshold for which the rate of the process in stressed plants starts to diverge from a reference value. Similarly, Eq (4) was used for RT and RL responses to PAW and h (kPa).

Results and Discussion

There were significant differences (P<0.01) between the effects of intensities of stress (mild and sever) and timing (mid-tillering, booting and 50% of flowering) on plant growth and yield components (Table 1).

Table 1. Analysis of variance for several plant and yield components.

Source	d.f.	Grain yield ($g\ m^{-2}$)	Panicles (per hill)	Filled grains (per panicle)	Unfilled grain (%)	1000-grain weight (g)	Plant height (cm)	Straw (g)	Root weight (g)
Treatment	6	353.456***	36.393***	3455.764***	5054.905***	9.731*	848.143***	353.456***	296.228ns
Residual	21	14.458	5.337	348.663	316.502	2.302	39.095	14.458	119.696
total	27								

nsnon significant.
***Significant at 0.001 significance level in F-tests.
Significant at 0.05 significant level in F-test.

Plant height

Plant height was significantly reduced by severe water stress compared to the well-watered plants (Table 2). In the severe water stress treatment (LR) plant height was significantly reduced at mid-tillering stage treatment (A), (121.5 cm). The decrease in height might be either due to inhibition of cell elongation or cell division by severe water stress. Plant height in mild water stress treatment (ER) did not decrease significantly at 0.05 level of probability (Table 2).

Table 2. Comparison of the means (four replicates) of plant and yield components under various treatments.

Treatment	Grain yield (g m^{-2})	Panicles (per hill)	Unfilled % of grain (per panicle)	1000-grain weight (g)	height (cm)	Straw (g pot^{-1})	Root weight (g pot^{-1})
Well -watered plant							
WW	494^{a}	21^{ab}	8^{a}	23.20^{a}	164.8^{a}	50.5^{bc}	19.3^{bc}
Stress at mid-tillering (A)							
AER	410.4^{a}	25.5^{a}	8^{a}	23.40^{a}	162.3^{ab}	47.4^{b}	17^{c}
ALR	157^{c}	16^{c}	46.45^{b}	23.06^{a}	121.5^{c}	28.3^{a}	35.3^{ab}
Stress at Booting (B)							
BER	234.4^{bc}	20.25^{bc}	65^{bc}	19.77^{b}	156.8^{ab}	54.8^{c}	27.8^{abc}
BLR	209.2^{bc}	18.3^{bc}	85^{c}	21.66^{ab}	150 b	48.2^{b}	22.9^{bc}
Stress at 50% of flowering (S)							
SER	301.2^{b}	20.5^{bc}	81.4^{bc}	21.3^{ab}	158.8^{ab}	57.4^{c}	40.4^{a}
SLR	204.3^{bc}	22.5^{ab}	92^{c}	19.43^{b}	150.5^{b}	48.9^{b}	22.2^{bc}

Water stress induced at A: Mid-tillering; B: Booting; S: 50% of flowering.
ER: early recovery; LR: late recovery.
Common letters within each column do not differ significantly ($P<0.05$) according to Duncan,s test.

The number of panicles

The number of panicles per hill under mild water stress at mid-tillering was the highest (25.5) (Table 2). It seems that mild water stress at mid-tillering affects assimilates translocation from the most plant part to the panicles, via altering source-sink relationships. The reduction in leaf cell expansion would decrease sink strength for vegetative growth and lessen the competition with panicle growth for assimilates. Under severe water stress at mid-tillering, the number of panicles per hill decreased significantly to 16 (Table 2).

Unfilled grain

The percentage of unfilled grain significantly increased with both intensity and postponed water stress toward flowering stage (Table 2). This might be due to the fact that water stress slowed down carbohydrate synthesis and / or weakened the sink strength at reproductive stages and abortion of fertilized ovaries (Rahman et al., 2002). This result is in agreement with those reported by Kumar et al. (2006) who showed that percentage of unfilled grains were significantly higher in sites that were affected by drought at reproductive stage. Water stress at flowering causes flower abortion, grain abscission and increasing of percentage of unfilled grain (Hsiao et al., 1976).

Grain yield

Grain yield significantly decreased by water stress imposed at three growth stages except by mild water stress at mid-tillering (Table 2). Water stress during booting and 50% of flowering produced similar effect, indicating high sensitivity of rice (Hashemi cultivar) to water stress with any intensity (mild or sever) during the reproductive stage (panicle initiation, booting and flowering) of growth. This effect might be due to decrease in translocation of assimilates towards reproductive organs (Rahman et al., 2002).

