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Differential Responses of Selected Soybean Cultivars to Drought Stress and Their Drought Tolerant Attributions

Aung Moe Myo Tint[1], Ed Sarobol[1]*, Sutkhet Nakasathein[1] and Witith Chai-aree[2]

ABSRACT

Seven soybean cultivars in Thailand were evaluated under well-watered and drought- stressed regimes. A randomized complete block design with three replications in greenhouses was used. Control pots were kept well watered. Imposing drought stress commenced at the vegetative growth stage 3 (V_3) for 15 d and then pots were re-watered. Shoot dry matter (SDM), root dry matter (RDM), nodule dry matter (NDM), shoot tissue moisture content (STM%) and electrolyte leakage from leaf tissue (EL%) of each tested cultivar under both water regimes were investigated. Physiological responses of the cultivars and their relationship were identified. Their drought tolerances were examined using a stress susceptibility index (SSI), mean productivity (MP), geometric mean productivity (GMP), stress tolerance (TOL) and a stress tolerance index (STI). SDM, RDM and NDM decreased with increasing water stress. SDM, NDM, STM%, and EL% showed significant correlations with seed yield. On the basis of the physiological responses and drought tolerance attributes of the cultivars studied, SJ-4 was the most drought tolerant cultivar indicating that SJ-4 is not only the appropriate genotype for cultivar improvement but also for cultivation in drought-prone areas. STI had a highly significant correlation with seed yield (r=0.66) and could distinguish better yielding genotypes under the drought-stress environment. The results also showed that STI was the most appropriate index to attain better yielding cultivars for a drought-stress environment, followed by GMP.

Keywords: soybean, drought stress, cultivar screening, electrolyte leakage, nodule dry weight, tolerant indices

INTRODUCTION

Drought is a major environmental factor determining crop yield, especially in the tropics and sub-tropics where crop production under rain-fed conditions can suffer due to erratic rainfall. Under the present scenarios of climate change, drought is more likely to occur and may decrease average yields of the most important economic crops globally (Bray *et al.*, 2000). In fact, improving drought tolerant cultivars has been undertaken with an integrated approach involving traditional through to molecular techniques (Hammer and Jordan, 2007; Manavalan *et al.,* 2009) as a priority with the ultimate goal of obtaining high grain yields. However, many mechanisms underlie plant response to drought (Chaves and Oliveira, 2005); therefore, many

[1] Department of Agronomy, Faculty of Agriculture, Kasetsart University, Bangkok 10900, Thailand.
[2] Department of Agronomy, Faculty of Agriculture at Kamphaeng Saen, Kasetsart University, Nakhon Pathom 73140, Thailand.
* Corresponding author, e-mail: agred@ku.ac.th

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screening techniques and criteria have been devoted to testing large numbers of samples.

A technique to measure the electrolyte leakage from leaf tissue in several crop species has been long established to quantify damage to cell membranes under various abiotic stress conditions (Bajji *et al.,* 2001). The technique is suitable for the development of a drought-tolerant rating in legume species and cultivars (Grzesiak *et al.,* 1996; Deshmukh and Kushwaha, 2002). It has been demonstrated that electrolyte leakage measurement was correlated with several physiological and biological parameters of plant response to environmental conditions (Franca *et al.,* 2000; Lauriano *et al.,* 2000).

Nitrogen fixation is more sensitive to water deficits than other processes (Serraj *et al.,* 1999) and this may restrict the nitrogen supply and subsequently the yield of soybean in many environments. In soybean, nitrogen fixation differed in response to water deficit and was dependent on both the inheritance of given genotypes and the severity of the water stress (Sinclair *et al.,* 2000). King and Purcell (2001) reported on the drought tolerance of the Jackson soybean cultivar, due to its larger nodules and its inherently greater supply of photosynthates to the nodules.

Drought tolerant mechanisms in legume crops are closely related to the root system or rooting pattern (Pandey *et al.,* 1984), in general. However, only a few studies have used them as screening criteria in crop improvement for drought tolerance because the difficulties in visualizing the root architecture are challenging (Myers *et al.,* 2007).

The ultimate goal of crop improvement is to achieve better yield. Therefore, several indices have been developed (Fischer and Maurer, 1978; Rosiselle and Hamblin, 1981; Fernandez, 1992) and widely used in crop breeding for target environments. However, Subbarao *et al.* (1995) considered that selection for drought resistance should not be based solely on seed yield as this alone could not assure gaining the desired physiological trait without physiological investigation of the crop improvement. Many studies on soybean response to drought with various physiological aspects have well documented. However there is a lack of information about the relationship between determining drought-tolerant parameters like electrolyte leakage of plant tissue, growth and development of shoot, root and nodules, with drought tolerance. An investigation and understanding of the relationships could help in developing improvements in soybean cultivars that are drought tolerant. The current research aimed to evaluate the response of some soybean cultivars to drought and to determine the relationships among observed drought parameters and seed yields.

