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Leaf Expansion and Transpiration Responses of Millet Species to Soil Water Deficit

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ABSTRACT

Plant processes, such as leaf expansion, stomatal conductance and transpiration, are affected by soil water, particularly in water-stressed environments. Quantifying the effects of soil water on plant processes, especially leaf expansion and transpiration, could be useful for crop modeling. In order to quantify the leaf expansion and transpiration in response to soil water deficit in three millet species, common (*Panicum miliaceum* L.), pearl (*Pennisetum glaucum* L.) and foxtail (*Setaria italica* L.) millets, a pot experiment was performed at the Gorgan University of Agricultural Sciences and Natural Resources, Gorgan, Iran. The soil water status was characterized by the fraction of transpirable soil water (FTSW). Leaf area and transpiration were measured daily. Relative leaf area expansion (RL) and relative transpiration (RT) data were plotted against FTSW. Finally the FTSW thresholds for RL and RT were calculated using linear-plateau and logistic models. The results showed that the thresholds for RL and RT were 0.68 and 0.62, respectively, based on all measured data of the three millet species using the linear-plateau model, indicating that RL and RT were constant when FTSW decreased from 1 to the threshold point. Thereafter, until FTSW = 0, RL and RT declined linearly with a slope of 1.48 and 1.43, respectively. Although millet is cultivated as a resistant crop in arid, semiarid and marginal lands, it showed an early response to soil water deficit at high FTSW thresholds. As leaf expansion and transpiration can be considered morphological and physiological variables, respectively, the results in this study indicate that millet has strong morphological flexibility when faced with soil water deficit.

Key Words: linear-plateau model, logistic model, morphological flexibility, plant process, resistant crop, soil water content, threshold

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INTRODUCTION

Water availability is an important determinant of crop growth, development and production, particularly in water-stressed environments (Seghatoleslami, 2008). Available soil water is generally considered to be the amount of water held by soil, ranging between its upper limit, field capacity (FC), and its lower limit, the permanent wilting point (PWP) (Wu *et al.*, 2011b). Within this range, soil water availability to the plant decreases linearly as the soil dries (Thornthwaite and Mather, 1955). Plant processes such as leaf expansion, stomatal conductance, photosynthetic activity, dry matter remobilization and transpiration are all affected by soil water availability (Takami *et al.*, 1981; Connor and Sadras, 1992; Poormohammad Kiani *et al.*, 2007). Cell expansion, cell wall synthesis and protein synthesis in rapidly growing tissues are the processes most sensitive to water deficit (Hsiao *et al.*, 1976, 1985; Lawlor and Leach, 1985; Sadras and Milroy, 1996). Among drought adaptation strategies, water loss can be minimized by reducing the leaf area, the transpiration per unit leaf area (stomatal conductance) or by reducing the energy load of the plant (extinction coefficient) (Sadras *et al.*, 1993; Weisz *et al.*, 1994; Williams II *et al.*, 2008; Gilbert *et al.*, 2011).

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Typical responses of leaf expansion and leaf gas exchange rate to plant-available soil water (PAW) can be described by two straight lines that intersect at $\mathrm{PAW_t}$, *i.e.*, the PAW threshold, or from the onset of the decline, for which the rate of the process in stressed plants starts to diverge from a reference value (Sadras and Milroy, 1996). Quantifying the effects of soil water on plant processes, especially leaf expansion and transpiration, will be useful to crop modeling (Lecoeur and Sinclair, 1996; Soltani *et al.*, 2000). Soil water status is characterized by the fraction of transpirable soil water (FTSW) that remains in the soil. Total transpirable soil water (TTSW) is defined as the difference between the soil water content at FC or pot capacity, and the soil water content when transpiration of the water deficit-stressed plants decreases to 10% or less of that of well-watered plants (Soltani *et al.*, 2000). Sadras and Milroy (1996) provide a review of the soil water thresholds of several plant processes, suggesting that the threshold for tissue expansion is higher than that for gas exchange. Several studies have been conducted to determine leaf expansion and transpiration in chickpea (Soltani *et al.*, 2000), sunflower (Casadebaig *et al.*, 2008), maize and winter wheat (Wu *et al.*, 2011a, b) under various conditions. These studies were often conducted in two locations, a greenhouse and a field, and growth conditions varied. Fitted models can be used to determine thresholds, and such models can either be logistic, linear-spline (Soltani *et al.*, 2000; Casadebaig *et al*, 2008), linear-plateau (Wu *et al.*, 2011a), inverse exponential (Devi *et al.*, 2009) or quadratic (Jefferies and MacKerron, 1993), among others.

