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Influence of Drought Stress on Several Root Traits and their Correlation with Seed Protein and Oil Contents in Soybean

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Abstract

The important crop soybean [*Glycine max* (L.) Merr.] is cultivated worldwide and the US is its number one exporter. However, farmers face many challenges in cultivating soybeans, including drought and diseases that reduce yields drastically. The root system is very important for plants, including crops, because it receives water and minerals from the soil so that the plant/crop can photosynthesize, grow, and increase its yield. The objective of this study was to grow the 'MD 96-5722' by 'Spencer' recombinant inbred line (RIL) population (n=86) in the greenhouse under normal (Group I) and drought stress (Group II) conditions, and compare the root length (RL), root surface area (RSA), average root diameter (ARD), and average root volume (ARV) in the two groups of plants. WhinRhizo software was used to measure the root traits and SPSSTM was used to evaluate population performance under normal and drought conditions. JMPTM was used to compare the root traits under normal and drought conditions, and to analyze the correlation between root traits, protein and oil contents. The results showed that there is a huge variation in these traits among the parents 'MD 96-5722' and 'Spencer', and among their RILs. For Group I plants, the RL of parents and RILs ranged from 20.67 cm to 2,327.88 cm; the RSA ranged from 4.57 cm^2 to 1,176.79 cm^2; the ARD ranged from 0.38 mm to 4.04 mm; and the ARV ranged from 0.08 cm^3 to 47.34 cm^3. For Group II plants, the RL of parents and RILs ranged from 15.70 cm to 3,562.42 cm; the RSA ranged from 4.15 cm^2 to 829.72 cm^2; the ARD ranged from 0.24 mm to 5.74 mm; and the ARV ranged from 0.03 cm^3 to 23.67 cm^3. It is clear from the results that Group I plants have higher means of RL [572.58 cm vs. 537.33 cm], RSA [201.20 cm^2 vs. 165.50 cm^2], ARD [3.96 mm vs. 1.45 mm], and ARV [6.31 cm^3 vs. 5.61 cm^3] compared to Group II plants which demonstrates that drought-stressed plants have reduced overall plant growth and development. However, statistically, these differences were not significant; therefore, further studies with several replicates should be conducted both in the greenhouse and the field in order to determine the effects of drought stress on the 'MD 96-5722' by 'Spencer' RILs. Moreover, studies of quantitative trait loci (QTL) mapping of the root traits studied here are underway to genetically map QTL for these root traits in this soybean RIL population.

Keywords: Root length (RL), Root surface area (RSA), Average root diameter (ARD), Average root volume (ARV), MD 96-5722, Spencer.

Introduction

Soybean [*Glycine max* (L.) Merr.] is a Leguminosae crop grown for its oil, proteins, isoflavones, and other bioactive compounds. It also widely used in the food industry and as a biofuel (Rosenthal et al., 2001; Kinney and Clemente, 2005).

According to USDA, North Carolina planted soybeans in 1.82 Million acres and produced 57.3 Million Bushels for a total of $487 Million in 2015 (USDA, 2015). In North Carolina, soybean production amount was 31 million bushels from 1.4 million acres and a total value of $174 million (NCSUCE, 2015). Soybeans are usually planted in early soybean production system (ESPS)

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(April) or conventional soybean production system (CSPS, May-June) across the US (Bowers, 1995; Taylor et al., 2005; Ouertani et al., 2011). Soybean plants grown in ESPS have increased yield and are drought-tolerant compared to plants grown in CSPS (Taylor et al., 2005; Ouertani et al., 2011).

Plant breeders and researchers are trying to develop cultivars that are resistant to diseases and drought stress. Drought stress reduces the ability of roots to absorb water and nutrients from the soil and it has been demonstrated that plants with vigorous and extensive root systems are able to cope with drought and become water deficit-tolerant (WDT) (Pandey et al., 1984; Benjamin and Nielsen, 2006; Reubens et al., 2006). During drought stress seasons, plants usually change the distribution of their roots and grow them deeper to absorb water and minerals as a mechanism of drought tolerance (Pandey et al., 1984; Benjamin and Nielsen, 2006). In another study, drought-stressed soybean plants have a sharp decrease in their photosynthetic rates, leaf water potentials, starch concentration, and leaf sucrose contents, and pod growth (Liu et al., 2004).