MATERIALS AND METHODS

Seven soybean cultivars in Thailand—namely, Nakhon Sawan 1 (NS-1), SJ-4, Sukhothai 1 (ST-1), Sukhothai 2 (ST-2), Sukhothai 3 (ST-3), Chiang Mai 60 (CM-60) and Chakkrabbandu 1 (CK-1) were tested. They were derived from various parents and varied in maturity from 90 to 110 d (Win *et al.,* 2009).

Using a greenhouse, treatments involving a control (well watered) and a treatment of 15 d of prolonged drought stress which started at the V_3 growth stage (V_3) and was followed by re-watering were arranged in a randomized complete block scheme with three replications. Pots were equally watered using a measuring beaker. The control plots were watered at three-day intervals. The stress plots received the same amount of water except during the drought-stress period. The experiment was conducted at the Central Laboratory and Greenhouses Complex, Kamphaeng Saen, Nakhon Pathom, Thailand, during October 2008–January 2009.

Garden soil enriched with nutrients was used as the growing medium in plastic pots (25 cm in diameter and 25 cm deep). Pots were filled with soil to a uniform weight of 3.5 kg. Seeds were inoculated with commercial peat-based rhizobium inoculum prior to sowing. Nine seeds at three seeding spots were sown in each pot. Germinants were thinned 11 d after sowing (DAS), maintaining three plants in each pot which was equivalent to 270,000 plants ha^{-1}. Re-randomization was carried out twice a week from emergence until imposing the treatments.

Data were collected at 0, 5, 10 and 15 d after the V_3 growth stage (DAV_3) for each cultivar under both water regimes which roughly coincided with V_3 and the reproductive growth stages R_2, R_3 and R_4 (Fehr *et al.,* 1977), respectively. Soils samples (80 cc) from the water-stressed pots were taken at each sampling time during the drought period. The soil moisture percentage was calculated based on the wet weight.

The first, uppermost, fully expanded leaf of each plant was collected, put in separate zip-plastic bags and kept in an ice box during the sampling process. Avoiding major veins, 20 leaf discs were obtained from each sample leaf using a 6 mm diameter single punch. Leaf-disc samples were placed in glass bottles and washed twice with fresh de-ionized water to clean cell lyses. Then, 60 mL of fresh de-ionized water was poured into each glass bottle and left for 5 h as bathing time on a mechanical shaker at 30 rpm. The first electrolyte measurements of the bathing solution were taken with a digital electro-conductivity meter (model: InoLab Cond Level 1) before bottles containing samples were subjected to autoclaving at 105 °C for 15 min. After autoclaving, bottles were left for 2 h to cool down to room temperature, and then the second electrolyte measurement was taken. Measurements were taken in an air-conditioned room with the temperature kept around 22 ± 2 °C. The percentage of electrolyte leakage (EL%) was calculated as the electro-conductivity (μS cm^{-1}) ratio between before and after autoclaving (Chen *et al.,* 2006).

Shoots of three plants from each pot were cut and sealed in plastic bags and kept in an icebox to avoid dehydration. Samples were collected during the period from 12:00 to 13:00 hours. In the laboratory, surface cleaning and drying were carried out using moisturized blotting tissue followed immediately by weighing on a Yamato digital balance to determine the fresh weight. Samples were oven dried at 70 °C for 72 h. The shoot moisture percentage (STM%) was calculated from the fresh weight and dried weight. Root-samples were obtained by breaking the soil clod and gently shaking it to obtain the root mass. Nodules were detached from roots after washing with tap water on a 1 mm screen, followed by weighing immediately on the digital balance to determine their fresh weight. Dry weight was determined after oven drying for 72 h at 70 °C. The relative growth rates of shoots, roots and the nodule dry matter accumulation between 0 and 15 DAV_3 under both water regimes were calculated using Equation 1 (Bajji *et al.,* 2001):

$$(Ln\ DWt_2 - Ln\ DWt_1)\ /\ \text{Days interval between two observed times} \quad (1)$$

where: $Ln\ DWt_2$ = natural logarithm of dry weight at present observed time; $Ln\ DWt_1$ = natural logarithm of dry weight at the previous observed time.

At physiological maturity, plants were harvested and seed yields were obtained. In order to evaluate the drought tolerance of the tested soybean cultivars, drought-tolerant indices were calculated using Equations 2 to 6:

Stress Susceptibility Index (SSI): (Fischer and Maurer, 1978), $SSI = \frac{1-(Ys/Yp)}{SI}$ (2)

where: SI (Stress Intensity) = $1-(\overline{Y}s/\overline{Y}p)$.