Millet has the potential to improve nutrition and boost food security, especially in semiarid regions (Mukarumbwa and Mushunje, 2010) because of their adaptability to such environments (Taylor, 2003). The grains of millet are rich in protein, mineral nutrients, and vitamins, so it is considered as food for humans in developed countries (Seetharam, 1999; Baltensperger, 2002; Dobránszki and Gondola, 2012).

Although many studies have widely indicated that millet species are tolerant to water deficit (Karou *et al.*, 2005; Seghatoleslami *et al.*, 2008; Heidari, 2012), other studies did not confirm this theory. Dai (2012) showed that leaf senescence, photosynthesis, chlorophyll content and the activity of antioxidative enzymes may be affected by water availability in foxtail millet (*Setaria italica* (L.) P. Beauvois). Singh and Singh (1995) showed that, under wet, moderately stressed and severely stressed conditions, water use efficiency in pearl millet (*Pennisetum glaucum* (L.) R. Br.) was lower than that in maize (*Zea mays* L.) and sorghum (*Sorghum bicolor* (L.) Moench). Maman *et al.* (2003) also agreed that, with respect to drought resistance, the seed yield of pearl millet was less stable than that of sorghum. Tfwala (2010) indicated that the water potential of pearl millet decreased to as low as -1.83 MPa after withholding rain for 11 d followed by water stress experienced by plants. The thresholds of leaf and stem expansion were less than 0.3 and 0.8, respectively, for pearl millet under field conditions when evapotranspiration was 6 and 9 mm $\mathrm{d^{-1}}$, respectively (McIntyre *et al.*, 1993).

Even though considerable research has been conducted to determine soil water thresholds for leaf expansion and transpiration of maize (NeSmith and Ritchie, 1992), wheat (Meyer and Green, 1980) and sorghum (Rosenthal *et al.*, 1987; Hammer and Muchow, 1990), few studies exist for that of millet species. Moreover, there are no studies on the quantification of soil water relations with leaf expansion and transpiration in millet as an alternative crop in poor and dry soils. Therefore, the objectives of this study were to quantify leaf expansion and transpiration of three millet species in response to soil water deficit and determine soil water thresholds using logistic and linear-plateau models.

MATERIALS AND METHODS

Experimental site, plant, and soil

A pot experiment was conducted in the summer of 2010 in a greenhouse at Gorgan University of Agricultural Sciences and Natural Resources (36° N, 54° E), Gorgan, Iran. Common millet (*Panicum miliaceum* L.), pearl millet (*Pennisetum glaucum* L.) and foxtail millet (*Setaria italica* L.), which are the main cultivated species in Iran, were used in this study. Their seeds were obtained from the Seed and Plant Improvement Institute, Karaj, Iran. The soil used was 60% (loam), 34% (clay) and 6% (silt) in texture.

Pot experiment

The pot experiment of this study was conducted following the methodology of Sinclair and Ludlow (1986), Lecoeur and Sinclair (1996), and Soltani *et al.* (2000). Thirty pots were used (15 pots each for water-stressed and well-watered treatments) for each millet species. The pot was 50 cm in height with a 30-cm radius, and each pot was filled with soil. The outer walls of the pots were covered with a thick layer of white paint to prevent excessive warming.

The seed germination test (percentage of normal seedling emerged) was performed as recommended by the International Seed Testing Association in three replications (ISTA, 1995). Common, foxtail and pearl millets had 95%, 98% and 92% normal seeds, respectively. Ten seeds were sown in each pot. Soil moisture was consistently maintained at FC during germination. During the period of emergence, the pot temperatures were kept at 25 to 35 °C in the greenhouse. After establishment, seedlings were thinned to four plants in each pot.

All the pots were well-watered until 6–7 leaves appeared (15–20 d after planting as an average across the three species). The pots had no bottom drainage. In the afternoon prior to the start of water-stress treatments, all pots were fully watered to FC (Miller and Donahue, 1990). On the next day, the soil surface of the pots was covered with 80 g of medium-size perlite to prevent soil evaporation. Two tubes were placed in each pot so that water could be added to the soil below the surface without wetting the perlite. Then, the pots were weighed to record initial pot weights. The experiment lasted for 12 to 16 d, depending on the species.

Implementation of water deficit and calculation of FTSW

Every evening throughout the pot experiment, each pot was weighed as daily pot weight. The difference in weight on successive days was considered to be daily transpiration. In well-watered plants, the amount of water reduced was added daily to pots. In water-stressed plants, the reduced water was not added to any pot until relative daily transpiration rate decreased to < 0.1 of that in well-watered plants.