Defending themselves against drought stress, soybean plants close their stomata to escape dehydration but the overall photosynthetic rate is reduced by limiting CO2 intake (via stomata), causing a reduced metabolism that might be reversible with enough supply or availability (Kramer et al., 1995; Specht et al., 2001; Flexas and Medrano, 2002; Liu et al., 2004; Gregory, 2006; Mastrodomenico et al., 2013). The reduced photosynthetic rate has a drastic effect on reducing grain yield. The physiological effects of drought can be estimated by measuring the leaf relative water contents (RWC), root architecture, and reactive oxygen species (ROS) (Hunt et al., 1987; Reddy et al., 2004; Chiante et al., 2006; Reubens et al., 2006; Miller et al., 2010; Comas et al., 2013). During seed fill and pod development stages, soybean plants, like other crops, need an adequate supply of water and any drought stress will decrease developmental and physiological functions that will lead to high decreased seed yields (Kadhem et al., 1985; Kramer et al., 1995; Chiante et al., 2006; Comas et al., 2013).

To withstand drought stress, soybean plants and other legumes use several important mechanisms. Among these are growing extensive root systems, water use efficiency, and high efficient nitrogen fixation (Nunberg et al., 2006; Mastrodomenico et al., 2013; Hussain et al., 2014). It is known that drought-stressed plants tend to grow extensive root systems with continuous elongation at low root water potentials (Westgate and Boyer, 1985; Kramer et al., 1995; Bing et al., 2005; Nunberg et al., 2006; Mastrodomenico et al., 2013; Hussain et al., 2014).

The objectives of this study are to (1) grow the 'MD 96-5722' by 'Spencer' recombinant inbred line population (n=86) of soybean under drought stress in the greenhouse, study the influence of drought stress on several root traits such as root length (RL), root surface area (RSA), average root diameter (ARD), and average root volume (ARV), and (2) investigate the correlation between root trait measurements, protein and oil contents of 'MD 96-5722' by 'Spencer'.

Materials and Methods

Plant Material

In this study, the 'MD 96-5722' by 'Spencer' recombinant inbred line (RIL) population (n=86) of soybean was used (Akond et al., 2013). These seeds were obtained at the National Soybean Research Laboratory (NSRL) in 2006 from Dr. Kantartzi. The parents of 'MD 96-5722' were from a cross between KS4644 and 'Corsica' KS4694, whose parents were 'Shermon and Toano'. 'Spencer' came from the crossings between A75-305022 by 'Century' (Akond et al., 2013).

Experimental Conditions

The experiment was performed during 2013 (June 2013 to September 2013) in a Greenhouse at Fayetteville State University, Fayetteville, North Carolina. Four seeds of parents, 'MD 96-5722', 'Spencer', and each RIL (n=86; n is the population size) were sown at 1.5–2.0 inches deep in 2-gallon pots (20.32 x 17.78 cm) filled with potting soil of organic material (Miracle Grow potting mix) under daylight temperatures of 24–34o C. The pots were set on a brown sheet, avoiding water capillarity from the bottom. The pots were divided into two groups, a control group (n=86) for normal growth and a treatment group (n=86) for drought conditions. The treatment group would undergo drought stress during the entire growth development. First week, normal watering was given to each seedling, 3.76 liters of water. Control group would receive normal watering throughout the whole study or when needed. Treatment group was submitted through intense drought stress for two weeks after normal watering. Afterwards, watering the plants at least once a week and at 1.5 liters of water.