Mean Productivity (MP): (Rosiselle and Hamblin, 1981), $MP = \frac{(Ys+Yp)}{2}$ (3)

Geometric Mean Productivity (GMP): (Rosiselle and Hamblin, 1981), GMP = $\sqrt{(Ys)(Yp)}$ (4)

Stress Tolerance (TOL): (Rosiselle and Hamblin, 1981), TOL = $(Yp - Ys)$ (5)

Stress Tolerance Index (STI): (Fernandez, 1992),

$$STI = \frac{(Ys)(Yp)}{(\bar{Y}p)2} \quad (6)$$

where: Yp = yield of a given genotype in non stress environment; Ys = yield of a given genotype in a drought-stressed environment; $\bar{Y}p$ = mean yield of all genotypes in a nonstressed environment; $\bar{Y}s$ = mean yield of all genotypes in stressed environment.

The dry matter of shoots, roots and nodules, EL%, STM% and soil moisture percentage (SM%), were collected at 0, 5, 10 and 15 DAV_3, and seed yields of the cultivars under the two watering regimes were subjected to analysis of variance, and treatment means were compared using least significant differences (LSD). The relationships among observed parameters of plant responses and the relationships among drought indices were analyzed using simple correlation.

RESULTS AND DISCUSSION

Moisture status of soil and plants

During 0–15 DAV_3, soil moisture of the control plants was maintained above 50% while the SM% had fallen to less than 47% under stress conditions since 5 DAV_3 and sharply declined at 10 DAV_3 (Figure 1a). However, SM% slowly declined at 15 DAV_3 due to reduced transpiration, and additional watering (100 mL plant^{-1}) was applied to stressed plants at 13 DAV_3 to avoid permanent wilting (Figure 1b). According to Wang *et al.* (2006), the leaf water potential and transpiration of soybean plants dropped quickly when soil moisture fell below 47%, whereas net photosynthesis dramatically declined below 26%. Therefore, it was obvious that the growth and development of the plants were affected by the water-stress conditions imposed in the current study.

The ability to maintain moisture in plant tissue is a key for plant survival under water stress, therefore, the shoot moisture of each tested soybean cultivar under both water regimes was determined (Figure 1b). The shoot tissue moisture content (STM%) of the stressed plants was significantly lower than for plants under the control treatment from 10 DAV_3. Among the tested cultivars at 15 DAV_3, ST-2, NS-1 and SJ-4 maintained significantly higher STM% at 69.02, 68.77 and 67.30%, respectively, under prolonged water stress compared to the other cultivars (Figure 1b).

Electrolyte leakage

Cell membranes are one of the first targets of many plant-stress syndromes and it is generally accepted that the maintenance of their integrity and stability under water-stress conditions is a major indicator of drought tolerance in plants. The occurrence of stress indicated by cell membrane injuries leads to an increased leakage of electrolytes. At 5 DAV_3, EL% was not significantly different between the two water regimes but was significantly higher in stressed plant tissue from 10 DAV_3 onwards (Figure 2).

The tested cultivars had already shown their genotypic differences at 0 DAV_3 and a significant strong interaction between cultivars and water regimes was observed at 10 and 15 DAV_3. Values of EL% affected not only genotypes, their age and level of stress intensity (Tsarouhas *et al.,* 2000) but also could vary with the mineral status of the plant which affected the solute concentration of cell sap (Bajji *et al.,* 2001). Nevertheless, the EL% values were consistent with STM%. The ST-2, NS-1 and SJ-4 cultivars held higher STM% and low EL% at the end of stress period. The results supported the fact that better cell membrane integrity under stress conditions helped to stabilize moisture in plant parts and organelles that may result in maintaining stomatal conductance and osmotic potential (Premachandra *et al.,* 1989) which regulate transpiration, and consequently improve water use efficiency (Franca *et al.,* 2000), or *vice versa.*

Plant growth and development

Dry matter accumulation of shoots, roots and nodules was collected at 0, 5, 10 and 15 DAV_3 to determine the growth and development of each cultivar under both water regimes. The results are presented in Tables 1, 2 and 3.

Dry matter accumulation in shoots (SDM) significantly declined at 10 DAV_3 under the drought-stressed regime (Table 1). In contrast, root dry matter accumulation (RDM) increased, indicating that drought-stressed plants partitioned large amount of assimilates to favor root growth. Among the tested soybean cultivars, SJ-4 and NS-1 showed the highest relative RDM compared with