Soil water status was characterized by the fraction of transpirable soil water (FTSW), which was calculated from Eq. 1:

$$\mathrm{FTSW} = \frac{\mathrm{ATSW}}{\mathrm{TTSW}} = \frac{W_{\mathrm{d}} - W_{\mathrm{f}}}{W_{\mathrm{i}} - W_{\mathrm{f}}} \tag{1}$$

where W_{i} (kg) is the initial pot weight determined by weighing each pot before the start of the water-stressed treatment (soil water content at FC); W_{f} (kg) is the final pot weight when daily transpiration rate in water-stressed plants decreased to < 0.1 of that in well-watered plants; W_{d} (kg) is the daily pot weight which was recorded every evening; ATSW (kg) is the actual transpirable soil water for each pot calculated as the difference between daily and final pot weights; and TTSW (kg) was the total transpirable soil water for each pot calculated as the difference between initial and final pot weights.

Leaf expansion and transpiration

Leaf area of all four plants in each pot was measured every afternoon by a portable leaf area meter (AM300, ADC Bio-scientific Ltd., Herts, UK) with no destructiveness. This was done for all three millet species. Daily transpiration was measured by weighing pots as explained in the previous section. Relative transpiration (RT) and relative leaf area expansion (RL) for individual water-stressed plants were expressed as ratios between the values obtained for stressed plants and the means of well-watered plants (Soltani *et al.*, 2000). For RL, the data of four individual plants (not averaged) in each pot were used. For RT, one value for each pot was used.

Models and parameters

To determine the soil water thresholds for leaf expansion and transpiration response, a linear-plateau model (Wu *et al.*, 2011a) was used to describe the responses of RL and RT to the fraction of transpirable soil water (FTSW) in Eq. 2:

$$\mathrm{RL} = \begin{cases} a_{\mathrm{L}} + b_{\mathrm{L}} \times \mathrm{FTSW} \ \textit{if} \ \mathrm{FTSW} < \mathrm{FTSW}_0 \\ a_{\mathrm{L}} + b_{\mathrm{L}} \times \mathrm{FTSW}_0 \ \textit{if} \ \mathrm{FTSW} \geq \mathrm{FTSW}_0 \end{cases} \tag{2}$$

where FTSW_0 is the threshold value of FTSW, a_{L} and

b_{L} are the intercept and slope, respectively, of the linear part of the model for RL; and a_{T} and b_{T} are the intercept and slope, respectively, of the linear part of the model for RT, and Eq. 3:

$$\mathrm{RT} = \begin{cases} a_{\mathrm{T}} + b_{\mathrm{T}} \times \mathrm{FTSW} \ \textit{if}\ \mathrm{FTSW} < \mathrm{FTSW}_0 \\ a_{\mathrm{T}} + b_{\mathrm{T}} \times \mathrm{FTSW}_0 \ \textit{if}\ \mathrm{FTSW} \geq \mathrm{FTSW}_0 \end{cases} \tag{3}$$

A logistic model (Muchow and Sinclair, 1991; Soltani *et al.*, 2000) was also used to describe their relations in Eq. 4:

$$\mathrm{RL} = \left\{ \frac{2}{1 + \exp[B_{\mathrm{L}}(\mathrm{FTSW} - A_{\mathrm{L}})]} \right\} - 1 \tag{4}$$

where B_{L} is a regression coefficient for RL; A_{L} is the FTSW value when RL reaches zero; B_{T} is a regression coefficient for RT; and A_{T} is the FTSW value when RT reaches zero, and Eq. 5:

$$\mathrm{RT} = \left\{ \frac{2}{1 + \exp[B_{\mathrm{T}}(\mathrm{FTSW} - A_{\mathrm{T}})]} \right\} - 1 \tag{5}$$

The parameters were estimated in Microsoft Excel software by using a Solver procedure based on iterative optimization procedure.

The coefficient of determination (R^2) and the root of mean square error (RMSE) were used to evaluate the precision of the simulations. The RMSE and R^2 were calculated in Eq. 6:

$$\mathrm{RMSE} = \sqrt{\frac{\sum_{i=1}^{n}(Y_i - \hat{Y}_i)^2}{n}} \tag{6}$$

where Y_i and $\hat{Y}_i$ are the measured and simulated values for the ith observation, respectively; n is the total number of observations; and $\bar{Y}$ is the mean of the observed data, and Eq. 7:

$$R^2 = \frac{\sum_{i=1}^{n}(Y_i - \hat{Y}_i)^2}{\sum_{i=1}^{n}(Y_i - \bar{Y})^2} \tag{7}$$

