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RESEARCH ARTICLE

Soybean (*Glycine max* (L) Merrill) Root Growth and Nodulation Responses to Different Soil Moisture Regimes

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Abstract

Climate change due to global warming is contributing to upward shifts in temperatures and reductions in rainfall leading to increased incidences of soil moisture stress. A greenhouse experiment was conducted over two seasons to determine the effect of varying soil moisture regimes on root growth and nodulation of selected soybean (*Glycine max* (L.) Merrill) cultivars. The experiment was conducted as a Randomized Complete Block Design (RCBD) in a 4 x 6 factorial treatment arrangement with moisture regimes (80, 60, 40, and 20% of field capacity) as first factor and cultivars (Gazelle, Nyala, EAI 3600, DPSB 8, Hill, and DPSB 19) as second factor. Collected data on root diameter, root length, root surface area, root volume, and nodulation were subjected to Analysis of Variance (ANOVA) using Linear Mixed Model in GENSTAT. Significantly different treatment means were separated using Tukey's test at 0.05 level of significance. Moisture stress significantly reduced soybean root diameter, root length, root surface area, root volume, root biomass, root to shoot ratio, and nodulation of all tested cultivars. The degree of stress however varied with soybean cultivars tested with cultivar EAI 3600 having highest root volume, root biomass, and number of nodules per plant compared to other cultivars. Results suggest that 40% moisture at field capacity could be a threshold moisture stress level for soybean beyond which adaptive soil moisture mitigation practices like supplementary irrigation and use of appropriate agronomic practices be employed to improve soybean yields.

Key words : Photosynthates, root nodules, seasons, soybean cultivars, soil moisture limitation

Introduction

Soybean [*Glycine max* (L) Merrill] is one of the most traded amongst tropical legumes contributing 83.3% annual revenue from legume crops which is valued at US $30.0 billion (Abate et al. 2012). Soybean is a good source of proteins (40%), carbohydrates (30%), oils (20%), vitamins, and minerals making the crop suitable for human consumption and livestock feed (Singh and Shivakumar 2010). Annual demand for soybean in Kenya exceeds 100,000 metric tons, the highest in the East African region (Tinsley 2009). However, annual production of the crop in the country is at 4,335 metric tons leaving a deficit of close to 95% (FAO 2013). Yields amongst smallholder farmers, which are key producers of the crop in Kenya, are low and range from 445-1200 kg per hectare (Collombert 2013). These low yields are largely attributed to soil moisture stress which, in recent times, has been associated with global climate change which has led to upward shifts in temperatures and reduction in rainfall (Hartman et al. 2011; Rosenzweig et al. 2001). Moisture stress is synonymous with soil compaction which affects soil air and water relations leading to limitation in plant growth (Sartoli et al. 2016). It is estimated that soil moisture stress cause between 28-45% reductions in soybean yields (Hartman et al. 2011), contributing to food insecurity at the household level.

Roots play a critical role in plant nutrition by absorbing water and mineral nutrients from the soil and conducting them to shoot system for production of assimilates for plant growth (Ryan et al. 2016). In leguminous crops like soybean, root nodulation defines extent of biological nitrogen fixation which serves as an important source of nitrogen for plant nutrition (Ciampitti and Salvagiotti 2018). In soybean, roots

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are also vital in the synthesis of phytohormones such as abscisic acid which help plants adapt to moisture stress through stomata closure and reduction of plant growth (Basu et al. 2016). Root growth in crop plants is therefore viewed as an important indicator of the extent to which plants may explore soil for water and nutrients and that under soil moisture limitations, water and nutrient uptake may be dependent on root size and morphology (Yang et al. 2016). Extent of morphological changes in root growth will however vary with degree of stress and level of tolerance of a crop cultivar. Adjustments in root growth under soil moisture limitation are considered as moisture stress avoidance mechanism which allow plants to maintain relatively higher tissue water content despite limitations in soil moisture level (Basu et al. 2016). While the response of the soybean shoot system to moisture stress has been extensively studied, the below ground system has received limited attention due to either challenges in controlling the growth environment or difficulties in accessing roots (Whitmore and Whalley 2009). However, in order to effectively optimize soybean yields under soil moisture limitations, it is vital to understand morphological adjustments in soybean root growth which may serve as adaptive mechanisms to soil moisture stress. This, in addition to identification and use of moisture stress tolerant cultivars, would help mitigate against adverse effects of soil moisture stress and narrow soybean yield gap for attainment of food, nutrition, and income security at the household and national levels. It is for this reason that this study was conducted to assess soybean root growth and nodulation responses to different soil moisture regimes under greenhouse conditions.