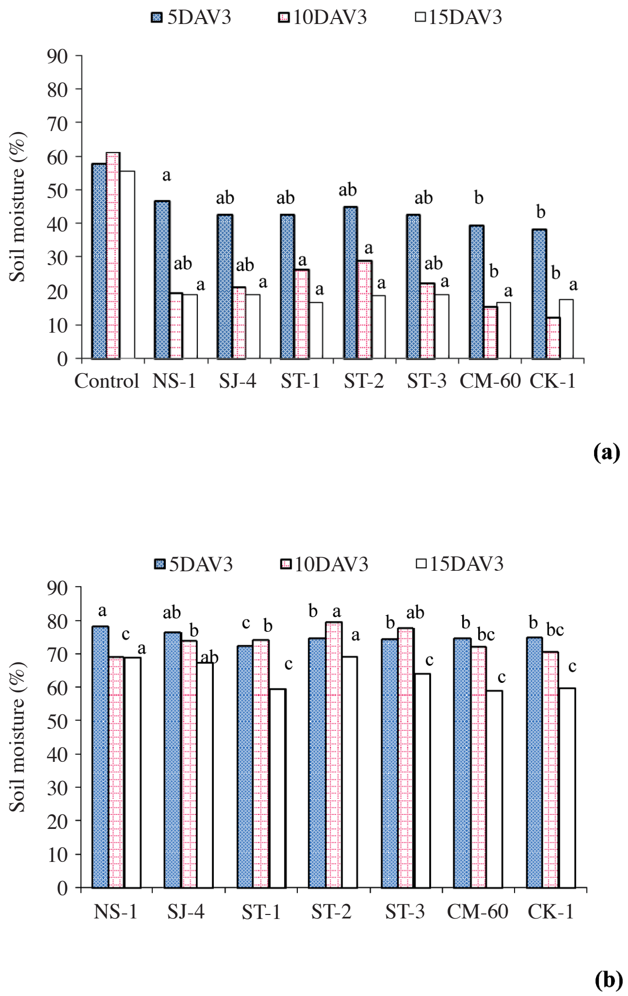

Figure 1 Soil moisture depletion in drought stressed pots of different soybean cultivars compared with controlled pots (a). Shoot tissue moisture content of different soybean cultivar under drought-stressed regime (b) at 5, 10 and 15 DAV3. Same letter above a bar indicates no significant difference at LSD 0.05 at the observed time.

the control water regime (Table 2), whereas ST-2 and ST-3 sustained SDM until 10 DAV_3 which was not a significant lag behind those under the control water regime. Simultaneously, the NDM of all cultivars was not significantly different (Table 3) at 10 DAV_3. However, SDM and NDM decreased dramatically at 15 DAV_3 under the drought-stressed regime, while RDM was still significantly higher under water stress regime. Although the increase in RDM was maintained in ST-2, NS-1 and SJ-4, it decreased in the other cultivars. At 15 DAV_3, ST-2, NS-1 and SJ-4 had the greatest relative SDM with 78.76, 78.59 and 77.13%, respectively.

The greater NDM of ST-2, SJ-4 and NS-1 under drought-stressed conditions (Table 3) resulted from their ability to maintain greater STM% through increasing root growth (Table 2). At 15 DAV_3, nodule growth was severely affected by drought stress up to 63% of the control (Table 3) while shoot growth was depressed up to 79.18% of the control (Table 1) and root growth was