RESULTS AND DISCUSSION

Leaf expansion of three millet species

Based on the linear-plateau model, the FTSW threshold for RL response to soil water deficit was predicted to be 0.78 (R^2 = 0.91**, RMSE = 0.114) in common millet, 0.50 (R^2 = 0.82**, RMSE = 0.165) in pearl millet, and 0.68 (R^2 = 0.88**, RMSE = 0.112) in foxtail millet, which implied that RL was constant when FTSW decreased from 1 to the threshold point (Table I, Figs. 1–3). Thereafter, until FTSW = 0, the

TABLE I

Parameter estimates[a)], coefficient of determination (R^2), and root of mean square error (RMSE) of the linear-plateau model fitting relative leaf area expansion (RL) and relative transpiration (RT) in response to soil water deficit in three millet species

Species	RL					
	FTSW_0	a_{L}	b_{L}	R^2	RMSE	n
Common millet	0.78	−0.055	1.37	0.91**	0.114	255
Pearl millet	0.50	−0.004	2.08	0.82**	0.165	388
Foxtail millet	0.68	−0.020	1.53	0.88**	0.112	620
Combined	0.68	0.014	1.48	0.83**	0.146	

Species	RT					
	FTSW_0	a_{T}	b_{T}	R^2	RMSE	n
Common millet	0.58	0.050	1.61	0.92**	0.096	88
Pearl millet	0.57	0.053	1.47	0.92**	0.084	73
Foxtail millet	0.64	−0.041	1.45	0.77**	0.111	48
Combined	0.62	0.059	1.43	0.88**	0.107	

**Significant at $P < 0.01$.

[a)] FTSW_0 is the threshold value of the fraction of transpirable soil water (FTSW); a_{L} and b_{L} are the intercept and slope, respectively, of the linear part of the model for RL; and a_{T} and b_{T} are the intercept and slope, respectively, of the linear part of the model for RT.

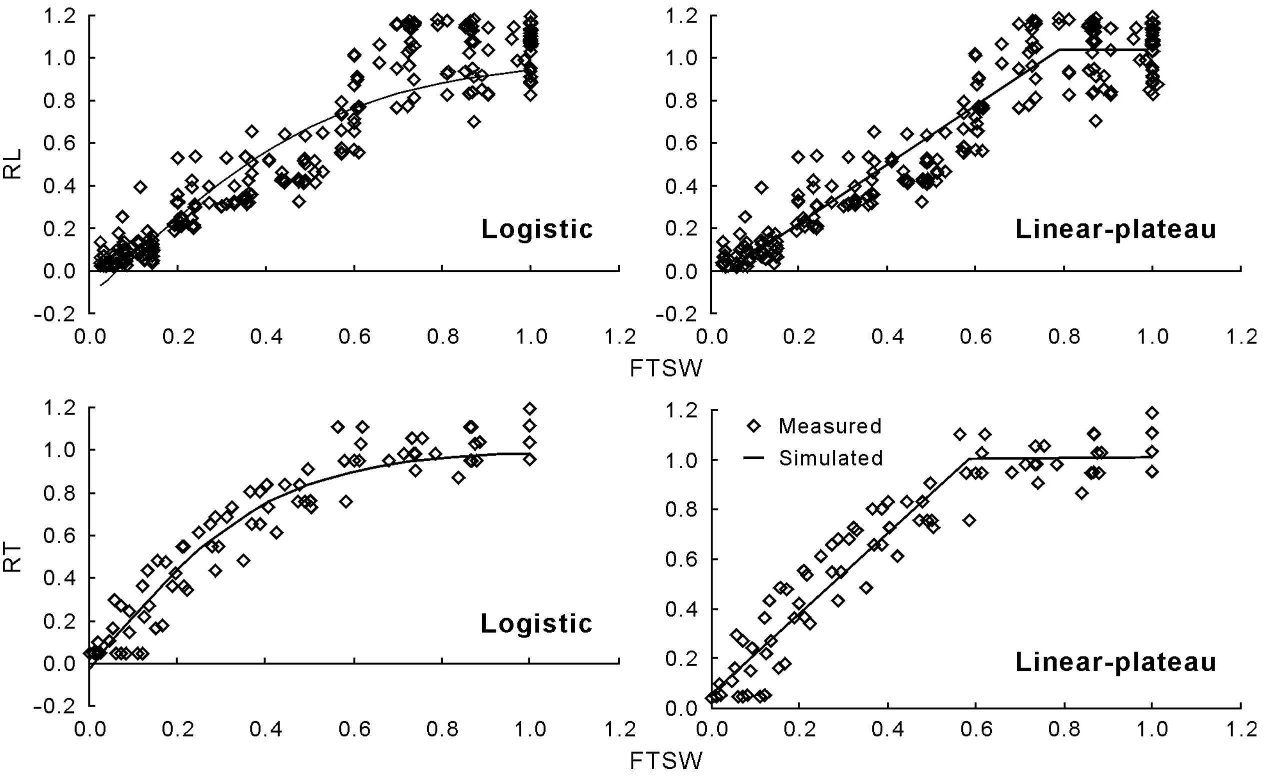

Fig. 1 Relative leaf area expansion (RL) and relative transpiration (RT) *vs.* the fraction of transpirable soil water (FTSW) for common millet fitted by logistic and linear-plateau models. Each point is related to one plant for RL and one pot for RT.

