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Responses of Physiological Traits of Maize to Water Deficit Induced at Different Phenological Stages

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ABSTRACT

Two field experiments were conducted to evaluate the physiological responses of maize to water deficit conditions. Five water regimes (control, water deficit from V10 to V13, V13 to V17, V17 to blister and blister to physiological maturity) and 3 maize genotypes including Pioneer 30B80, NK 40 and Suwan 4452 were tested under moderate water deficit (MWD). Based on their better physiological performance, NK 40 and Suwan 4452 were further evaluated under severe water deficit (SWD) levels (control, water deficit from V10 to anthesis, anthesis to milk and milk to physiological maturity). The omission of irrigation in the moderate and severe water deficit regimes decreased the soil water potential and resulted in a significant decrease in the relative water content (RWC), chlorophyll content, leaf area (LA) and dry matter (DM) accumulation compared to the control. A greater decrease in the RWC (13.66 and 29.78%) at the V17 and anthesis stages, chlorophyll content (12.75 and 49.44%) at the V17 and late grain filling stages, LA (50.01 and 36.64%) at the V13 and milk stages and DM (15.98 and 14.60%) at the V17 and late grain filling stages was found under moderate and severe water deficit, respectively. The most susceptible stage to MWD and SWD was the V13 to V17 stage and the anthesis to milk stage, respectively in terms of grain yield reduction. After rewatering, the RWC fully recovered or was close to the control level under both water deficits while recovery of chlorophyll was relatively higher in the moderate water stress regime. Rewatering after water deficit at an early stage resulted in a recovery in leaf area but rewatering after anthesis failed to recover leaf area under both experiments. NK 40 demonstrated better performance regarding sustaining a relatively higher RWC and chlorophyll content and a higher yield under both stress environments compared to the other genotypes. The relative water content, chlorophyll content and grain yield showed negative relationships with the available soil water depletion (%), while the grain yield showed a positive relationship with the relative water content and chlorophyll content under both water deficit experiments which can be used as an index for drought screening.

Keywords: water deficit, rewatering, genotypes, physiological traits, maize

INTRODUCTION

Drought is one of the major causes for crop loss worldwide, reducing average yields by 50% or more (Wang *et al.*, 2003). The lack of adequate soil moisture or water deficit, affect the ability of plants to grow and complete a normal life cycle (Moussa and Abdel - Aziz, 2008). The reaction of plants to drought differs significantly at various organizational levels depending upon

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the intensity and duration of stress as well as the plant species and the stage of development (Chaves *et al.*, 2003). It is well established that drought stress impairs numerous metabolic and physiological processes in plants (Levitt, 1980). The water content has been widely used to quantify water deficits in leaf tissues. The leaf water content is a useful indicator of plant water balance since it expresses the relative amount of water present in the plant tissues (Yamasaki and Dillenburg, 1999). Atteya (2003) found that drought stress significantly altered the internal water status in maize by lowering the osmotic potential and the relative water content, which inhibited the photosynthetic rate. Xu *et al*. (2008) reported that approximately two thirds of the decline in net photosynthetic rate is attributable to stomatal limitations under mild-to-moderate water stress, which limits CO_2 assimilation. A species that can sustain a higher relative water content shows better adaptation to water deficit environments (Atteya, 2003). Chlorophyll is one the major chloroplast components for photosynthesis and the relative chlorophyll content has a positive relationship with the photosynthetic rate (Baker and Rosenqvist, 2004). Therefore assessment of the chlorophyll content can become an effective means of monitoring plant growth and estimating the photosynthetic productivity under stress (Chen *et al*., 2007). It has been established that water deficit is a very important limiting factor at the initial phase of plant growth and establishment and that it affects both elongation and expansion growth (Anjum *et al*., 2003). Greater plant fresh and dry weights under water deficit conditions are desirable characters. It would seem that breeding for difficult and complex traits such as drought tolerance could be simplified by identifying agronomic traits and morphological or physiological characters that are closely linked to yield in water-limited environments. In order to improve the agricultural productivity within water-limited areas, it is imperative to ensure higher crop yields under drought stress. A physiological approach using knowledge of crop responses to water deficits would be the best option for crop production, yield improvement and yield stability under soil moisture deficits conditions. However, the physiological basis for tolerance of maize genotypes to drought induced at different stages and any subsequent recovery has not been well investigated. Therefore the present study was carried with the following objectives: 1) to assess the effect of water deficit on the physiological traits of maize induced at different growth stages and 2) to identify measured physiological traits which could be used for screening maize genotypes for drought tolerance.

MATERIALS AND METHODS

Experimental site

Two field experiments with a split plot arrangement were carried out at the National Corn and Sorghum Research Center (latitude 14.5^{0}N, longitude 101^0 E 360 m above sea level) located in Pak Chong, Nakhon Ratchasima, Thailand during the growing seasons of 2010-2011 and 2011-2012. Soils at the experimental site belong to the Pak Chong (PC) soil series.