Materials and Methods

Site description

The experiment was conducted in pots in a greenhouse at Egerton University, Njoro campus in Kenya during 2017 and 2018 seasons. Egerton University is 0^0 22'S; 35^0 56'E and at an altitude of 2267 meters above sea level (m.a.s.l) with annual mean temperature of 15.9°C.

Determination of moisture at field capacity

A sample of 10 planting pots used in the experiment were filled with soil and then saturated for several hours with water until all micro-pores were filled with water. The top of the pots were then covered with black plastic sheets to avoid evaporation. After overnight, moisture content at 100% field capacity (FC) was determined using IMKO-HD2 time domain reflectometer (TDR) by inserting TDR probes vertically in the pot soil. The amount of moisture held by the soil at subsequent field capacities were then determined with reference to mean soil moisture level at 100% FC which was then used to come up with the following: 80, 60, 40, and 20% of FC. After sowing, moisture levels in all treatments were maintained close to 100% field capacity for 30 days after which respective soil moisture treatment regimes were initiated up to physiological maturity of the crop. After initiation of moisture regime treatments, soil moisture regimes at respective field capacities were monitored using TDR and changes in soil moisture were corrected by supplying additional water.

Table 1. Characteristics of soybean cultivars used in the experiment.

	Cultivar name	Characteristics
1	Gazelle	indeterminate, medium maturity
2	Nyala	determinate, early maturity
3	EAI 3600	determinate, early maturing
4	DPSB 8	indeterminate, promiscuous, late maturity
5	Hill	determinate, medium maturity
6	DPSB 19	indeterminate, promiscuous, medium maturity

Experimental design and treatments

The experiment was conducted using a randomized complete block design (RCBD) with a 4 x 6 factorial treatment arrangement with three replicates. Treatments consisted of two factors: factor 1 being moisture regimes and factor two being soybean cultivars. Soil moisture regimes were at 80, 60, 40, and 20% of soil moisture content at field capacity. Soybean cultivars used in the experiment were Gazelle, Nyala, EAI 3600, DPSB 8, Hill, and DPSB 19. Characteristics of soybean cultivars used in the study are shown in Table 1.

Planting and crop management

Growth medium was a mixture of clay loam soil and river sand in a 2:1 ratio. Soil analyses were performed at the soil science laboratory at Egerton University to determine initial quantities of total nitrogen (N), extractable potassium (K), and available phosphorous (P) prior to mixing with river sand. The growth medium was put in planting pots measuring 18 cm in height and 22 cm in diameter giving a pot volume of 6,842 cm^3. Planting pots were placed on a bench 100 cm above greenhouse floor. Natural lighting was used for plant growth and daily minimum and maximum temperatures were taken using a minimum and maximum bulb thermometer. Soybean seeds were inoculated with BIOFIX *(Bradyrhizobium japonicum)* inoculant strain USD 110 from Mea Limited–Kenya at the rate of 10 g per kg of seed prior to sowing. Three soybean seeds were sown in each pot and thinned to one plant per pot 14 days after emergence. Each treatment had four plants per replicate. Triple Super Phosphate (TSP) and Muriate of Potash (MOP) were applied as basal dressing fertilizers at the rates of 0.68 g per pot (30 kg P_2O_5 ha^{-1}) and 0.27 g per pot (30 kg K_2O ha^{-1}), respectively. Hand weeding was done in pots as weeds appeared.

Measurement of root growth parameters

Root diameter, root length, root surface area, root volume, root biomass, root to shoot ratio, and nodulation were determined at 50% flowering and one plant from each treatment was soaked in a 20 l bucket of water for 5 min to loosen the soil. A plant with loosened soil was then put on 2 mm screens and cleaned until all soil and plant debris were removed. Separation of roots and shoot was done at the crown level. All leaves were plucked leaving stems and branches. Plucked leaves were put in plastic bags while stems and branches were cut into 5 cm pieces and placed in separate plastic bags. Nodule counts and function were determined and active nodules were pink to red in color when cut open while inactive nodules were green to brown in color (Station et al. 2011). Root volume, root length, root diameter, and root surface area were determined by scanning plant roots using Epson Expression 10000XL color image scanner and analyzed using Winrhizo software (LA 2100-Regent Instruments Inc.). Separated shoot and root plant parts for determination of leaf, root and nodule biomasses were dried separately in an oven to constant weights at 60°C for 24 h (Hossain et al. 2014). Mean weights of dried samples were taken as leaf, root, and nodule biomass per plant.