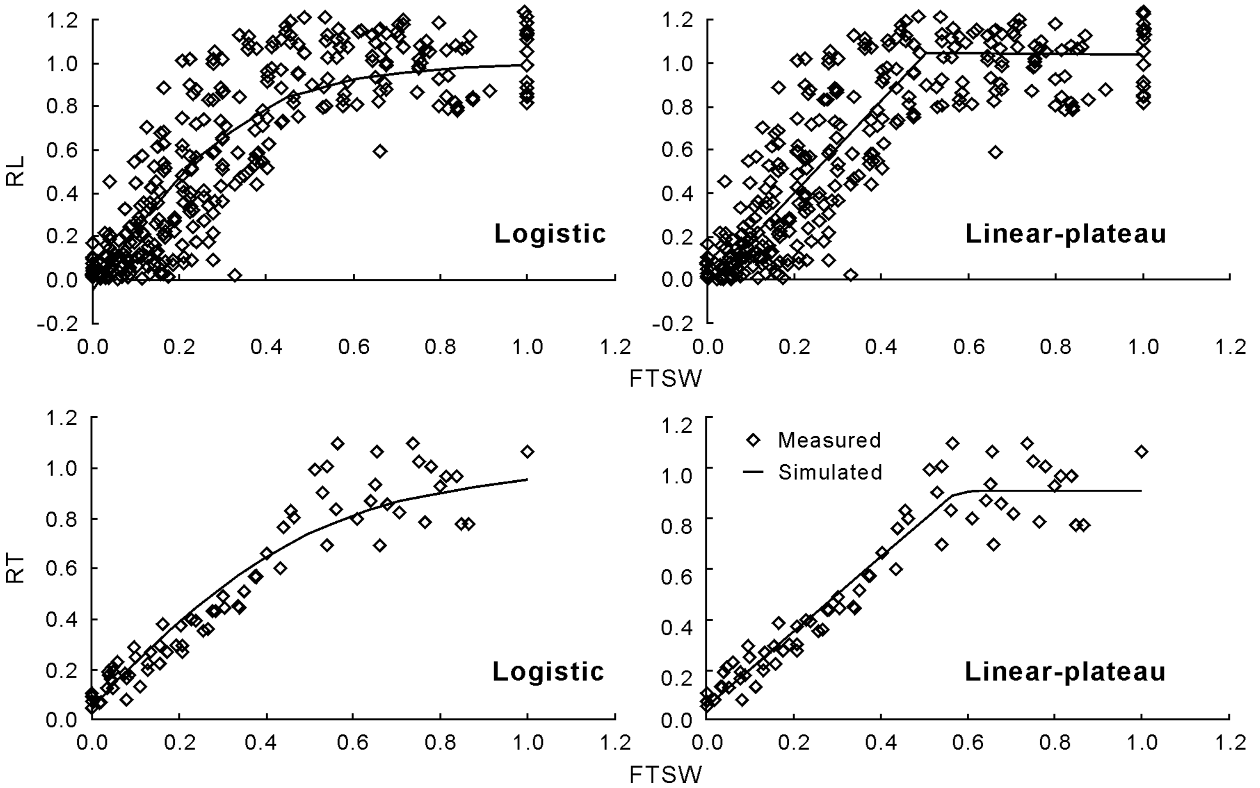

Fig. 2 Relative leaf area expansion (RL) and relative transpiration (RT) *vs.* the fraction of transpirable soil water (FTSW) for pearl millet fitted by logistic and linear-plateau models. Each point is related to one plant for RL and one pot for RT.

RL declined linearly with a slope of 1.37, 2.08, and 1.53 for common, pearl and foxtail millets, respectively (Table I). Based on the logistic model, the parameter A_L was predicted to be 0.063 ($R^2 = 0.91^{**}$, RMSE = 0.128) in common millet, 0.018 ($R^2 = 0.80^{**}$, RMSE = 0.160) in pearl millet, and 0.063 ($R^2 = 0.85^{**}$, RMSE = 0.111) in foxtail millet (Table II).