Root Extraction Method

After eight weeks of planting, roots were carefully extracted from the pots one by one, placed inside a tray filled with water and washed by hand. Later, the roots were left to dry and have just enough moisture in order to separate the lateral roots from the primary root. Roots were separated by using a plastic transparent wrap, the wraps texture allowed for lateral roots to separate easily without damaging the root and minimizing loss of fine lateral roots. Afterwards, to preserve the roots, they were placed inside Ziploc bags and placed in a refrigerator for later analysis. Several root traits such as root length (RL), root surface area (RSA), average root diameter (ARD), and average root volume (ARV) were measured.

Protein and Oil Contents Quantification

Seed protein and oil contents have been measured by Nacer Bellaloui at the USDA-ARS, Stoneville, MS according to Bellaloui et al. (2009). Briefly, 25 g of seed from each plant were grinded using a Lab Mill 3600 (Perten, Springfield, IL). Near infrared reflectance was used for analyses using a diode array feed analyzer AD 7200 (Perten, Springfield, IL) (Bellaloui et al., 2009).

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Root Trait Analysis

The root traits root length (RL), root surface area (RSA), average root diameter (ARD), and average root volume (ARV) were measured in both groups (Control and Experimental Groups) using an Epson Scanner and the WhinRhizo software Package 3.10 version (Regent Instruments Inc. Quebec, Canada). The images were visualized and root data analyzed using the Epson Scanner and the WhinRhizo software. Root traits analyzed were root length (RL), root surface area (RSA), average root diameter (ARD), and average root volume (ARV).

Statistical Analysis

A distribution chart was constructed based on the differences in root trait measurements in (RIL) population. SPSSTM statistical software package was used to evaluate population performance under normal and drought conditions. The evaluation was based on mean differences, estimation of variance and descriptive comparisons. JMPTM was used to compare the root length (RL), root surface area (RSA), and average root diameter (ARD) and average root volume (ARV) under normal and drought conditions. Also, JMPTM statistical software package was used to analyze the correlation between root traits, protein and oil content. Recombinant inbred lines of the parents were also compared along with the RILs evaluation. T-Test and Pearson correlations were performed to compare the root traits in plants grown in the two conditions and between the root traits and protein and oil contents.

Results and Discussion

Comparison of Root Traits Data

Examples of scanned images of the root system of RIL 2 under normal water regime and drought stress are shown in Figure 1. Measurements of root length (RL), root surface area (RSA), average root diameter (ARD), and average root volume (ARV) of 'MD 96-5722 by 'Spencer' recombinant inbred lines root systems under normal (Group I) and drought (Group II) growth conditions have been recorded.

For control plants (Group I), the root length (RL) of parents and RILs ranged from 20.67 cm (RIL 63) to 2,327.88 cm (RIL 2); the root surface area (RSA) parents and RILs ranged from 4.57 cm^2 (RIL 41) to 1,176.79 cm^2 (RIL 2); the average root diameter of parents and RILs ranged from 0.38 mm (RIL 80) to 4.04 mm (RIL 43); and the average root volume (ARV) of parents and RILs ranged from 0.08 cm^3 (RIL 41) to 47.34 cm^3 (RIL 2).

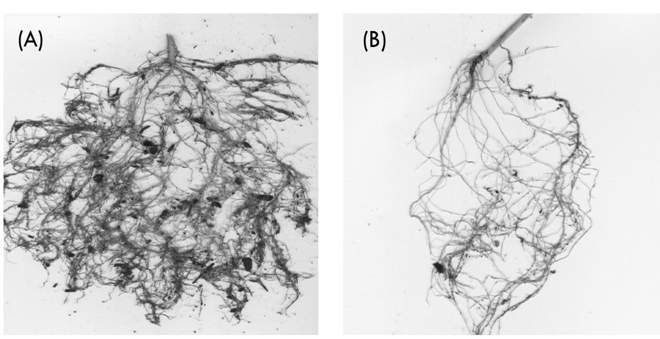

Figure 1. Scanned images of the root system of RIL 2 under normal water regime (A) and drought stress (B).