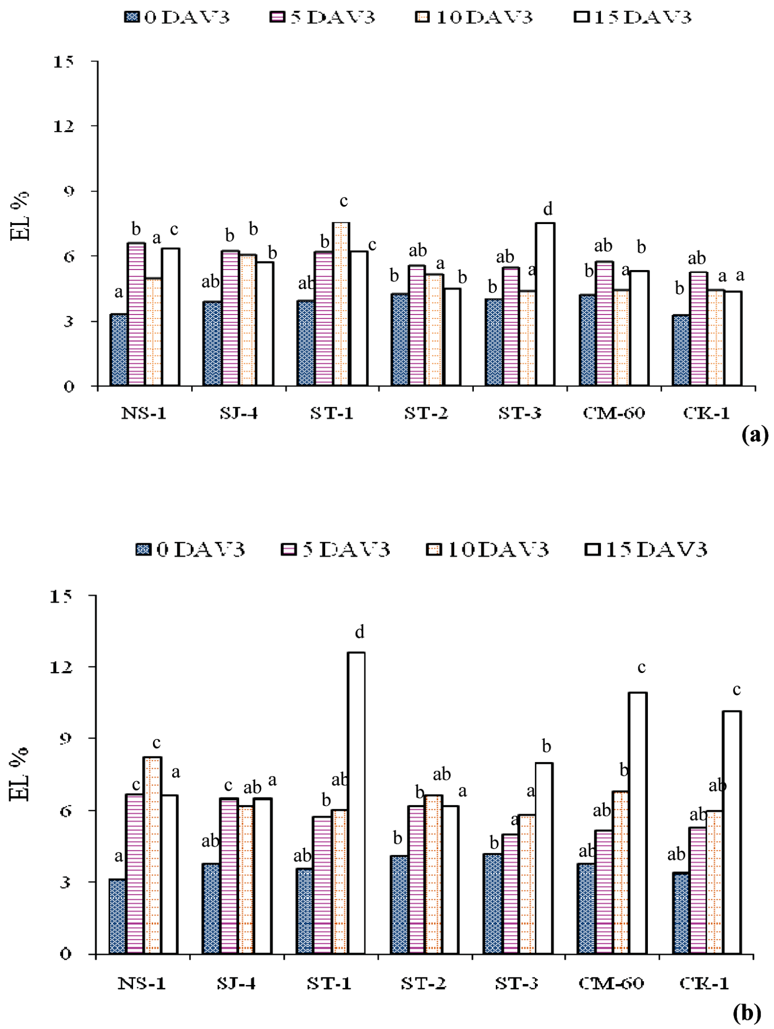

Figure 2 Electrolyte leakage (EL%) of leaf tissue of different soybean cultivars under controlled water regime (a) and under drought-stressed water regime (b) at 5, 10 and 15 DAV3. Same letter above a bar indicates no significant difference at LSD 0.05 at the observed time.

increased up to 100.96% of the control (Table 2). Similar results were also observed for the dry matter accumulation rates during the imposed drought-stressed period (0–15 DAV_3) as shown in Table 4.

The accumulation rates of SDM, RDM, NDM during 0–15 DAV_3 ($SDAR_{0-15}$, $RDAR_{0-15}$, $NDAR_{0-15}$) and seed yield (SYd) shown in Table 5, showed that SDM was significantly correlated with EL%, STM%, NDM and finally with SYd. Although RDM showed a significant correlation only with SDM, it may contribute indirectly to others since SDM had a significant and broad correlation with most of the observed parameters.

Table 1 Shoot dry matter accumulation (g plant $^{-1}$) of different soybean cultivars (Cr) at 0, 5, 10 and 15 DAV_3 under controlled (Control) and drought-stressed (Stress) water regimes (W).

Cultivar	0 DAV_3		5 DAV_3		10 DAV_3		15 DAV_3	
	Control	Stress	Control	Stress	Control	Stress	Control	Stress
NS-1	0.57 ^{b}	0.63 ^{b}	1.27 ^{c}	1.24 ^{b}	2.27 ^{b}	2.10 ^{a}	2.99 ^{b}	2.35 ^{ab}
SJ-4	0.55 ^{b}	0.60 ^{b}	1.18 ^{c}	1.20 ^{bc}	2.16 ^{b}	1.84 ^{a}	3.28 ^{b}	2.53 ^{a}
ST-1	0.68 ^{b}	0.63 ^{b}	1.22 ^{c}	1.00 ^{bc}	1.9^{bc}	1.79 ^{ab}	3.45 ^{b}	2.07 ^{b}
ST-2	0.62 ^{b}	0.59 ^{b}	0.98 ^{c}	1.09 ^{bc}	1.42 ^{c}	1.30 ^{b}	2.59 ^{b}	2.04 ^{b}
ST-3	0.52 ^{b}	0.45 ^{b}	0.93 ^{c}	0.89 ^{c}	1.49 ^{c}	1.37 ^{b}	2.65 ^{b}	1.92 ^{b}
CM-60	0.86 ^{ab}	0.88 ^{a}	1.59 ^{b}	1.50 ^{a}	2.45 ^{a}	2.19 ^{a}	3.96 ^{a}	2.26 ^{ab}
CK-1	1.05 ^{a}	1.02 ^{a}	2.05 ^{a}	1.80 ^{a}	2.95 ^{a}	2.15 ^{a}	4.47 ^{a}	2.46 ^{ab}
Mean	0.69	0.69	1.32	1.25	2.09	1.65	3.34	2.23
CV %	16.9	14.5	17.4	12.5	14.0	17.1	15.2	7.8
$LSD_{0.05\ (Cr)}$	0.21	0.18	0.42	0.31	0.52	0.41	0.90	0.31
$LSD_{0.05\ (W)}$	0.07		0.14		0.16		0.24	
$LSD_{0.05\ (Cr\ xW)}$	0.18		0.36		0.43		0.25	

Means followed by the same letter in a column are not significantly different at $LSD_{0.05}$

Table 2 Root dry matter accumulation (g plant $^{-1}$) of different soybean cultivars (Cr) at 0, 5, 10 and 15 DAV_3 under controlled (Control) and drought-stressed (Stress) water regimes (W).