Root weight

Root weight per pot was highest (40.4 g) under mild water stress at 50% of flowering followed by severe stress at mid-tillering (35.3 g) comparatively with the well-water plants (Table 2). In addition, root weight increased from 19.9 g pot^{-1} at the start of early recovery from drought stress at 50% of flowering to 40.4 g pot^{-1} at harvest stage. O'Toole and Moya (1981) reported that drought might induce more rapid root growth. Hsiao and Xu (2000) reported that roots are capable of growing at low matric potential, down to -1.5 MPa and even lower. The raising of root weight under water stress may be considered as the adaptive mechanism that alleviates the water uptake reduction under drought condition as a result of extra root growth. In this adaptive mechanism, assimilates accumulate and its partitioning from leaves and stems to roots can renew root growth and resulted in exploration of more soil volume which enable plant to obtain more soil water (Hsiao et al., 1976).

Carbohydrate partitioning between shoot and root under water stress is generally altered in favour of the root biomass (O'Toole and Moya, 1981). When leaves stop expanding, photosynthesis still continues and the level of reserve carbohydrates increases, which makes more of them available for growth of the root system (van Keulen and Seligman, 1987).

Delay in flowering

Water stress decreased yield and increased the delay of 50% flowering (DEL in Table 3) in day at mid-tillering and booting stages as compared to well-watered plants (Tables 2 and 3). Turner et al. (1986) showed that water deficit during the vegetative growth stage delays flowering and it is negatively associated with grain yield (Kumar et al., 2006). Woperies et al., (1996) showed that the delay in flowering was reduced if drought was induced at later growth stages. Postponement of flowering in this study was in relative agreement with the number of days between the date of zero leaf expansion and the date of recovery onset (DIF, Table 3). Delay in flowering increased with increasing of DIF. Bouman et al. (2001) indicate that, if the soil is too dry to produce new leaves, the rate of the crop growth and development would be brought to a standstill as well.

Transpiration response to soil water stress

The behavior of combined relative transpiration (RT) data obtained in different water stress treatments as a function of soil-water availability (FTSW, PAW and h) criteria are shown in Figure 1. The linear spline model provided good descriptions of the relationships as indicated by high R^2 values (Table 4). Variation of relative transpiration (RT) below and above 1.0 at moist soil can be explained by micro- environmental variation in and between experiments and error in estimating daily LAI values for well-watered and stressed plants from a limited number of observations (Wopereis et al., 1996). Water stress affected transpiration rates by closure of stomata and change in leaf morphology.

Table 3. Duration of water stress (Du), delay in dates of 50% flowering (DEL) under water deficit compared to well-watered treatment, and the number moment of days between of zero leaf expansion to recovery (DIF). Data are averages of at least 4 replicates.

Treatment	**DU**	**DEL**	**DIF**
	day	**day**	**day**
Stress at Mid-tillering (A)			
AER	11	2	4
ALR	22	23	15
Stress at Booting (B)			
BER	11	3	7
BLR	16	3	11
Stress at 50% of Flowering (S)			
SER	10	0	5
SLR	13	0	7

Water stress induced at A: Mid-tillering; B: Booting and S: 50% of flowering.
Er: early recovery; LR: late recovery.
Du: Duration of water stress (day); DEL: Delay in date of 50% flowering of drought treatments as compared to the well-watered treatment (day) and DIF: the number of days between moment of zero leaf expansion and recovery (day) for rice Hashemi cultivar.

Relative transpiration started to decrease from 1.0 with soil-water tension of about 78 kPa and approached 0.0 at around 185 kPa (Table 4, Figure 1. c). The upper limit of h for relative transpiration was close to 70 kPa as reported by Bouman et al., (2001) but the lower limit was much lower than 1500 kPa as reported by the same authors. These threshold values are different from those reported in literature. Therefore, these values should be determined for other local cultivars as well.

Relative transpiration (RT) did not decline until FTSW and PAW fell below around the critical thresholds of about 0.46 and 0.9, respectively (Table 4). These critical thresholds values were generally higher than those reported in literatures by Sadras and Milroy (1996). The effect of drought timing on RT indicated that booting stage was the most sensitive to water deficit and 50% of flowering being in the next place (Table 5). It is probably due to the larger leaf and plant size and higher transpiration demand of the older plants.

Table 4. Estimates of parameters for rice (Hashemi cultivar) in relative transpiration (RT) and relative leaf development (RL) response to the fraction of transpirable soil water (FTSW), plant available water (PAW) and soil-water tension (h) using linear spline model.

	FTSW			PAW			h (kPa)		
	A	C_T	R^2	A	C_T	R^2	A	C_T	R^2
RT	0	0.46	0.95	0.3	0.9	0.98	185	78	0.81
RL	0	0.44	0.98	0.24	0.91	0.90	180	74.6	0.95

A: is the criteria value when RL and RT reached to zero; CT: is the upper limit of soil-water criteria for which the rate of the process in the stressed plants starts to diverge from a reference value.