For drought-stressed plants (Group II), the root length (RL) of parents and RILs ranged from 15.70 cm (RIL 80) to 3,562.42 cm (MD, 2,497.9 cm for RIL 87); the root surface area (RSA) parents and RILs ranged from 4.15 cm^2 (RIL 46) to 829.72 cm^2 (MD, 669.62 cm^2 for RIL 87); the average root diameter of parents and RILs ranged from 0.24 mm (RIL 7) to 5.74 mm (RIL 80); and the average root volume (ARV) of parents and RILs ranged from 0.03 cm^3 (RIL 46) to 23.67 cm^3 (RIL 32).

Our results showed that both RL, RSA, ARD, and ARD have been significantly reduced by drought stress which is in agreement with several studies reporting the influence of drought on root traits (Xiong et al., 2006, Pandey and Shukla 2015). For example, Xiong et al. (2006) reported that drought stress reduced significantly lateral root growth in Arabidopsis thaliana as a mechanism of drought adaptation (Xiong et al., 2006). Garay and Wilhelm (1982) studies the effect of drought stress on root traits of two soybean isolines of 'Harosoy' (Harosoy normal (HN) and Harosoy dense (HD)) and found that the root systems have been concentrated in the upper 0.15 m of the soil. However, after one month of drought stress, the root systems were denser at 0.90-1.2 m layer of the soil which means that the root system grew deeper into the soil to pump more water and mineral (Garay and Wilhelm, 1982). However, another study reported effect of drought stress on root distribution (Benjamin and Nielsen, 2006).

Statistical Data Analysis

Root traits data for the two groups (Control plants – Group I and Drought Stressed plants – Group II) were analyzed for the mean values, standard deviation, range, and coefficient of variation and the results are shown in Table 1.

In Group I plants (normal water conditions), the mean of the average of root length (RL) was 572.58 cm with a coefficient of variance of (CV) of 0.95; the mean of the average of root surface area (RSA) was 201.20 cm^2 with a coefficient of variance of (CV) of 1.13; the mean of the average root diameter (ARD) was 3.96 cm with a coefficient of variance of (CV) of 6.01; and the mean of the average root volume (ARV) was 6.3 cm^3 with a coefficient of variance of (CV) of 8.02 (Table 1).

In Group II plants (water stress conditions), the mean of the average of root length (RL) was 537.33 cm with a coefficient of variance of (CV) of 1.25; the mean of the average of root surface area (RSA) was 165.5 cm^2 with a coefficient of variance of (CV) of 1.01; the mean of the average root diameter (ARD) was 1.45 cm with a coefficient of variance of (CV) of 7.89; and the mean of the average root volume (ARV) was 5.6 cm^3 with a coefficient of variance of (CV) of 1.03 (Table 1).

It is clear from the results that Group I plants have higher means of root length (RL) [572.58 cm vs. 537.33 cm], root surface area (RSA) [201.20 cm^2 vs. 165.50 cm^2], average root di-

Table 1. Comparison of root trait measurements of 'MD 96-5722 by 'Spencer' RILs under normal growth conditions and drought. N: Population size (69 plants in group I and 75 plants in groups II survived among 86 planted plants in total).

Root Traits	N	Range	Minimum	Maximum	Mean	SD	CV%
Normal Growth							
Length (cm)	69	2307.201	20.679	2327.881	572.580	548.901	0.958
Surface Area (cm^2)	69	1172.221	4.572	1176.793	201.208	227.754	1.131
Average Diameter (mm)	69	3.653	0.388	4.042	1.090	0.537	4.927
Average Root Volume (cm^3)	69	47.260	0.080	47.340	6.311	8.028	1.272
Drought Conditions							
Length (cm)	75	2482.200	15.700	2497.901	497.001	582.135	1.171
Surface Area (cm^2)	75	665.496	4.156	669.653	156.646	150.044	0.957
Average Diameter (mm)	75	5.499	0.245	5.745	1.449	1.154	7.961
Average Root Volume (cm^3)	75	23.638	0.039	23.677	5.610	5.796	1.033

Table 2. T-Test showing summary of paired statistics for the two experimental conditions for each of the four root traits listed. For each condition we display the mean, number of participants (N), the standard deviation and standard error. N: Population size.