In general, based on all measured data of three spe-

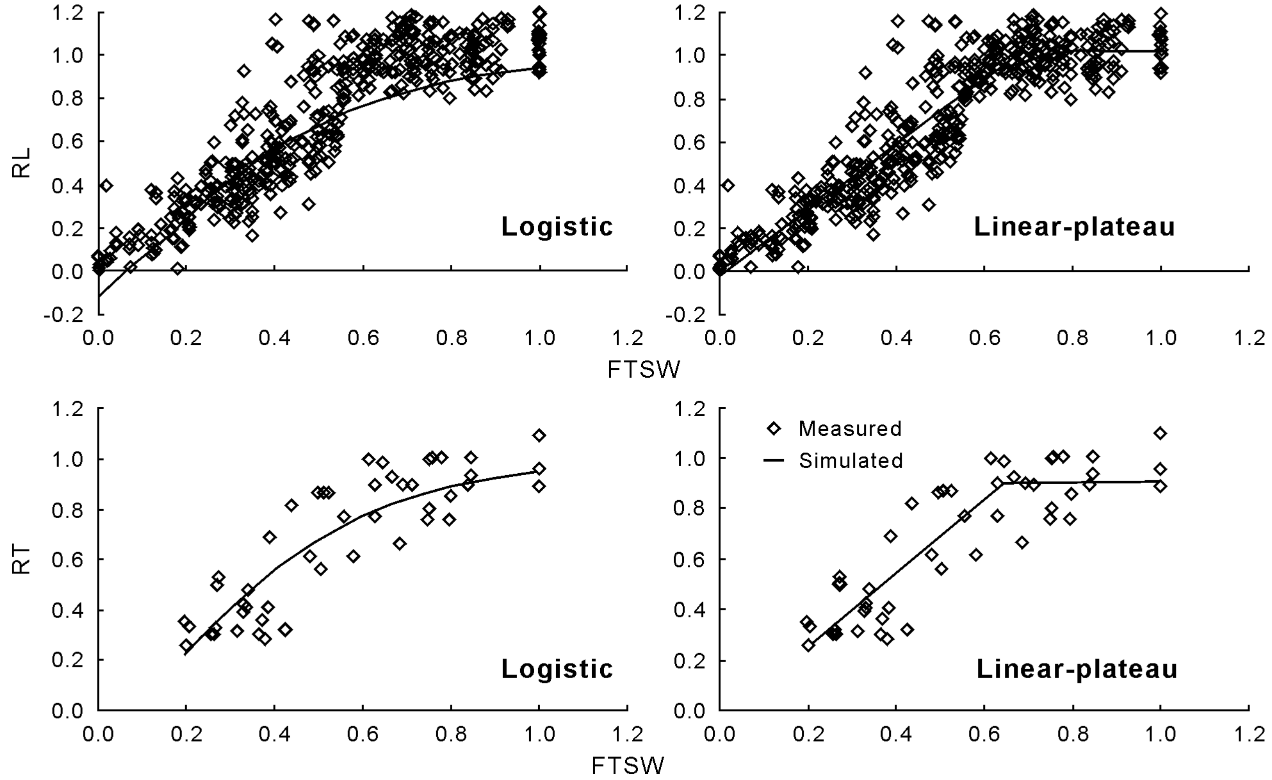

Fig. 3 Relative leaf area expansion (RL) and relative transpiration (RT) *vs.* the fraction of transpirable soil water (FTSW) for foxtail millet fitted by logistic and linear-plateau models. Each point is related to one plant for RL and one pot for RT.

TABLE II

Parameter estimates[a)], coefficient of determination (R^2), and root of mean square error (RMSE) of the logistic model fitting relative leaf area expansion (RL) and relative transpiration (RT) in response to soil water deficit in three millet species

Species	RL				
	B_L	A_L	R^2	RMSE	n
Common millet	−3.748	0.063	0.91**	0.128	255
Pearl millet	−5.560	0.018	0.80**	0.160	388
Foxtail millet	−3.748	0.063	0.85**	0.111	620
Combined	−4.320	0.029	0.80**	0.146	

Species	RT				
	B_T	A_T	R^2	RMSE	n
Common millet	−4.960	0.011	0.92**	0.092	88
Pearl millet	−3.618	−0.025	0.92**	0.087	73
Foxtail millet	−4.00	0.085	0.77**	0.108	48
Combined	−3.96	−0.002	0.87**	0.108	

**Significant at $P < 0.01$.

[a)] B_L is a regression coefficient for RL; A_L is the FTSW value when RL reaches zero; B_T is a regression coefficient for RT; and A_T is the FTSW value when RL reaches zero.

cies using the linear-plateau model, the threshold for RL response to soil water deficit was predicted to be 0.68 (R^2 = 0.83**, RMSE = 0.146), which indicated that RL was constant when FTSW decreased from 1 to 0.68 (Fig. 4, Table I). Thereafter, until FTSW = 0, the RL declined linearly with a slope of 1.48 (Table I). Based on the logistic model, the parameter A_{L} was predicted to be 0.029 (R^2 = 0.80**, RMSE = 0.146) (Table II).