Cultivar	0 DAV_3		5 DAV_3		10 DAV_3		15 DAV_3	
	Control	Stress	Control	Stress	Control	Stress	Control	Stress
NS-1	0.15 ^{a}	0.15 ^{a}	0.35 ^{a}	0.32 ^{b}	0.44 ^{b}	0.55 ^{a}	0.57 ^{ab}	0.61 ^{a}
SJ-4	0.14 ^{a}	0.15 ^{a}	0.31 ^{a}	0.32 ^{b}	0.43 ^{b}	0.58 ^{a}	0.62 ^{a}	0.60 ^{a}
ST-1	0.11 ^{b}	0.09 ^{c}	0.29 ^{a}	0.27 ^{c}	0.40 ^{b}	0.43 ^{b}	0.61 ^{a}	0.55 ^{a}
ST-2	0.15 ^{a}	0.15 ^{a}	0.33 ^{a}	0.34 ^{b}	0.36 ^{bc}	0.44 ^{b}	0.50 ^{a}	0.58 ^{b}
ST-3	0.12 ^{b}	0.12 ^{b}	0.29 ^{a}	0.23 ^{c}	0.32 ^{c}	0.56 ^{a}	0.51 ^{b}	0.51 ^{c}
CM-60	0.10 ^{c}	0.10 ^{bc}	0.39 ^{a}	0.34 ^{b}	0.45 ^{b}	0.62 ^{a}	0.72 ^{a}	0.68 ^{a}
CK-1	0.12 ^{b}	0.11 ^{bc}	0.40 ^{a}	0.44 ^{a}	0.59 ^{a}	0.61 ^{a}	0.71 ^{a}	0.68 ^{a}
Mean	0.13	0.12	0.34	0.32 ^{b}	0.43	0.54	0.61	0.60
CV %	8.20	13.4	22.3	13.2	14.9	11.1	16.2	4.70
$LSD_{0.05\ (Cr)}$	0.02	0.03	0.13	0.07	0.11	0.10	0.17	0.05
$LSD_{0.05\ (W)}$	7.84		11.02		17.23		22.09	
$LSD_{0.05\ (Cr\ xW)}$	20.73		29.17		45.58		58.45	

Means followed by the same letter in a column are not significantly different at $LSD_{0.05}$

NDM also significantly correlated with SDM, STM%, EL% and SYd. Moreover, there was a significant relationship between NDM and $SDAR_{0-15}$ (r =0.67). In addition, maintaining STM% and membrane integrity resulted in significant correlations with SDM, NDM and SYd. Therefore, it was obvious that nodule growth and biological nitrogen fixation (BNF) depended not only on the ability to maintain moisture status (Serraj and Sinclair, 1998; King and Purcell, 2001)

Table 3 Nodule dry matter accumulation (mg plant $^{-1}$) of different soybean cultivars (Cr) at 0, 5, 10 and 15 DAV_3 under controlled (Control) and drought-stressed (Stress) water regimes (W).

Cultivar	0 DAV_3		5 DAV_3		10 DAV_3		15 DAV_3	
	Control	Stress	Control	Stress	Control	Stress	Control	Stress
NS-1	90.8 ^{ab}	88.8 ^{b}	123.0 ^{b}	116.4 ^{b}	166.2 ^{ab}	177.4 ^{ab}	234.4 ^{ab}	171.4 ^{a}
SJ-4	86.8 ^{ab}	87.9 ^{b}	133.4 ^{ab}	124.0 ^{ab}	177.2 ^{ab}	184.9 ^{a}	223.6 ^{ab}	167.4 ^{a}
ST-1	101.2 ^{ab}	86.7 ^{b}	138.4 ^{ab}	116.0 ^{b}	159.9 ^{b}	144.9 ^{ab}	252.6 ^{ab}	122.3 ^{b}
ST-2	67.3 ^{b}	66.3 ^{b}	99.2 ^{c}	100.9 ^{b}	134.6 ^{b}	126.6 ^{b}	187.1 ^{b}	153.0 ^{ab}
ST-3	85.1 ^{b}	85.0 ^{b}	110.9 ^{b}	112.0 ^{b}	165.3 ^{ab}	147.7 ^{ab}	277.7 ^{a}	153.8 ^{ab}
CM-60	110.8 ^{a}	120.2 ^{a}	134.4 ^{a}	141.4 ^{a}	188.3 ^{ab}	168.9 ^{ab}	270.0 ^{a}	160.1 ^{ab}
CK-1	109.8 ^{a}	119.2 ^{a}	147.2 ^{a}	150.2 ^{a}	203.2 ^{a}	169.4 ^{ab}	250.1^{ab}	134.1 ^{b}
Mean	93.03	93.44	126.6	123.0	170.7	160.0	242.2	151.7
CV %	14.5	9.90	14.6	14.0	13.2	19.8	18.4	11.6
$LSD_{0.05\ (Cr)}$	24.04	16.54	22.20	30.73	40.2	56.28	79.3	31.31
$LSD_{0.05\ (W)}$	7.84		11.02		17.23		22.09	
$LSD_{0.05\ (Cr\ xW)}$	20.73		29.17		45.58		58.45	

Means followed by the same letter in a column are not significantly different at $LSD_{0.05}$

Table 4 Dry matter accumulation rate of shoot, root and nodule of different soybean cultivars (Cr) during 0-15 DAV_3 under controlled (Control) and drought-stressed (Stress) water regimes (W).