	Root Traits	Mean	N	SD
Pair 1	Length-Normal	587.753	62	568.043
	Length-Drought	529.145	62	608.654
Pair 2	Surface Area-Normal	209.915	62	235.000
	Surface Area-Drought	167.590	62	158.028
Pair 3	Average Diameter-Normal	1.112	62	.556
	Average Diameter-Drought	1.417	62	1.105
Pair 4	Volume-Normal	6.726	62	8.351
	Volume-Drought	5.663	62	5.660

Table 3. The Pearson correlation between the two conditions, whether the difference between the means of the two conditions was large enough not to result, and last, 95% confidence interval was calculated. N: Population size.

	Root Traits	N	Correlation	Significance Level
Pair 1	Length (Normal)-Length (Drought)	62	-.141	.276
Pair 2	Surface Area (Normal) & Surface Area (Drought)	62	-.165	.200
Pair 3	Average Diameter (Normal) & Average Diameter (Drought)	62	-.131	.310
Pair 4	Volume (Normal) & Volume (Drought)	62	-.053	.685

ameter (ARD) [3.96 mm vs. 1.45 mm], and average root volume (ARV) [6.31 cm^3 vs. 5.61 cm^3] compared to Group II plants (Table 1) which demonstrate that drought-stressed plants have reduced overall plant growth and development.

A paired-samples t-Test shown in Table 2 was used to demonstrate whether there was a significant mean difference of root measurements (RL, RSA, ARD, ARV) between normal and drought growth in 'MD 96-5722' by 'Spencer' population planted under greenhouse conditions. Levels of root trait measurements for root length elicited a difference of 58.60821 (95% Confidence Interval (CI), -167.15727 to 284.37370) cm when comparing normal and drought growth conditions, $t(61) = .519$, $p > .005$. The comparison for root surface area (cm^2) displayed a difference of 42.32496 (95% CI, -34.88817 to 119.53809) and a $t(61) = 1.096$, $p > .005$. The average root diameter in comparison showed a difference of -.30523 (95% CI, -.63563 to .02518) mm and $t(61) = -1.847$, $p < .005$. Last, when comparing average root volume, the measurements demonstrated a difference of 1.06339 (95% CI, -1.56043 to 3.68721) cm^3 with a $t(61) = .810$, $p > .005$. There is no significant difference between root length, root surface area, and average root volume. However, there was statistical difference between normal and drought growth conditions for average root diameter. A paired statistic test was used to determine the different effects between two experimental conditions for each of the four root traits. In (Table 2), results indicate a decrease for root measurements of length (cm) (529.14 -77.299), surface area (cm^2) (167.59- 20.069), root volume (cm^3) (5.66- 0.719), and an increase in average diameter (1.42-0.140). In normal growth conditions there was a slight increase in measurements in length (587.75-72.141),

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Table 4. Paired Samples Test. The Pearson correlation between the two conditions, whether the difference between the means of the two conditions was large enough not to result, and last, 95% confidence interval was calculated. Sig.: significance level.

	Root Traits	Mean	SD	Std. Error Mean	95% Confidence Interval of the Difference		t	df	Sig.
					Lower	Upper			
Pair 1	Length (Normal) – Length (Drought)	58.608	889.006	112.903	-167.157	284.373	.519	61	.606
Pair 2	Surface Area (Normal) – Surface Area (Drought)	42.324	304.045	38.613	-34.888	119.538	1.096	61	.277
Pair 3	Average Diameter (Normal) – Average Diameter (Drought)	-.305	1.301	.165	-.635	.025	-1.847	61	.070
Pair 4	Volume (Normal) – Volume (Drought)	1.063	10.331	1.312	-1.560	3.687	.810	61	.421

surface area (209.91-29.845), volume (6.73-1.060) and a decrease in average diameter (1.11-.071). A paired sample correlation test was used to determine the significance between the two conditions and the root traits demonstrated no correlation between RL, RSA, ARD, and ARV under drought and normal conditions. There is no correlation when compared to parents of RIL (Tables 3 and 4).