Water deficit treatments

For experiment I, the main plots consisted of five water regimes: D1, the control, with the soil water status maintained near field capacity; D2, with water deficit from the V10 to V13 stage; D3, with water deficit from the V13 to V17 stage; D4, with water deficit from the V17 to blister stage; and D5, with water deficit from the blister stage to physiological maturity. Three hybrid field corn genotypes—V1 (Pioneer 30B80), V2 (NK 40) and V3 (Suwan 4452)—were selected as subplots. For experiment II, four water regimes were used for the main plots: D1, control soil water status maintained near field capacity; D2, water deficit from V10 to anthesis stage; D3, water deficit from anthesis to milk stage; and D4, water deficit from milk to physiological maturity stage. The two better performed genotypes from experiment I (NK 40 and Suwan 4452) were selected as subplots. In each experiment, water management for the early establishment of the crop was continued with sprinkler irrigation up to 41 d after planting (before the onset of the water deficit treatments). Water deficit under the different treatments was imposed on plants at 42 d after planting (V10 stage) by withholding irrigation for a specific duration (in the main plots) followed by rewatering up to the physiological maturity stage with weekly flood irrigation. To avoid lateral movement of water between the main plots, plots were separated by about 7.5 m and a deep furrow was made between the main plots under different water deficit treatments. Tensiometers of two different sizes were installed at 0-30cm and 0-60 cm soil depth to monitor the daily soil water tension in the experimental plots throughout the crop cycle. Both experiments were carried out during the winter season which was characterized by very low and no rainfall. Therefore, the experiments were not affected by seasonal rainfall.

Field and crop management

Soil preparation was performed in accordance with conventional approaches at the Research Station, including disc harrow plowing followed by leveling. The plot was finally prepared with ridges and furrows maintaining the 75 cm spacing. Mixed fertilizer (N:P =16:20) was applied at the rate of 156 $kg.ha^{-1}$ during the final land preparation and properly incorporated into the soil. On 1 December 2010 and 14 January 2011, the seeds of each maize genotype were sown by hand with two seeds per hill in 10 rows in each plot 7.5 m long, with a spacing of 75 cm and 25 cm between rows and plants, respectively. On the day after planting, sprinkler irrigation was applied to the plots for better germination of seeds and thereafter irrigation was continued at weekly intervals until the maize plants reached the knee-high stage. The same amounts of mixed fertilizer (as an application) were applied as top dressing with a mechanical applicator during the 8–10 leaf stage. Sprinkler irrigation was applied immediately after top dressing with fertilizer. The plants were thinned at the 4-leaf stage to maintain one plant per hill.

Measurement of physiological parameters

Physiological parameters were initially measured prior to the onset of treatments and then weekly after initiation of the water deficit treatments. Five plants per plot were randomly selected from the two central rows for measuring physiological traits. The relative water content (RWC) was measured using flag leaves and ear leaves after imposing drought conditions. Immediately after cutting at the base of the lamina, leaves were sealed within polythene bags and quickly placed in an ice box and then transferred to the laboratory. The fresh weight (FW) was determined within 30 min after excision. The turgid weight (TW) was obtained after soaking the leaves in distilled water in plastic pots for 16 to 18 hr at room temperature. After soaking, the leaves were quickly and carefully blotted dry with a towel before determining the turgid weight. The dry weight (DW) was obtained after oven drying the leaf samples for 72 hr at 70 ºC. According to Atteya (2003), the RWC can be calculated from the formula: RWC (%) = (FW – DW)/ (TW – DW) × 100, where FW is the fresh weight, DW is the dry weight and TW is the turgid weight, all measured in the same unit. The *in vivo* relative chlorophyll concentrations of the flag leaves and ear leaves of five plants per plot were assessed using a portable chlorophyll meter (SPAD-502; Minolta; Tokyo, Japan). The leaf area was determined manually by measuring the length and maximum breadth and multiplying by 0.75. The dry matter was measured before the initiation of water deficit and thereafter weekly from all the plots (control and water deficit treatments). Five plants per plot were randomly harvested from the two central rows excluding the roots and divided into tassels, ears, stems, leaves and husks, and then oven-dried at 80 ^{0}C to constant weight in a forced-air circulation oven. The procedure was repeated for dry matter measurement on five plants per plot at maturity. The weights of the individual plant parts were combined to obtain the total aboveground biomass dry weight.

Statistical analysis

The experiment was conducted according to a randomized complete block design with a split-plot arrangement and three replications. Data were analyzed using analysis of variance which was performed with the MSTATC software (Version 1.2; Michigan State University; MI, USA). The significant differences between treatment means were compared at ($P < 0.05$) by Duncan's multiple range test.

RESULTS AND DISCUSSION

Changes in soil water potential under water deficit condition

For both experiments, changes in the soil water potential and soil water depletion were monitored through the installation of tensiometers at soil depths of 0-30 and 0-60 cm. In experiment I, the soil water potential ranged from -22 to -36 KPa and from -41 to -96 KPa in the control (field capacity) and water deficit conditions, respectively (Table 1). In experiment II, the range in the soil water potential was from -31 to -39 KPa in the control and from -190 to -252 KPa under a water deficit (Table 2). Though the control conditions produced quite similar soil water potential values in both experiments, the severe water deficit in experiment II accounted for the remarkably higher soil water potential there. The available soil water depletion was also higher in experiment II compared to experiment I.

Effect of water deficit on physiological parameters

Relative water content

In experiment I, during all stages of growth, the results indicated a substantial decrease in the leaf relative water content (RWC) of Pioneer 30B80, NK 40 and Suwan 4452 under

Table 1 Changes in soil water potential and soil water depletion at soil depths of 0-30 and 0-60 cm under control and water deficit treatments for experiment I carried out in Pak Chong Nakhon Ratchsima during 2010-2011.

	Treatment	Growth and development stages of maize							
		V10 to V13		V13 to V17		V17 to blister		Blister to PM	
Soil depth (cm)		0-30	0-60	0-30	0-60	0-30	0-60	0-30	0-60
Soil water potential (Kpa)	Control	-24	-22	-39	-35	-34	-35	-38	-36
	Water deficit	-84	-41	-96	-88	-82	-80	-83	-82
Available soil water depletion (%)		24	11	27.5	24	23.6	22.5	23.8	23.7

Table 2 Changes in soil water potential and soil water depletion at soil depths of 0-30 and 0-60 cm under control and water deficit treatments for experiment II carried out in Pak Chong Nakhon Ratchasima during 2011-2012.