Table 5. The upper (UL) and lower limits (LL) of soil water availability criteria (FTSW, PAW and h) relative transpiration (RT), and relative leaf development (RL) for occurring water stress at different growth stage.

Growth stage	RT						RL					
	FTSW[1]		PAW[2]		h(kPa)[3]		FTSW		PAW		h(kPa)	
	UL	LL	UL	LL	UL	LL	UL	LL	UL	LL	UL	LL
Mid-tillering	0.48	0.0	0.44	0.0	73.5	171.6	0.98	0.44	0.91	0.24	73.6	185.0
Booting	0.73	0.0	0.81	0.31	45.0	205.0	Non determined					
Flowering (50%)	0.51	0.0	0.86	0.0	63.7	191.0	Non determined					

[1]FTSW: Fraction of transpirable soil water
[2]PAW: Plant available water.
[3]h (kPa): Soil water tension.

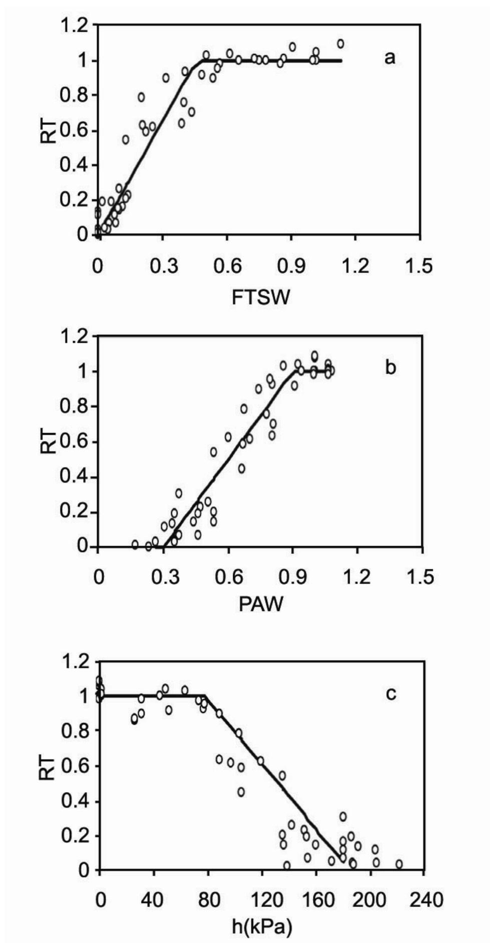

Figure 1. Relative transpiration (RT) as a function of a) Fraction of transpirable soil water (FTSW), b) plant available water (PAW), and c) soil-water tension (h) for Hashemi cultivar. The solid line is the fitted curve to the observed data by the linear spline model.

Leaf development response to soil water stress

Responses of relative leaf development (RL) to soil water stress criteria at mid-tillering stage are shown in Figure 2. At this stage, the upper and lower limits of FTSW and PAW for RL were higher than those for RT (Table 5). These results indicated that leaf area development is considered to be more sensitive to water deficits than transpiration rate due to inhibition of leaf cell expansion or division by water stress. Apparently, this is the consequence of the critical role of the turgor in the leaf cells expansion process (Hsiao et al., 1976). It significantly attributes to reduction in LAI by the effects of translocation via altered source-sink relationships for assimilate. Further, closing of stomata and photosynthesis inhibiting by the stress would be the second factors in this regard. Leaf area development may be hampered due to leaf rolling and early senescence too (O'Toole and Baldia, 1982). Large decline in leaf area under mild water stress is disadvantageous to plants because it leads to reduced nutrient uptake, because of reduced transpiration (O'Toole and De Datta, 1986). Reduced leaf area also decreases carbon assimilation per unit land area (Schulze, 1986).

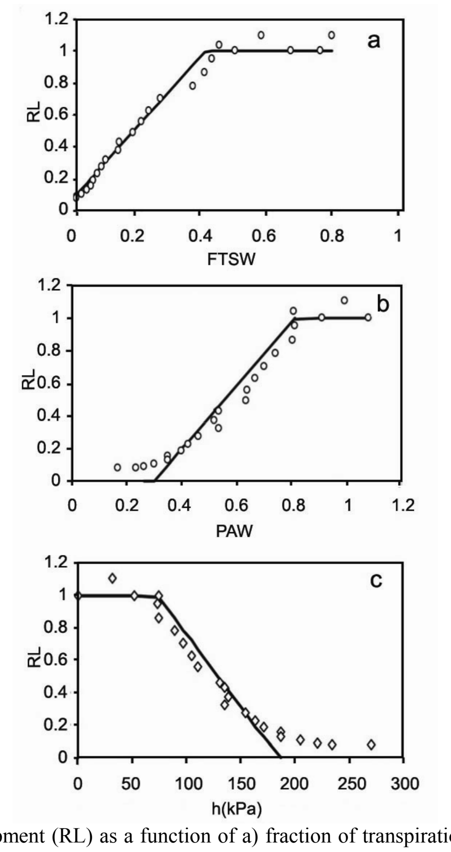

Figure 2. Relative leaf development (RL) as a function of a) fraction of transpiration soil water (FTSW), b) plant available water (PAW), and c) soil-water tension (h) for Hashemi cultivar at mid-tillering stage. The solid line is the regression fit to the data by the linear spline model.