Statistical analysis

Collected data were checked for fulfilment of analysis of variance (ANOVA) assumption of normality by using Shapiro-Wilk normality test in Genstat release 18.1. Data that did not meet the aforesaid ANOVA assumption were subjected to a square root transformation before analysis. Data were then subjected to ANOVA using the linear mixed model for RCBD with factorial treatment arrangement in Genstat (Restricted Maximum Likelihood-REML) and statistically significant treatment means were separated using Tukey's test at 0.05 significance level.

Results

Root diameter

Root diameter was significantly ($P < 0.01$) influenced by the interaction of soil moisture regimes and cultivars (Table 2). In the two seasons, all soybean cultivars had thicker roots at higher soil moisture regime of 80% FC, with root diameter progressively decreasing with increasing soil moisture limitation. All cultivars had a proportionate root thickness response at the lowest moisture regime of 20% FC.

Root surface area

Soil moisture regimes significantly ($P < 0.001$) influenced root surface area both in 2017 and 2018 seasons (Fig. 1). Highest root surface area of 829 cm^2 in 2017 and 1079 cm^2 in 2018 were achieved at 80% FC representing 69.60 and 82.02% increases over lowest root surface areas of 252 cm^2 (2017) and 194 cm^2 (2018) attained at 20% FC. Soybean cultivars did not have a significant effect on root surface area in both seasons.

Table 2. Effect of soil moisture regimes and soybean cultivars on root diameter (mm) during 2017 and 2018 seasons.

	Root diameter (mm)		
Soil moisture (% FC)	Cultivar	2017	2018
80	Gazelle	0.82	0.69
	Nyala	0.95	0.85
	EAI 3600	0.77	0.63
	DPSB 8	0.84	0.80
	Hill	0.63	0.68
	DPSB 19	0.81	0.62
60	Gazelle	0.66	0.68
	Nyala	0.75	0.69
	EAI 3600	0.71	0.72
	DPSB 8	0.75	0.69
	Hill	0.66	0.64
	DPSB 19	0.74	0.65
40	Gazelle	0.62	0.56
	Nyala	0.62	0.55
	EAI 3600	0.64	0.54
	DPSB 8	0.68	0.67
	Hill	0.61	0.55
	DPSB 19	0.62	0.60
20	Gazelle	0.61	0.49
	Nyala	0.54	0.54
	EAI 3600	0.52	0.52
	DPSB 8	0.66	0.58
	Hill	0.54	0.55
	DPSB 19	0.52	0.50
p-value		0.007	0.009
LSD (0.05)		0.097	0.088
CV (%)		8.8	8.6

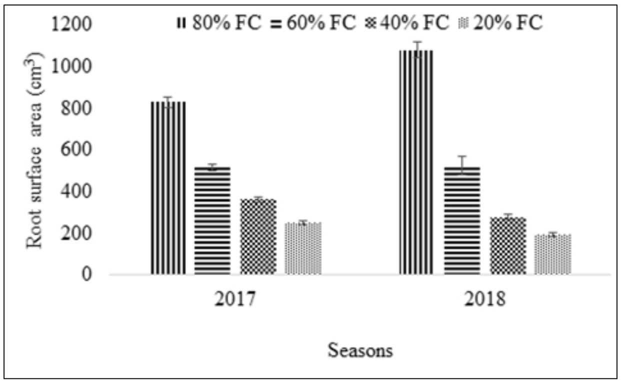

Fig. 1. Response of root surface area to different soil moisture regimes during 2017 and 2018 seasons (error bars represent standard error).

Root length

Soil moisture regimes significantly ($P < 0.001$) increased soybean root length in both seasons. In both cases, root length significantly increased with reduced soil moisture stress (Fig. 2). The effect of soybean cultivars on root length varied with seasons. In the 2017 season, cultivars did not have a significant influence on root length. In 2018, root length was significantly dependent on cultivar type with cultivar EAI 3600 having longest root length of 2957 cm which was 24.52% more than shortest root length registered by cultivar Nyala.