	Treatment	Growth and development stages of maize					
		V10 to anthesis		Anthesis to milk		Milk to PM	
Soil depth (cm)		0-30	0-60	0-30	0-60	0-30	0-60
Soil water potential (-Kpa)	Control	-36	-32	-39	-36	-33	-31
	Water deficit	-252	-200	-210	-198	-195	-190
Available soil water depletion (%)		54	48	49	47.5	47	45

water deficit conditions compared to the control (Table 3). This result was in agreement with the findings of Efeoglu *et al*. (2009). A relatively higher reduction in leaf RWC under water deficit for Pioneer 30B80 (16.09%), NK 40 (12.72%) and Suwan 4452 (12.15%) was recorded with an average of 13.66% where the water deficit was imposed before anthesis (V17 stage) and the water deficit at subsequent stages showed a relatively lower reduction in the RWC compared to the control. After anthesis, the RWC declined gradually under the control conditions. Among the tested varieties, the RWC was statistically similar in all growth stages except for Pioneer 30B80 which exhibited the lowest RWC at the mid grain filling stage. NK 40 retained a higher RWC under the control and water deficit conditions that were imposed at different growth stages compared to Pioneer 30B80 and Suwan 4452 (Table 3). Under experiment II, the severe water deficits imposed at different stages significantly decreased the RWC of the genotypes compared to the control. A reduction in the leaf RWC of NK 40 (15.01%) and Suwan 4452 (21.19%) was noted under severe water deficit at anthesis, with values of 14.24 and 18.63% at the milk stage and of 19.11 and 20.58% at the late grain filling stage, respectively, compared to the control indicating that NK 40 retained a relatively higher RWC than Suwan 4452. NK 40 retained a significantly higher RWC under the control and severe water deficit treatments at all stages compared to Suwan 4452 (Table 4).

Table 3 Interaction effect of moderate water deficit and genotypes on relative water content, chlorophyll content, leaf area and dry matter accumulation of maize for experiment I at Pak Chong, Nakhon Ratchasima during 2010-2011.

Genotype	V13 stage		V17 stage		Blister stage		Mid grain filling stage	
	Control	Drought	Control	Drought	Control	Drought	Control	Drought
Relative water content (%)								
Pioneer 30B80	91.39	81.88	93.58	78.52	88.58	78.35	86.11	76.75
NK 40	94.35	82.41	94.55	82.52	89.61	79.73	87.22	79.04
Suwan 4452	92.69	81.52	92.51	81.27	90.03	78.5	86.33	80.06
LSD (P = 0.05)	8.44		2.54		6.34		4.31	
Chlorophyll content (SPAD value)								
Pioneer 30B80	51.08	48.66	53.96	45.43	51.66	47.73	52.96	46.95
NK 40	52.61	49.68	53.87	47.50	55.57	49.20	52.57	47.00
Suwan 4452	50.02	47.82	49.83	44.62	49.87	44.13	50.83	45.48
LSD (P = 0.05)	2.58		1.63		1.43		2.19	
Leaf area (cm^2 per plant)								
Pioneer 30B80	2263	1071	7323	6681	6177	5167	5189	5013
NK 40	2346	1165	5636	4834	5185	4900	4921	4704
Suwan 4452	3426	1835	7151	6929	6569	5874	6472	5438
LSD (P = 0.05)	244.10		285.60		101.10		176.60	
Dry matter accumulation (g per plant)								
Pioneer 30B80	53.01	41.50	83.95	73.76	142.30	122.70	252.80	207.60
NK 40	71.00	68.00	93.06	81.84	140.40	128.30	213.30	187.30
Suwan 4452	76.84	64.00	118.40	92.60	145.00	123.60	235.00	209.90
LSD (P = 0.05)	3.474		7.94		10.10		16.20	

SPAD = Soil and plant analysis development.

Table 4 Interaction effect of severe water deficit and genotypes on relative water content, chlorophyll content, leaf area and dry matter accumulation of maize for experiment II at Pak Chong, Nakhon Ratchasima during 2011-2012.

Genotype	Anthesis		Milk stage		Late grain filling stage	
	Control	Drought	Control	Drought	Control	Drought
Relative water content (%)						
NK 40	93.57	79.52	87.03	74.64	79.42	64.24
Suwan 4452	90.90	71.64	84.40	68.68	75.66	60.09
LSD (P = 0.05)	0.65		9.14		0.57	
Chlorophyll content (SPAD value)						
NK 40	49	46.95	55.05	38.88	34.90	19.00
Suwan 4452	45	42.20	53.28	30.40	33.05	15.35
LSD (P = 0.05)	1.47		0.79		2.37	
Leaf area (cm^2 per plant)						
NK 40	7469	6640	7428	4862	5668	4337
Suwan 4452	8080	7133	7965	4892	6197	3793
LSD (P = 0.05)	196.80		95.52		476.60	
Dry matter accumulation (g per plant)						
NK 40	118.40	86.08	175.80	154.80	232.30	194.80
Suwan 4452	121.90	82.71	165.30	149.90	220.00	191.50
LSD (P = 0.05)	9.19		3.29		7.89	

SPAD = Soil and plant analysis development.