Monitoring leaf morphology vs. soil water stress

The results of relationship between leaf rolling (LR) score and the soil water criteria (FTSW, PAW, and h) are given in Table 6. Leaf rolling started at soil- water tension around 31.3 kPa and it increased sharply at soil water tension of 154 kPa. These results are much lower than those reported (200- 300 kPa for upper limit and 400- 1000 kPa for lower limit) by Bouman et al., (2001). It indicates that Hashemi cultivar is very sensitive to water stress and its threshold values are different from those reported in literature. Therefore, these values should be determined for other local cultivars as well.

The upper and lower limits of soil-water criteria of zero leaf expansion (Table 6) were compared to those of relative transpiration (Table 5). The upper limits of FTSW for zero leaf expansion are close to the upper limits of relative transpiration at mid-tillering. The threshold values of FTSW and PAW for zero leaf expansion were higher than that obtained for relative transpiration. However, the threshold value for h (kPa) was lower for relative transpiration.

The duration of severe water stress in different growth stages were high (22 day in mid-tillering, 16 day in booting and 13 day in 50% of flowering). However, the observed soil-water tension at the end of these stress periods is much lower (mid-tillering =134, booting=153 and 50% of flowering =180 kPa) than that commonly defined for the permanent wilting point, i.e., 1500 kPa. Thus, it seems that PAW can not be a suitable soil-water availability criterion for rice plants that are very sensitive to water deficit. Sadras and Milory (1996) indicated that PAWT, the threshold of PAW, vary widely. Sources of variation in this threshold could be due to physiological process, plant factor, soil factor and evaporative demand. However, the use of soil water tension, h, as a main index should be used with precaution; because it is, only, on the base of thermodynamic characterization of soil water and not on hydraulic conductivity of soils. In the clay soils, unsaturated hydraulic conductivity might be low even at high soil water content. Thus, movement of water to roots became slow and caused water stress on plant.

These results indicated that physiological and morphological responses for different rice cultivars should be investigated under local conditions and and different soil textures.

Table 6. The upper (UL) and lower limits (LL) of soil water availability criteria (FTSW, PAW and h) for water stress effects on zero leaf expansion and leaf rolling.

	FTSW[1]		PAW[2]		h (kPa)[3]	
	UL	LL	UL	LL	UL	LL
Leaf rolling	0.65	0.11	0.94	0.46	31.3	154
Zero leaf expansion	0.48	0.22	0.91	0.67	52.0	104

[1]FTSW: Fraction of transpirable soil water.
[2]PAW: Plant available water.
[3]h (kPa): Soil water tension.

Conclusion

Experiment was carried out to investigate water-stress responses (intensity and timing) of rice grown in puddle clay soil and determine the thresholds of rice plant physiological and morphological responses during drying cycles, when plant responses were monitored as the soil dried progressively in mid-tillering, booting and 50% of flowering growth stages. The severe water stress at mid-tillering significantly decreased plant height, the number of panicles per hill and delayed flowering. The severe water stress at different growth stages resulted to substantial yield losses, caused by large percentage of unfilled grains.

The number of panicles per hill under mild water stress at mid-tillering was highest but their yields were not significantly different from well-watered plants. Root weight was highest under mild water stress at 50% of flowering followed by severe water stress. The thresholds of the fraction of transpirable soil water (FTSW), plant available water (PAM) and soil water tension (h) for relative transpiration (RT) were approximately close to those of relative leaf development (RL). These results indicated that RT and RL have the same sensitivity to water deficits. However, at the mid-tillering, relative leaf development was more sensitive than relative transpiration.

Most of the reduction in leaf area appears to be the consequence of slowed cell expansion, the closing of stomata and inhibition of photosynthesis. The results of thresholds for relative transpiration and relative leaf development at different growth stages indicated that booting stage is more sensitive than other stages. It is concluded that water tension of 1500 kPa as considered for permanent wilting point is not suitable for rice. Therefore, PAW can not be a suitable soil-water criteria for rice plants that are sensitive to water deficit. Furthermore, It is concluded that Hashemi variety is very sensitive to mild and severe drought stress during reproductive stage.

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