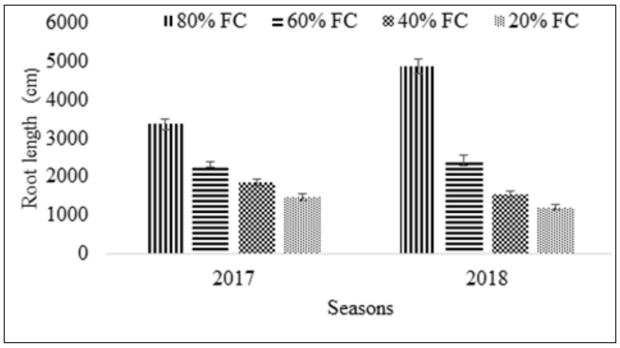

Fig. 2. Response of root length to soil moisture regimes during 2017 and 2018 seasons (error bars represent standard error).

Root volume

Interaction effect of soil moisture regimes and cultivars had a significant ($P < 0.001$) effect on volume of soybean roots. The interaction of the highest soil moisture regime of 80% FC and all cultivars led to a significant increase in root volume. Corresponding interactive effects between cultivars and soil moisture regimes at lower soil regimes reduced root volume (Table 3). Cultivar Nyala had highest percent reduction in root volume at the lowest soil moisture regime of 20% FC both in 2017 (85.47%) and 2018 (91.39%) seasons. On the other hand, cultivars Hill and EAI 3600 maintained highest

Table 3. Effect of soil moisture regimes and soybean cultivars on soybean root volume (cm^3) and root biomass (g plant^{-1}) during 2017 and 2018 seasons.

		Root volume (cm^3)		Root biomass (g plant^{-1})	
Soil moisture (% FC)	Cultivar	2017	2018	2017	2018
80	Gazelle	18.88	18.76	2.85	3.00
	Nyala	21.20	26.03	3.24	3.17
	EAI 3600	17.01	16.02	2.72	2.19
	DPSB 8	16.46	21.70	2.89	3.61
	Hill	12.17	17.76	2.09	2.22
	DPSB 19	14.68	15.38	2.50	2.38
60	Gazelle	7.98	8.60	1.72	1.35
	Nyala	9.32	7.04	2.26	1.25
	EAI 3600	9.00	14.56	1.90	1.91
	DPSB 8	9.69	8.56	2.46	1.69
	Hill	8.31	7.57	1.47	1.20
	DPSB 19	10.68	8.25	2.15	1.39
40	Gazelle	5.75	4.45	124	0.82
	Nyala	5.56	3.47	1.21	0.64
	EAI 3600	6.13	4.04	1.22	0.81
	DPSB 8	5.88	4.42	1.31	0.83
	Hill	5.26	3.15	1.34	0.63
	DPSB 19	5.68	4.63	1.18	0.68
20	Gazelle	3.25	2.30	0.84	0.50
	Nyala	3.09	2.24	0.77	0.46
	EAI 3600	3.76	3.11	0.73	0.60
	DPSB 8	4.14	3.08	0.77	0.58
	Hill	3.23	2.28	0.69	0.49
	DPSB 19	3.64	2.17	0.81	0.40
p-value		0.004	0.002	< 0.001	< 0.001
LSD (0.05)		2.853	4.310	0.317	0.382
CV (%)		19.8	30.0	11.5	17.0

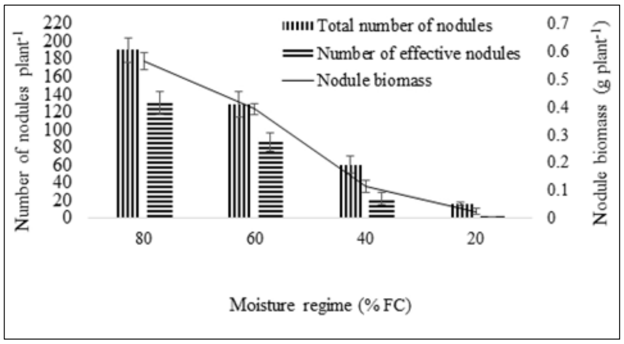

Fig. 3. Effect of soil moisture regimes on total number of soybean nodules, number of effective nodules and nodule biomass during 2017 season (error bars represent standard error).

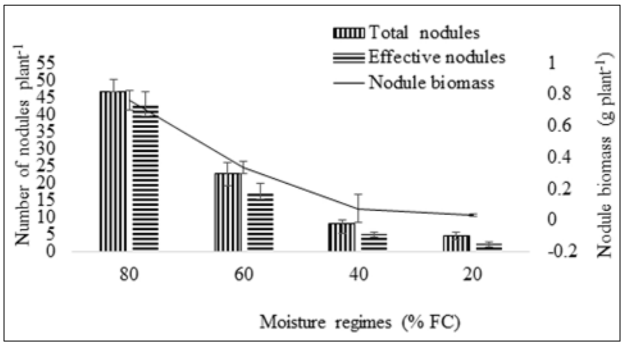

Fig. 4. Effect of soil moisture regimes on total number of soybean nodules, number of effective nodules and nodule biomass during 2018 season (error bars represent standard error).