Chlorophyll content

The moderate water deficit in experiment I significantly reduced the chlorophyll content across the growth stages. Comparatively higher chlorophyll reduction under water deficit (12.75 and 12.05%) irrespective of genotypes was noted before anthesis (V17 stage) and the mid grain filling stage, respectively, compared to the control (Table 3). Among the genotypes, NK 40 and Pioneer 30B80 showed significantly higher chlorophyll contents at the V13, V17 and mid grain filling stages compared to Suwan 4452 but at the blister stage, NK 40 sustained a significantly higher chlorophyll content compared to the other genotypes averaged over the water regimes. Suwan 4452 exhibited the lowest chlorophyll content at all stages (Table 3). The results indicated that NK 40 exhibited a relatively higher chlorophyll content under the control and water deficit conditions compared to the other varieties. In a similar manner to NK 40, Pioneer 30B80 had a relatively higher chlorophyll content compared to Suwan 4452 (Table 3). In experiment II, the severe water deficit in the growth stages exerted a significant effect on the chlorophyll content. Compared to the control, the reduction in the chlorophyll content was 5.15%, 36.04% and 49.44% at the anthesis, milk and late grain filling stages, respectively, across the genotypes (Table 4). This result indicated that after the anthesis stage, the severe water deficit had a profound effect on chlorophyll degradation. It revealed that under the control and severe water deficit treatments imposed at different growth stages, NK 40 sustained a significantly higher chlorophyll content compared to Suwan 4452 (Table 4).

Leaf area

The leaf area varied significantly under the moderate water deficit at different growth stages. The water deficit significantly reduced the leaf area across the growth stages. The maximum leaf area reduction (50.01%) was noted due to water deficit at the V10 to V13 stage (Table 3). This result suggested that the leaf area is susceptible to water deficit in an early growth stage. Among the genotypes, Suwan 4452 showed significantly higher leaf area at all stages whereas NK 40 exhibited the lowest leaf area (Table 3). The results showed that Suwan 4452 exhibited a significantly higher leaf area under the control and water deficit conditions compared to the other genotypes. In a similar manner to Suwan 4452, Pioneer 30B80 showed a relatively higher leaf area compared to NK 40 (Table 3). In experiment II, the severe water deficit in the different growth stages induced a significant effect on the leaf area. The higher reductions of leaf area were 36.64% and 31.48% at the milk and late grain filling stages, respectively, compared to the control irrespective of genotypes (Table 4). This result indicated that after the anthesis stage, the severe water deficit had a profound effect on chlorophyll degradation and finally reduced the green leaf area. Of the two genotypes, Suwan 4452 had a significantly higher leaf area compared to NK 40 under the control and water deficit regimes imposed from V10 to the anthesis stage (Table 4). NK 40 had a relatively higher leaf area at the late grain filling stage compared to Suwan 4452 probably due to the higher leaf senescence in Suwan 4452.

Dry matter accumulation

The results in experiment I indicated that dry matter accumulation reduced significantly due to the moderate water deficit at the different growth stages compared to the control. The highest reduction in dry matter was 15.98% observed in the case of a water deficit imposed before the anthesis (V17 stage) irrespective of genotypes (Table 3). This result was in agreement with Sah and Zamora (2005) and Cakir (2004). The water deficit caused a significant variation in the above ground dry matter of the genotypes at different stages except for the blister stage. Suwan 4452 retained relatively higher above ground dry matter under the control at the V13 and V17 stages compared to Pioneer 30B80 and NK 40 while at the mid grain filling stage, Suwan 4452 and Pioneer 30B80 exhibited relatively higher above ground dry matter compared to NK 40. Suwan 4452 and NK 40 exhibited relatively higher dry matter under the water deficit at the V13 and V17 stages whereas Suwan 4452 and Pioneer 30B80 showed significantly higher dry matter under water stress at the mid grain filling stage (Table 3).

Under the severe water deficits in experiment II, dry matter was significantly decreased compared to the control. The highest reduction (14.6%) was found where the water deficit was induced at the late grain filling stage averaged over all genotypes (Table 4). NK 40 exhibited significantly higher dry matter at all growth stages compared to Suwan 4452 except for the anthesis stage irrespective of water deficit treatments (Table 4). A similar response with regard to dry matter was noted for NK 40 under the control conditions. The severe water deficit imposed at different stages showed a similar effect with all genotypes at all growth stages except for the milk stage where NK 40 exhibited significantly higher dry matter accumulation.

Recovery of physiological traits under moderate water deficit

Figure 1 represents the recovery pattern of physiological traits under moderate water deficit. Rewatering after withholding water deficit demonstrated a different pattern of recovery of physiological parameters at following growth stages. Fourteen days after rewatering, the relative water content attained its full recovery to the level of the control at each stage of growth irrespective of genotypes (Figure 1). A decrease in the water potential under water stress associated with a quick return to control levels after re-watering was also reported by other workers (Kameli and Loesel, 1996). Water deficit following rewatering sustained the chlorophyll content at 92.98, 92.08 and 95.56% of the control at three consecutive growth stages which indicates that before anthesis (the V10 to V13 and the V13 to V17 stages), a water deficit induced faster degradation and inhibited the formation of new chlorophyll molecules compared to the V17 to blister stage. Rewatering after water deficit at the V13 to V17 stage produced a leaf area of 94.95% of the control which was higher than at other stages. The dry matter accumulation per plant