In a recent study, Fenta et al. (2014) studied three soybean cultivars: A drought-sensitive (A5409RG), a drought-tolerant ('Jackson'), and an intermediate drought-tolerant cultivar ('Prima 2000'). They found that Prima 2000 outperformed the other cultivars under drought stress with the highest grain yield, shoot biomass, and nodules. They also found a positive correlation between nodule size and seed yield and shoot biomass in both control and water stressed plants (Fenta et al., 2014). In general, drought stress is a negative environmental condition affecting soybean production, growth and development (Garay and Wilhelm, 1982; Benjamin and Nielsen, 2006; Du et al., 2009; Fenta et al., 2014). This demonstrates that the carefully chosen root traits can be used to screen for drought tolerance in soybean.

Increasing water deficit tolerance (WDT) increases agricultural plant productivity. Since the roots are the main organs for water and minerals uptake, they play a vital role in agricultural plant productivity. Water stress or water deficit (WD) also decreases shoot biomass, leaf cuticular waxes, seed yield, nitrogen fixation, and seed development (Purcell and King, 1996; Serraj et al., 1999; Kim et al., 2007). Root systems are reported to be critical to cope with WD and increase yield. For example, deep and dense roots with high abilities of penetration and branching into the soil help rice plants to be drought tolerant (Pandey and Shukla, 2015).

Correlation Between Root Traits and Seed Protein and Oil Contents

A Pearson correlations test was done between roots traits of Group I (normal) and Group II (drought), protein and oil content as shown in Table 5 and Table 6. The frequency distribution charts for all root traits showed different measurement distributions. In Group I plants, a positive correlation was observed between all root traits studied (RL, RSA, ARD, and ARV) and seed protein content while a negative correlation was observed between all these root traits and seed oil content (Table 5). In Group II plants, a negative correlation was observed between RL, RSA, and ARV and seed protein content while a positive correlation was observed between ARD and protein content. A negative correlation was observed between RL, RSA, and ARV and seed oil content while a positive correlation was observed between ARD and seed oil content (Table 6).

Table 5. The Pearson correlation between root traits from Group I (normal growth), protein and oil content. Sig.: significance level.

	N	Correlation	Sig.
Pair 1 Length & Protein	69	0.086	0.480
Pair 2 Length & Oil	69	-0.240	0.047
Pair 3 Surface Area & Protein	69	0.113	0.354
Pair 4 Surface Area & Oil	69	-0.301	0.012
Pair 5 Average Diameter & Protein	69	0.084	0.492
Pair 6 Average Diameter & Oil	69	-0.293	0.015
Pair 7 Volume & Protein	69	0.077	0.531
Pair 8 Volume & Oil	69	-0.294	0.014

Table 6. The Pearson correlation between root traits from Group II (drought growth), protein and oil content. Sig.: significance level.

	N	Correlation	Sig.
Pair 1 Length & Protein	75	-0.225	0.052
Pair 2 Length & Oil	75	0.221	0.057
Pair 3 Surface Area & Protein	75	-0.304	0.008
Pair 4 Surface Area & Oil	75	0.246	0.034
Pair 5 Average Diameter & Protein	75	0.029	0.804
Pair 6 Average Diameter & Oil	75	-0.026	0.827
Pair 7 Volume & Protein	75	-0.233	0.044
Pair 8 Volume & Oil	75	0.148	0.204

Several studies reported correlations between shoot traits and protein and oil contents in soybean (Johnson et al., 1955; Mansur et al., 1995; SoyBase, 2016); however, studies reporting correlations between root traits and protein or oil contents are non-existent our knowledge to date.

In conclusion, we have demonstrated that water deficit decreased RL, RSA, and ARV but not ARD in soybean. It is very important to understand the root architecture and root traits under WD to be able to increase seed yield, seed quality, and crop productivity which will enhance the development of WDT varieties and ensure food security.

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