Table 4. Effect of soybean cultivars on total number of nodules, nodule efficiency and nodule biomass during 2017 and 2018 seasons.

Cultivars	Total nodules plant $^{-1}$			Effective nodules plant^{-1}			Nodule biomass g plant^{-1}		
	2017	2018	Mean	2017	2018	Mean	2017	2018	Mean
Gazelle	85.19	20.16	52.68	41.99	14.85	28.42	0.24	0.25	0.25
Nyala	71.40	18.32	44.86	18.84	13.76	16.30	0.30	0.26	0.28
EAI 3600	103.22	16.81	60.02	58.37	12.04	35.21	0.33	0.18	0.26
DPSB 8	66.75	15.21	40.98	31.80	11.76	21.78	0.31	0.27	0.29
Hill	65.12	11.70	38.41	38.32	7.34	22.83	0.25	0.11	0.18
DPSB 19	96.24	14.98	55.61	45.02	12.18	28.60	0.22	0.20	0.21
Mean	81.32	16.20		39.06	11.99		0.28	0.21	
p-value	0.045	0.175		0.005	0.016		0.009	0.001	
LSD$_{(0.05)}$	33.31	7.90		26.65	6.237		0.067	0.105	
CV (%)	21.7	25.3		31.6	26.1		29.8	25.0	

root volume at lowest soil moisture level of 20% FC in 2017 and 2018, respectively.

Root biomass

Root biomass was significantly ($P < 0.001$) responsive to interaction of soil moisture regimes and soybean cultivars (Table 3). In both seasons, all soybean cultivars accumulated more root biomass at higher soil moisture regime of 80% FC with root biomass decreasing with increasing soil moisture stress. Cultivar Nyala had highest percent reduction in root biomass in 2017 (76.23%) and 2018 (85.49%) seasons.

Root nodulation and nodule biomass

Number of nodules per plant, nodule efficiency and nodule biomass were significantly ($P < 0.001$) responsive to variations in soil moisture regimes (Figures 3 and 4) and type of cultivar used (Table 4). Total number of nodules per plant at 80% FC were 91.57% (2017) and 90.13% (2018) higher compared to number of nodules registered at 20% FC. Moisture stress significantly reduced number of effective nodules per plant in both seasons. Cultivar EAI 3600 and Gazelle gave highest total number of nodules per plant in 2017 and 2018, respectively. Cultivar Hill gave the lowest total number of nodules per plant in both seasons. Cultivar Nyala had the lowest number of effective nodules in 2017 while cultivar DPSB 8 registered the least number of effective nodules in 2018 season. Nodule biomass was responsive to cultivar type with cultivar EAI 3600 and Nyala having highest nodule biomass in 2017 and 2018, respectively.

Root to shoot ratio

Root to shoot ratio significantly varied with soil moisture regimes ($P < 0.001$) and cultivars ($P < 0.05$). In both seasons, root to shoot ratio was significantly higher at 80% FC compared to root to shoot ratios obtained at 60% FC, 40% FC, and 20% FC moisture levels (Fig. 5). Soil moisture regime at 40% FC had the least root to shoot ratio in 2017. During 2018 season, non-significant differences were registered amongst 60% FC, 40% FC, and 20% FC. Although cultivar DPSB 8 had the highest root to shoot ratio (0.48) in 2017, this was not significantly different from cultivars Gazelle (0.45), EAI 3600 (0.43), DPSB 19 (0.43), and Nyala (0.42). Cultivar Hill had the lowest root to shoot ratio (0.37) in 2017. In 2018, cultivar EAI 3600 had highest root to shoot ratio (0.32) with cultivar DPSB 19 (0.23) having the lowest. Overall, results indicate that there was a preferential allocation of biomass to shoot system over root system at all moisture regimes and by all soybean cultivars.