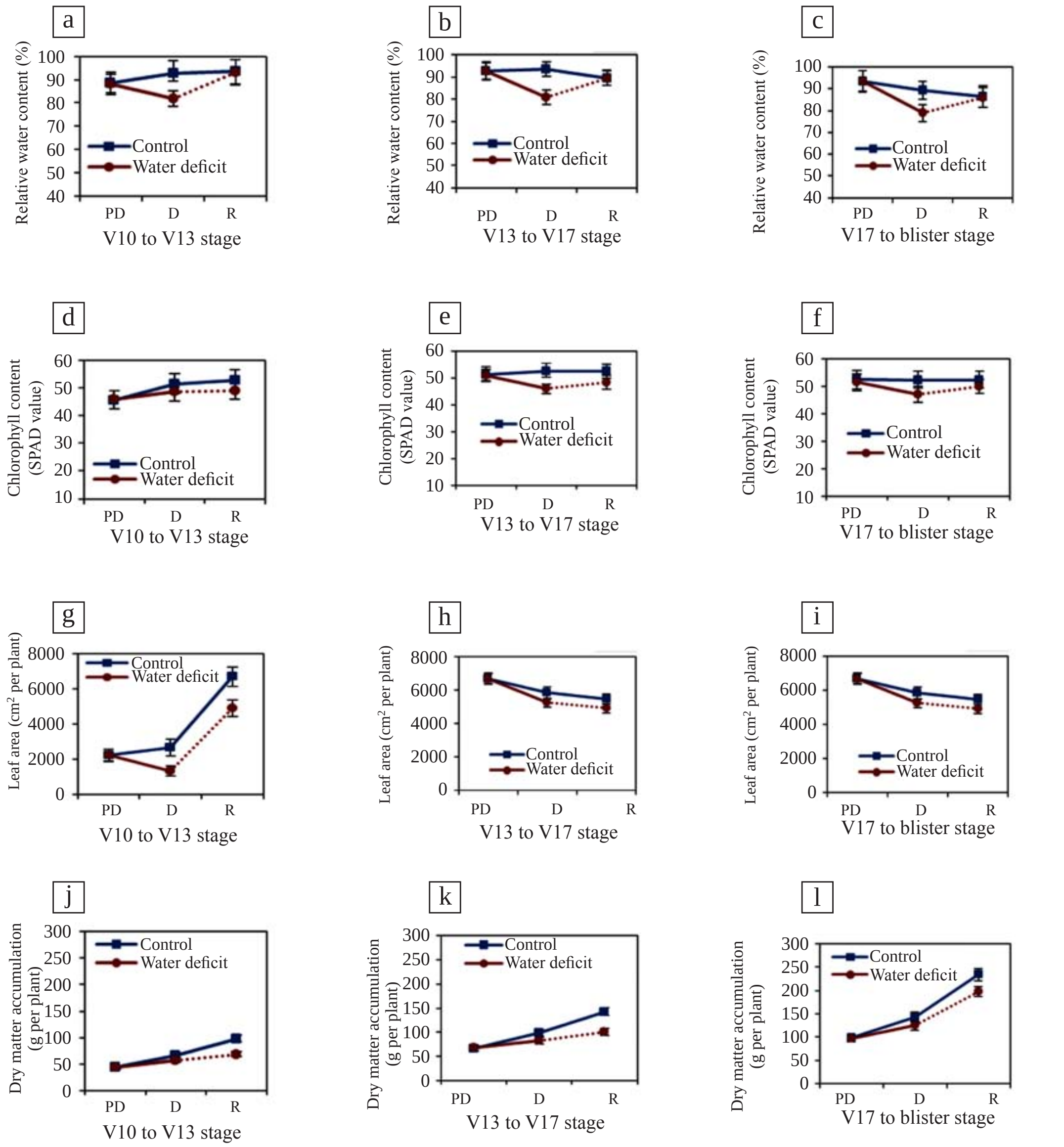

Figure 1 Recovery pattern of: (a, b and c) Relative water content; (d, e and f) Chlorophyll content; (g, h and i) Leaf area; (j, k and l) Dry matter accumulation of maize (averaged over three genotypes) under rewatering for 14 d after moderate water deficit imposed at V10 to V13, V13 to V17 and V17 to blister stages, respectively, in moderate water deficit (Experiment I) during 2010–2011. Vertical bars indicate the standard deviation of the means and least significant differences at $P \leq 0.05$. PD = Pre drought period, D = Drought period and R = Rewatering period. SPAD = Soil and plant analysis development.

showed progressive recovery due to rewatering after the V13 to V17, V17 to blister and blister to mid grain filling stages (69.73, 70.76 and 84.33%, respectively) indicating that water deficit followed by rewatering at these growth stages resulted in higher recovery compared to the early growth stages.

Recovery of physiological traits under severe water deficit

The relative water content (RWC) of leaves was significantly lower for water deficit plants compared to control plants, either at the V10 to anthesis, anthesis to milk or milk to physiological maturity stages. The RWC of rewatered plants was similar to well-watered ones (Figure 2). Under severe water stress conditions, the chlorophyll content of the leaves decreased significantly at all growth stages studied, although at the milk and late grain filling stages, the differences between the control and water-stressed plants were more evident. After the anthesis stage, rewatering slightly increased the chlorophyll content compared to the stress conditions but it declined progressively even after rewatering following the milk stage which indicated that water deficit during the anthesis to milk stage induced severe chlorophyll degradation which did not recover under rewatering (Figure 2). The leaf area decreased significantly under stress at all the stages and was more evident at the milk stage. Rewatering after anthesis failed to recover leaf area after the stress conditions. Severe water deficit exerted a significant decrease in the dry matter accumulation with a dominant effect at anthesis. Rewatering increased the dry matter accumulation per plant at all the growth stages compared to deficit conditions but was lower than the control.