The results of this study showed that the FTSW threshold for RL of pearl millet (FTSW_0 = 0.50) was lower than those of the other two millet species (foxtail millet, FTSW_0 = 0.68; common millet, FTSW_0 = 0.78). In contrast, the decline in RL of pearl millet after the threshold point (b_{L} = 2.08) was faster than that of the other two millet species (foxtail millet, b_{L} = 1.53; common millet, b_{L} = 1.37) (Table I). Although pearl millet had a lower FTSW threshold than the other two species, it responded quickly to reduce leaf area expansion after the threshold point. The leaf area expansion stopped (RL = 0) at a lower FTSW in pearl millet (A_{L} = 0.018) than foxtail millet (A_{L} = 0.063) and common millet (A_{L} = 0.063) (Table II).

Many studies have shown stability in the daily transpiration of plants and in the responses of leaf expansion to drying soil over a wide range of conditions, but plants' thresholds may vary in different conditions (Sadras and Milroy, 1996; Sinclair, 2005). McIntyre *et al.* (1993) indicated that the plant-available soil water (PAW) threshold for leaf and stem expansion of pearl millet under field conditions (with reference evapora tion of < 6 and < 9 mm d^{-1}) are estimated at less than 0.3 and 0.8, respectively (quoted from Sadras and Milory, 1996), which were comparable with our study's findings for pearl millet. The physiology and water requirements of maize, sorghum and millet may be similar. Rosenthal *et al.* (1987) reported that the thresholds for sorghum leaf area expansion under glasshouse-pot and field-lysimeter conditions were 0.5 and 0.44, respectively. Wu *et al.* (2011a) used a linear-plateau model to predict the threshold for RL response to soil water deficit in maize and found that the threshold was 0.72 with the declining slope of 1.94 after the threshold point.