Cultivar	Shoot (g plant $^{-1}$ day^{-1})		Root (g plant $^{-1}$ day^{-1})		Nodule (mg plant $^{-1}$ day^{-1})	
	Control	Stress	Control	Stress	Control	Stress
NS-1	0.33 ^{a}	0.26 ^{a}	0.016 ^{d}	0.017 ^{c}	0.062 ^{ab}	0.044 ^{a}
SJ-4	0.36 ^{a}	0.29 ^{a}	0.018 ^{c}	0.019 ^{b}	0.063 ^{ab}	0.043 ^{a}
ST-1	0.32 ^{a}	0.24 ^{ab}	0.021 ^{b}	0.022 ^{a}	0.060 ^{ab}	0.022 ^{b}
ST-2	0.28 ^{b}	0.25 ^{ab}	0.015 ^{d}	0.016 c	0.068 ^{ab}	0.055 ^{a}
ST-3	0.32 ^{a}	0.29 ^{a}	0.017 ^{cd}	0.017 ^{c}	0.077 ^{a}	0.039 ^{a}
CM-60	0.31 ^{ab}	0.19 ^{b}	0.024 ^{a}	0.022 ^{a}	0.060 ^{ab}	0.019 ^{b}
CK-1	0.29 ^{b}	0.18 ^{b}	0.023 ^{a}	0.022 ^{a}	0.055 ^{b}	0.008 ^{b}
Mean	0.32	0.24	0.019	0.019	0.064	0.033
CV %	10.3	15.5	9.6	10.7	19.0	29.7
$LSD_{0.05\ (Cr)}$	0.06	0.07	0.0003	0.0004	0.022	0.017
$LSD_{0.05\ (W)}$	0.002		0.001		0.008	
$LSD_{0.05\ (Cr\ xW)}$	0.006		0.003		0.021	

Means followed by the same letter in a column are not significantly different at $LSD_{0.05}$

but also on the energy and carbon supplied by photosynthesis from the top parts (Fellows *et al.*, 1987). Likewise, the results suggested that nodule growth was more sensitive to drought stress than shoot growth regarding their relative growth under different water regimes.

Drought tolerance attributes of the cultivars

The yield-based cultivar evaluation was also analyzed to support further breeding programs in this study. The stress-tolerant attributes for the tested soybean cultivars estimated from Yp and Ys under the control and drought-stress (SI=0.34) regimes are presented in Table 6 and their relationship is shown in Table 7. The intensity of imposed stress (SI) was 0.34. The results of the current study clearly indicated that ST-1, which was in the top rank of TOL and SSI, had low potential yield in both environments. In addition, the ranks of tested cultivars based on MP, GMP and STI values were similar. Their ranking by SSI and TOL were similar to one another, but different from the former tolerance indices. Although all indices showed a significant relationship with Yp and Ys in this study (Table 7), SSI and TOL failed to distinguish the cultivars which gave lower

Table 5 Correlation coefficient between observed the parameters and seed yield (g plant^{-1}) of soybean cultivars under different water regimes at 15 DAV_3.

Parameter	SDM	RDM	NDM	$SDAR_{0-15}$	$RDAR_{0-15}$	$NDAR_{0-15}$	STM%	EL%
SYd	0.76^{**}	0.21^{ns}	0.81^{**}	0.60^{*}	0.07^{ns}	0.49^{ns}	0.78^{**}	-0.66^{**}
SDM		0.57^{*}	0.78^{**}	0.45^{ns}	0.43^{ns}	0.35^{ns}	0.65^{*}	-0.60^{*}
RDM			0.15^{ns}	-0.36^{ns}	0.77^{**}	-0.04^{ns}	-0.14^{ns}	-0.01^{ns}
NDM				0.67^{**}	0.07^{ns}	0.48^{ns}	0.86^{**}	-0.63^{*}
$SDAR_{0-15}$					-0.37^{ns}	0.42^{ns}	0.82^{**}	0.67^{**}
$RDAR_{0-15}$						-0.25^{ns}	-0.33^{ns}	0.35^{ns}
$NDAR_{0-15}$							0.58^{*}	-0.49^{*}
STM%								-0.85^{**}

SYd = Seed yield (g plant^{-1}); *SDM* = Shoot dry matter; *RDM* = Root dry matter; *NDM* = Nodule dry matter; $SDAR_{0-15}$ = Shoot dry matter accumulation rate during 0–15 DAV_3; $RDAR_{0-15}$ = Root dry matter accumulation rate during 0–15 DAV_3; $NDAR_{0-15}$ = Nodule dry matter accumulation rate during 0–15 DAV_3; *STM%* = Shoot tissue moisture %; *EL%* = Electrolyte leakage % of leaf tissue.

ns = Not significant at $P \leq 0.05$; * = Significant at $P \leq 0.05$; ** = Significant at $P \leq 0.01$

Table 6 Mean of drought tolerance indices and seed yields (g plant^{-1}) of tested soybean cultivars under controlled and drought-stressed (SI = 0.37) regimes.