Grain yield under moderate and severe water deficit

The effect of water regimes on grain yield of maize was significant in both experiments (Figures 3a and 3b). The moderate water deficit in experiment I caused 6.2, 15.75, 10.6 and 6.55% reduction in grain yield in the D2 (water deficit from V10 to V13), D3 (water deficit from V13 to V17), D4 (water deficit from V17 to blister stage) and D5 (water deficit from blister to physiological maturity) treatments, respectively, compared to the control conditions. The severe water deficit in experiment II resulted in 19.35, 24.86 and 11.80% grain yield reduction in the D2 (water deficit from V10 to anthesis), D3 (water deficit from anthesis to milk) and D4 (water deficit from milk to physiological maturity) treatments, respectively, compared to the control. These results indicated that anthesis is the most sensitive phenological stage to water deficit. Before anthesis, the moderate water deficit reduced kernel setting and after anthesis the severe water deficit resulted in more kernel abortion and these factors might have been the cause of the higher yield reduction. Many researchers who investigated drought occurrence in relation to the anthesis stage reported a substantial reduction in yield and yield components. (Araus *et al*., 2002; Blum *et al*., 1989; Borras *et al*.,2002; Yadav and Bhatnagar, 2001; Seghatoleslami *et al*., 2008). It may be postulated that when maize genotypes encounter water deficit in the reproductive stage, although yield is decreased compared to normal conditions, dry matter translocation and the translocation efficiency and contribution of stored assimilate to grain increases. These traits could be selected to screen maize genotypes for yield potential under water limited conditions.

As shown in Figure 3, the grain yield of maize varied significantly due to the interaction effect of the moderate water deficit and genotype. NK 40 and Suwan 4452 produced significantly higher grain yields under the control, water deficit from the V10 to V13 and the V17 to blister stages which were similar to Pioneer 30B80 under the control conditions. NK 40 also showed higher grain yields under water deficit from the V13 to V17 stage (D3) and V17 to blister

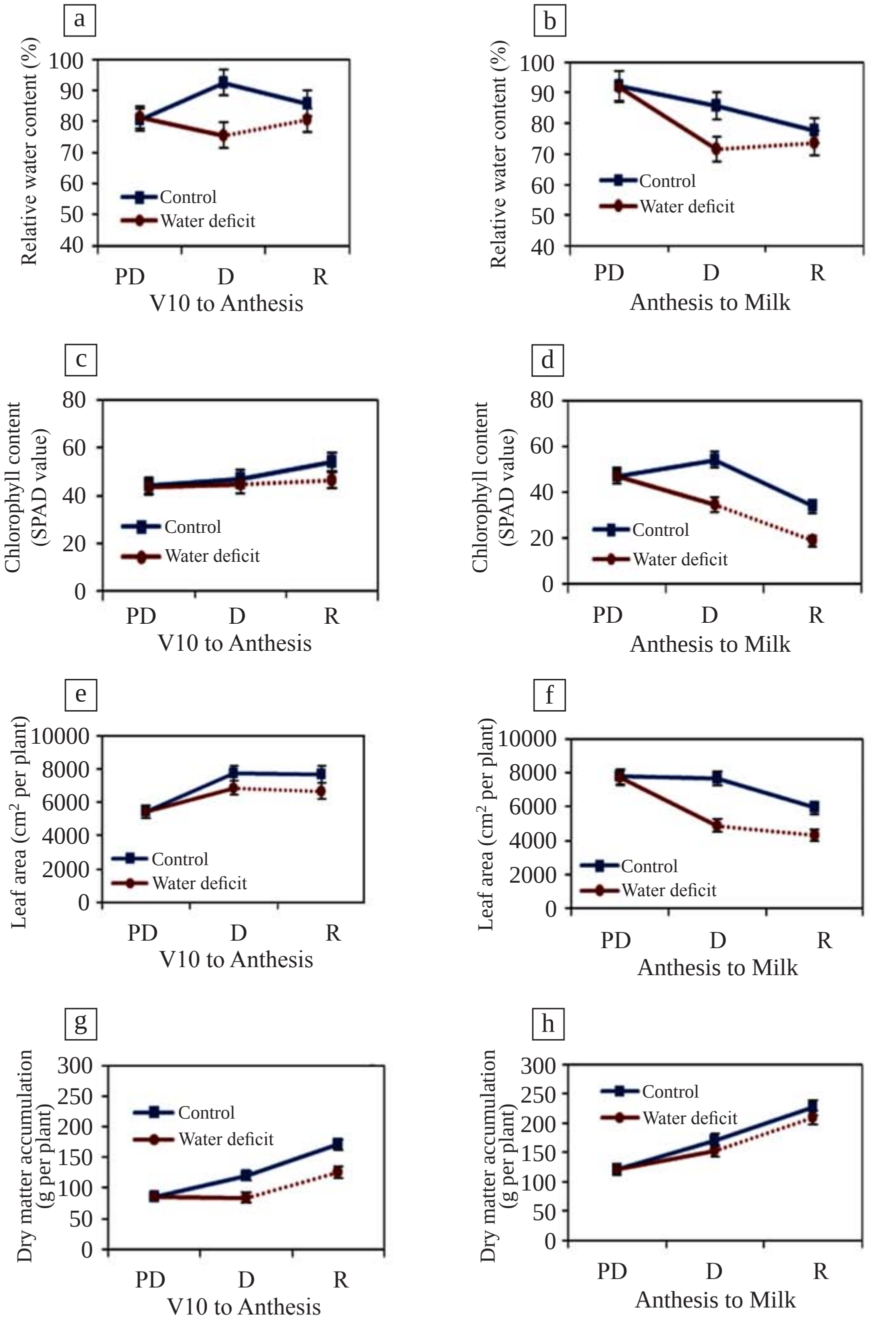

Figure 2 Recovery pattern of: (a and b) Relative water content; (c and d) Chlorophyll content; (e and f) Leaf area; (g and h) Dry matter accumulation of maize (averaged over three genotypes) under rewatering up to succeeding stage after severe water deficit imposed at V10 to anthesis and anthesis to milk stages, respectively, in experiment II during 2011–2012. Vertical bars indicate the standard deviation of the means and least significant differences at $P \leq 0.05$. PD = Pre drought period, D = Drought period and R = Rewatering period. SPAD = Soil and plant analysis development.