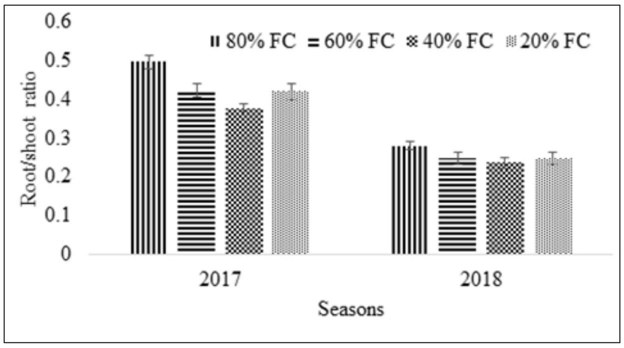

Fig. 5. Response of root to shoot ratio to soil moisture regimes during 2017 and 2018 seasons (error bars represent standard error).

Discussion

Roots play an important role in plant survival under moisture stress via a combination of morphological, osmotic, and cell wall adaptations (Wu and Cosgrove 2002). Results of the study have indicated that root surface area, root diameter, root length, root volume, and root biomass were all reduced with increased soil moisture stress. Studied root characteristics varied with soybean cultivars but growth habit seemed to have non-significant influence on root surface area, root diameter, root length, root biomass, number of nodules per plant, and nodule efficiency. These findings are in agreement with observations by Sartori et al. (2016) who reported an increase in soybean root length, root diameter, root surface area, and root volume in irrigated soybean plants compared to non-irrigated plants. While results of this study have shown that root biomass was significantly reduced by moisture stress, Machado et al. (2017) reported that root dry matter accumulation amongst determinate and indeterminate soybean genotypes was not negatively affected by moisture stress. Unlike results of this study which have indicated reduced root diameter at lower moisture levels, Foloni et al. (2006) reported increased root diameter at lower soil moisture levels which was linked to increased force exerted in the process of stretching root meristem cell to penetrate compacted soil. Studies on wheat by Saidi et al. (2010) indicated that moisture stress did not have significant effect on wheat root length unlike root surface area which was significantly reduced at lower moisture levels. Reduced root growth at low soil moisture levels as found in this study may be attributed to imbalances in the allocation of photosynthates to root system from shoots and reduction in the uptake of nutrients to sustain root growth and development (Masoumi et al. 2014). Reduced root growth at lower soil moisture regimes may also arise from suppressed division, elongation and expansion of root cells coupled with increased root penetration resistance offered by drier soil (Bengough et al. 2005).

Number of soybean nodules per plant, nodule biomass and efficiency of nodules to fix nitrogen were all dependent on available soil moisture. Increases in number of soybean nodules per plant, nodule efficiency and nodule biomass at minimal moisture stress were reported by Streeter (2003) and Madhu and Hartfield (2015). Reductions in number of nodules and the efficiency with which nodules fix nitrogen at lower soil moisture levels may be associated with impairment of nitrogenase activity. Impairment of nitrogenase activities is caused by either a compromised uptake of nutrients by roots to drive symbiotic nitrogen fixation, breakdown of oxygen diffusion barrier or loss of leghemoglobin (Arrese-Igor et al. 2011; Kunert et al. 2016). In addition, moisture deficit promotes accumulation of ureides in soybean shoot system causing a feedback reduction in the efficiency with which root nodules fix nitrogen (Kunert et al. 2016; Purcell et al. 2000).

Root to shoot ratio decreased with increased soil moisture stress amongst soybean plants during both seasons. Much as root to shoot ratio varied with type of cultivar used, no cultivar had a distinct advantage over others in dry matter partitioning to root and shoot systems. Previous studies have reported significant increases in root to shoot ratio at lower soil moisture levels (Dos Santos et al. 2018; Saidi et al. 2010) which contradict the findings of this study. Under water stress, plants are known to invest more dry matter in roots over shoot systems and gradually shift the allocation in favor of shoots when moisture stress becomes less limiting (Munns and Crammer 1996). Current results can be explained by the fact that root to shoot ratios are varied as plant response index to factors influencing carbon synthesis and nutrient acquisition. Higher moisture stress could have caused a reduction in use of photosynthates and uptake of soil nutrients for root growth which was then offset by an increase in the mass of leaves so that the quantity of photosynthate produced by leaves is increased to sustain plant growth and pod development (Linker and Johnson-Rutzke 2005; Szaniawski 1982).

Conclusion

Soil moisture stress reduced soybean root growth and nodulation. Cultivar EAI 3600 maintained higher root volume and root biomass at lower soil moisture in addition to having the highest number of nodules compared to other cultivars. Results suggest that 40% moisture at field capacity could be a threshold moisture stress level for soybean beyond which adaptive soil moisture mitigation practices like supplementary irrigation and use of appropriate agronomic practices be employed to improve soybean yields.

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