Cultivar	Yp	Ys	MP	GMP	SSI	TOL	STI
NS-1	$8.51c^{5}$	$6.96b^{3}$	$7.74bc^{6}$	$7.67cd^{6}$	$0.49a^{3}$	$1.55a^{2}$	$0.56bc^{6}$
SJ-4	$10.93b^{4}$	$9.10a^{1}$	$10.02a^{1}$	$9.89a^{1}$	$0.35a^{2}$	$1.82a^{3}$	$0.92a^{1}$
ST-1	$7.63c^{7}$	$5.80b^{7}$	$6.72c^{7}$	$6.65d^{7}$	$0.65a^{4}$	$1.83a^{4}$	$0.42c^{7}$
ST-2	$8.47c^{6}$	$7.86a^{2}$	$8.16b^{5}$	$8.14c^{5}$	$0.19a^{1}$	$0.61a^{1}$	$0.63b^{4}$
ST-3	$12.31ab^{2}$	$5.63b^{7}$	$8.97a^{3}$	$8.31b^{4}$	$1.47b^{7}$	$6.68b^{7}$	$0.65b^{3}$
CM-60	$11.51ab^{3}$	$5.82b^{5}$	$8.66b^{4}$	$8.15bc^{3}$	$1.32b^{5}$	$5.69b^{5}$	$0.63b^{4}$
CK-1	$12.88a^{1}$	$6.38b^{4}$	$9.63a^{2}$	$9.04ab^{2}$	$1.36b^{6}$	$6.49b^{6}$	$0.77ab^{2}$
$LSD_{0.05}$	1.67	1.75	1.07	1.16	0.65	2.67	0.18

Yp = Seed yield under control water regime; Ys = Seed yield under drought stress regime; MP = Mean productivity; GMP = Geometric mean productivity; SSI = Stress susceptibility index; TOL = Stress tolerance; STI = Stress tolerance index.

Means followed by the same letter in a column are not significantly different at $LSD_{0.05}$

In a column, superscripted numbers show the rank of the cultivar.

Table 7 Correlation coefficient among drought tolerance indices and seed yield under control and drought-stressed regimes.

	Yp	Ys	MP	GMP	SSI	TOL	STI
Yp	1	-0.20^{ns}	0.78^{**}	0.61^{**}	0.75^{**}	0.86^{**}	0.59^{**}
Ys		1	0.46^{*}	0.65^{**}	-0.79^{**}	-0.68^{**}	0.66^{**}
MP			1	0.97^{**}	0.17^{ns}	0.34^{ns}	0.96^{**}
GMP				1	0.06^{ns}	0.13^{ns}	0.99^{**}
SSI					1	0.98^{**}	0.09^{ns}
TOL						1	0.06^{ns}
STI							1

Yp = Seed yield under control water regime; Ys = Seed yield under drought stress regime; MP = Mean productivity; GMP = Geometric mean productivity; SSI = Stress susceptibility index; TOL = Stress tolerance; STI = Stress tolerance index.
ns = Not significant at $P \leq 0.05$; * = Significant at $P \leq 0.05$; ** = Significant at $P \leq 0.01$.

yields under both water regimes, while STI, GMP and MP could distinguish better yielding genotypes. Moreover, SSI and TOL resulted in low potential in genetic aspects such as heritability, general combining ability and specific combining ability in wheat (Saba *et al.,* 2001). Most studies with various crops pointed out that selection based on TOL and SSI identified the drought-tolerant genotypes with low yield. However, MP, GMP and STI identified the drought-tolerant genotypes with high yield (Fernandez, 1992; Sanjari and Yazdansepas, 2008) and showed a consistent correlation with yields in seasonal variations (Golabadi *et al.,* 2006) and locations (Pourdad, 2008).

CONCLUSION

Dry matter accumulation in the shoots and nodules were major parameters for selection and evaluation for drought-tolerant soybean cultivars and yield improvement. Shoot tissue moisture content and electrolyte leakage were also effective for the monitoring and evaluation of drought-tolerant cultivar improvement by obtaining better yield potential under both nonstressed and water-stress conditions, due to all parameters showing a good correlation with seed yield. Among the tested soybean cultivars, SJ-4 was the most appropriate cultivar not only for cultivar improvement but also for crop production in drought-prone areas because its physiological properties responded to drought and showed better yield potential in drought-stressed environments. Among the drought-tolerance indices, STI was the most appropriate index for selecting a drought-tolerant cultivar, followed by GMP.

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