(D4) stage indicating that this genotype retains potential physiological traits which favor the yield process. Except for the control, Pioneer 30B80 demonstrated significantly lower grain yields under all water deficit conditions. Under severe water deficit, although both genotypes produced significantly higher grain yields under the control, NK 40 showed relatively higher yields in the severe water stress treatments imposed at the V10 to anthesis and anthesis to milk stages compared to Suwan 4452. Among the tested genotypes in both experiments, NK 40 exhibited relatively higher yield potentials under moderate and severe water deficit probably due to sustaining its higher relative water content and chlorophyll content which helped the dry matter accumulation and substantial grain filling through photosynthesis. Under stress conditions, the superior performance of NK 40 might have been due to retaining a relatively higher RWC and chlorophyll content.

Relationship between soil water depletion and physiological parameters (experiment I and experiment II)

The depletion of available soil water from the root zone impaired many physiological traits of maize. The immediate effect of the soil water deficit was evident in tissue dehydration. Under the conditions in experiment I and experiment II, the results indicated that the relative water content had significant negative relationships (R^2 = 0.83 and 0.67, respectively) with the available soil water depletion (Figures 4a and 5a, respectively). This indicated that the soil water deficit limits water uptake and subsequently reduces the water content of the leaf tissues. A more severe water deficit causes a greater reduction in the RWC. The chlorophyll content also showed significant negative relationships (R^2 = 0.86 and 0.57, respectively, for the two experiments) with soil water depletion under both experiments (Figures 4b and 5b) indicating that increasing the water deficit progressively promotes the degradation of chlorophyll molecules. In contrast, significant positive relationships (R^2 = 0.88 and 0.89, respectively) were found between the chlorophyll content and the relative water content (Figures 4d and 5d). Negative relationships were found between the grain yield and soil water depletion (R^2 = 0.74 and 0.80 in Figures 4c and

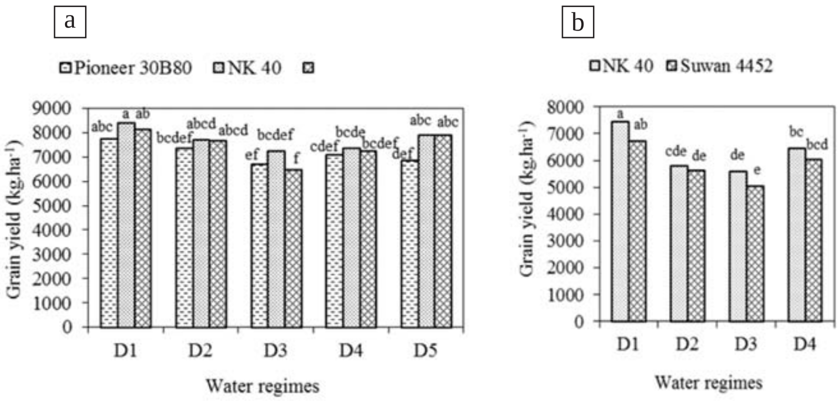

Figure 3 Grain yield of maize genotypes affected by different levels of water regimes under: (a) Moderate water deficit (D1 = control, D2 = Water deficit from V10 to V13, D3 = Water deficit from V13 to V17, D4 = Water deficit from V17 to blister stage and D5 = Water deficit from blister to physiological maturity stage.); (b) Severe water deficit (D1= Control, D2 = Water deficit from V10 to anthesis, D3 = Water deficit from anthesis to milk and D4 = Water deficit from milk to physiological maturity stage). Different letters above the bars indicate significant differences at $P < 0.05$ level.

5c, respectively), whereas the grain yield was positively correlated with the chlorophyll content and relative water content under both experiments being more evident under the moderate water deficit (Figures 4e and 4f, and Figures 5e and 5f, respectively for experiments I and II.).

CONCLUSION

Moderate and severe water deficit impaired the physiological traits of maize but the magnitude of the damage depended on the duration and severity of the water deficit at critical growth stages. Under both experimental conditions, optimum water management (the control) showed better exposure of physiological traits and subsequent higher grain yield irrespective of genotype. Although the water deficit was imposed for different periods at different growth stages under the two experiments, the severe water deficit had a more damaging effect on the RWC and chlorophyll content and eventually grain