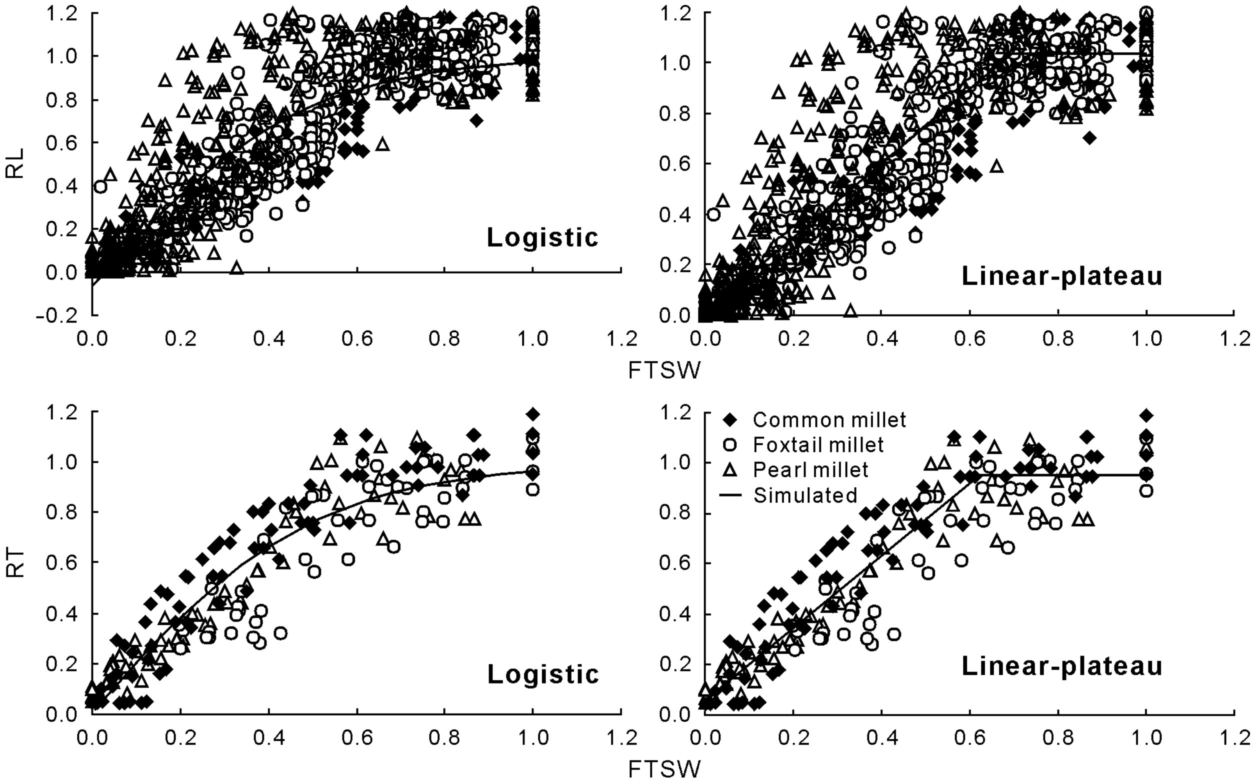

Fig. 4 Relative leaf area expansion (RL) and relative transpiration (RT) *vs.* the fraction of transpirable soil water (FTSW) for three millet species fitted by logistic and linear-plateau models. Each point is related to one plant for RL and one pot for RT.

Transpiration of three millet species

Based on the linear-plateau model, the threshold for RT response to soil water deficit was predicted to be 0.58 ($R^2 = 0.92^{**}$, RMSE = 0.096) in common millet, 0.57 ($R^2 = 0.92$, RMSE = 0.084) in pearl millet, and 0.64 ($R^2 = 0.77$, RMSE = 0.111) in foxtail millet, which indicated that RT was constant when FTSW decreased from 1 to the threshold point (Table I, Figs. 1–3). Thereafter, until FTSW = 0, the RT declined linearly with a slope of 1.61, 1.47 and 1.45 for common, pearl and foxtail millets, respectively (Table I). Based on the logistic model, the parameter A_{T} was predicted to be 0.011 ($R^2 = 0.92^{**}$, RMSE = 0.092) in common millet, −0.025 ($R^2 = 0.92^{**}$, RMSE = 0.087) in pearl millet, and 0.085 ($R^2 = 0.77$, RMSE = 0.108) in foxtail millet (Table II).

In general, based on all measured data of three species using the linear-plateau model, the threshold for RT response to soil water deficit was predicted to be 0.62 ($R^2 = 0.88^{**}$, RMSE = 0.107), which indicated that RT was constant when FTSW decreased from 1 to 0.62 (Fig. 4, Table I). Thereafter, until FTSW= 0, the RT declined linearly with a slope of 1.43 (Table I). Based on the logistic model, the parameter A_{T} was predicted to be −0.005 ($R^2 = 0.87^{**}$, RMSE = 0.108) (Table II).

The results of this study also showed that the threshold for RT in pearl millet ($\mathrm{FTSW}_0 = 0.57$) was lower than that of the other two species (common millet, $\mathrm{FTSW}_0 = 0.58$; foxtail millet, $\mathrm{FTSW}_0 = 0.64$), while the decline in RT of foxtail millet (b_{T} =1.45) after the threshold point was lower than that of the other two species (pearl millet, $b_{\mathrm{T}} = 1.47$; common millet, $b_{\mathrm{T}} = 1.61$) (Table I). Wu *et al.* (2011a) used a linear-plateau model for predicting the threshold for daily transpiration of maize (0.85), and found that the decreasing slope after the threshold point was 1.24. Wu *et al.* (2011b) obtained a threshold and slope of 0.80 and 1.28, respectively, in their another study. The threshold for RT predicted from all measured data of three millet species (*i.e.*, $\mathrm{FTSW}_0 = 0.62$) in this study was lower than the average threshold predicted by Wu *et al.* (2011a, b) and higher than the average of 0.37 calculated by Sadras and Milroy (1996) across species, growing conditions and methods.

The leaf expansion and transpiration thresholds predicted from the all measured data of the three millet species were 0.68 and 0.62, respectively. Even though millet is cultivated as a water deficiency-resistant crop in arid, semiarid and marginal lands (Dai *et al.*, 2008, 2009; Tfwala, 2010; Heidari, 2012), the millet species investigated in this study had a quick response to soil water deficit at high FTSW thresholds. Relative transpiration began to decrease at a lower FTSW threshold than RL, except in pearl millet (Table I). As leaf expansion and transpiration are considered as morphological and physiological variables, millet has strong morphological flexibility since transpiration started to decline at a lower FTSW threshold than leaf expansion.

CONCLUSIONS

Three millet species showed different responses to soil water deficit in terms of leaf expansion and transpiration. Even though millet is traditionally categorized as a water deficiency-resistant crop, the results in this study, specifically the inflection points, indicated that this crop responded to soil water deficit at high FTSW thresholds. These important thresholds and related decreasing slopes (1.48 and 1.43, respectively) could be used in simulation models which are involved in quantifying the effects of soil water deficit on leaf expansion and crop yield.

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