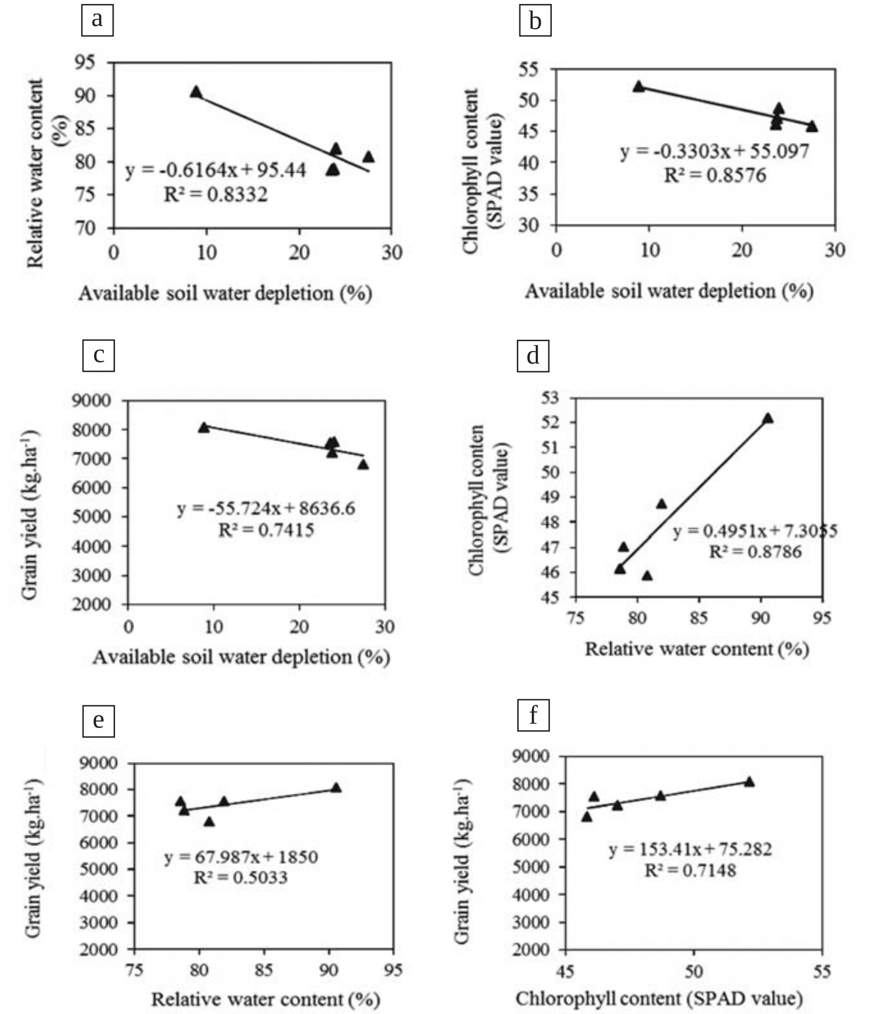

Figure 4 Relationship of available soil water depletion with: (a) Relative water content; (b) Chlorophyll content; (c) Grain yield. Relationship of relative water content under moderate water deficit with: (d) Chlorophyll content; (e) Grain yield; (f) Relationship of chlorophyll content with grain yield. SPAD = Soil and plant analysis development R^2 = Regression co-efficient.

yield compared to the moderate water deficit. Re-watering led to a recovery of the RWC to the control level under both water deficit experiments, while the recovery of chlorophyll was relatively higher in the moderate water stress treatment. Rewatering after a water deficit at an early stage led to a recovery in the leaf area but rewatering after water stress around anthesis failed to produce a recovery in the leaf area under both experiments. Rewatering increased the dry matter accumulation per plant at all the growth stages compared to deficit conditions but was lower than the control. NK 40 demonstrated better performance due to sustaining a relatively higher RWC and chlorophyll content under the control and water deficit conditions which made it tolerant against drought compared to the other genotypes. The relative water content, chlorophyll content and grain yield showed negative relationships with the available soil water depletion (%) while the grain yield showed a positive relationship with the relative water content and chlorophyll content in both water deficit experiments.

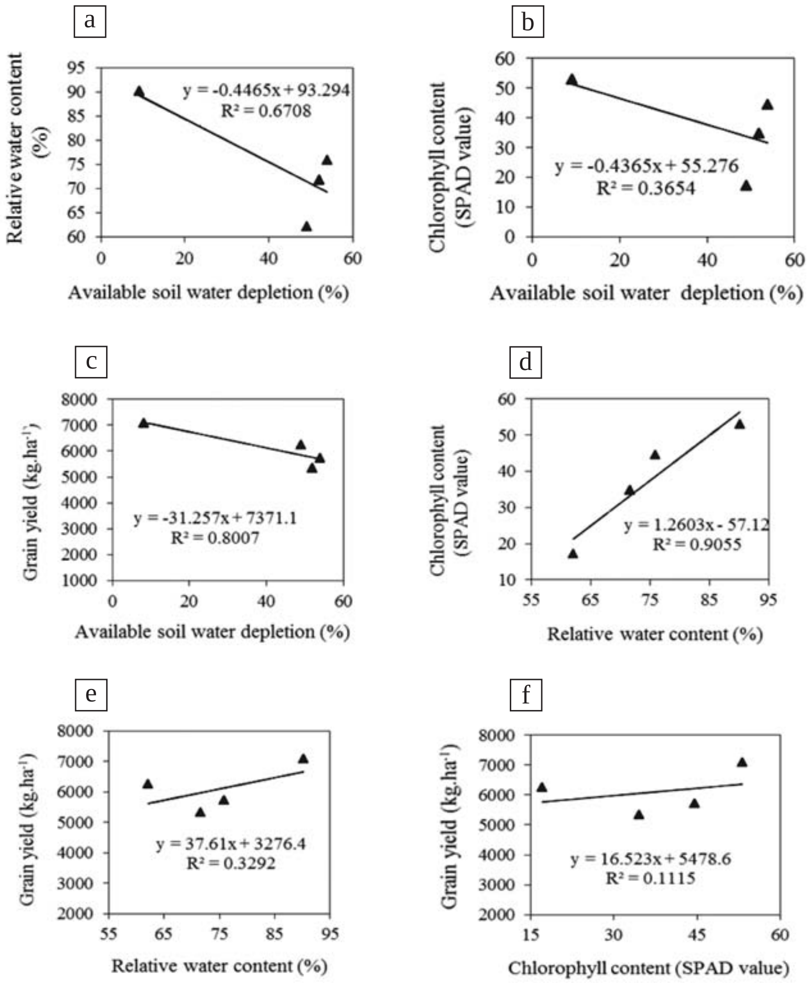

Figure 5 Relationship of available soil water depletion with: (a) Relative water content; (b) Chlorophyll content; (c) Grain yield. Relationship of relative water content under severe water deficit with: (d) Chlorophyll content; (e) Grain yield; (f) Relationship of chlorophyll content with grain yield. SPAD = Soil and plant analysis development, R^2 = Regression co-efficient.

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