Above-Ground, Below-Ground, and Biochemical Properties of Soybeans Seedlings (*Glycine max* L.) under Drought Stress

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Summary

Drought is one of the major obstacles to the cultivation of soybean. In the event of limited water supply, a functional root system provides biological advantages in case of drought and limited nutrient intake. It is therefore critical to understand how above-ground, below-ground, and physio-biochemical drought responses relate to one another in soybean during drought. Twenty genotypes of soybeans were exposed to drought stress in randomized complete block design experiment for a period of 14 days. Measurements were made of the above-ground parameters (AGP): shoot height, leaf breadth, length and number, canopy wilting, and shoot dry weight. Measurements for below-ground parameters (BGP) were root dry weight, diameter, length and number of lateral roots. Chlorophyll *a* (Chlr *a*), Chlorophyll *b* (Chlr *b*), carotenoids, and proline concentrations were evaluated as biochemical parameters (BP). All parameters were measured and compared to find out which of the 20 genotypes of soybeans were drought-tolerant. There was a positive relationship between AGP and BGP. The Principal Component 1 (PC1), which is positively and significantly correlated with the genotypes TGm-4015, TGm-4400, TGm-951, and TGm-1326, were also positively and significantly correlated with canopy wilt, Chlr *a* and *b*, and carotenoids, as well as root length and dry weight, shoot dry weight, shoot height and high concentrations of Chlorophyll *a* and *b* and carotenoids during drought conditions. Genotypes TGm-1326, TGm-95, TGm-4414, TGm-1678, and TGm-99 had significant ABG and BGP benefits under drought, according to a principal component analysis (PCA) biplot. Therefore, soybean cultivars with advantageous BG and BP under drought will be useful in germplasm improvement.

Key words

legume, soybean, drought stress, root architecture, below-ground, above-ground

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Introduction

Soybean is an important staple crop with high nutritional and agronomical importance. Its proteinaceous benefit makes it suitable as food for humans and as animal feed (Rahman et al., 2021; FAOSTAT, 2019). Its production is yearly affected by some biotic and abiotic factors (Twizeyimana et al., 2011; Ajayi-Oyetunde and Bradley, 2017). Drought as a result of inadequate rainfall is reported to decrease its yield yearly (Khojely et al., 2018). There have been several research efforts in breeding drought tolerance soybean. Many of such studies were carried out on above-ground morphology, physiological and molecular approaches in selecting drought tolerance soybean.

Root phenotype and physiological adjustments at the seedling stage are attributes useful in selecting drought-tolerant cultivars of crops (Fenta et al., 2011; Fenta, et al., 2014; Esan et al., 2023). As several studies have suggested plant adaptability to drought is usually determined by the physio-biochemical adjustment tendency of the plant at the seedling stage (Obisesan et al., 2021). Few studies have reported on soybean root architectural structures under drought stress. Some factors are reported to confer sensitivity or tolerance on soybean cultivars. Delayed canopy wilting confers drought tolerance ability on soybean genotypes by allowing for high CO_2 assimilations along with partial closure of stomata in leaves (Sadok et al., 2012; Sinclair et al., 2010). Soybean with slow canopy wilting is high yielding even under drought conditions (Bagherzadi et al., 2017). The slow canopy wilting trait is documented to be positively correlated to fibrous root morphology, an increase in lateral root and a massively growing root system in legumes (Hudak and Patterson 1996; Wang et al., 2020).

Amongst the important functional roles of roots in plants are water and nutrient absorptions, therefore the need for a substantial root system architecture to improve crop sustenance under drought. The root architecture includes its biomass, length, angle, length of the hair, depth, diameter, robust taproot and more lateral roots (Gilbert et al. 2011; Ye et al. 2018; Kou et al., 2022). Drought stress reduces root dry weight by 26.5% and length by 3.4% (Kou et al., 2022). Under water deficit, the ability of the plants to absorb water from deep soils depends on the depth of the roots (Nardini et al., 2016), which is essential for drought tolerance. It has also been reported that longer roots are only possible if there is a sustainable root growth irrespective of the levels of water availability in the soil. At low water concentration, the roots must face the hardiness of the soil and be able to penetrate deep in soil for capturing water indispensable for physiological reactions and plant growth (Rich and Watt, 2013).

Few improved soybean cultivars have been introduced by research institutes to be adopted by farmers (Okogun et al., 2004). Unpredictable or irregular rainfall due to climate change still negatively affects the production of soybean in the country (Ati et al., 2002; Bebeley, et al., 2022). To increase the productivity of soybean, there is need for selecting cultivars highly adapted to drought. As there have been predicted future unfavorable climatic conditions, continual use of soybean with high water requirements and productivity will affect soybean yield as soybean farming is basically relying on rainfed soils in Nigeria (Durodola and Mourad, 2020). Therefore, there is need for low-water requiring soybean with strong root system incorporation into the farming system.

Although few studies have reported drought sensitivity and tolerance in soybean by studying root architecture and relating it to above-ground biomass and physiological response of the plant (Fental et al., 2014; Wang et al., 2020), some studies reported below-ground architectural responses of soybean to drought (Sinclair, 2008; Fenta et al., 2014; Wang et al., 2020). Most of these studies made use of polyethylene glycol-simulated drought, while others used few soybean cultivars in their experiments. Many of such made use of few numbers of cultivars in their report. This research made use of larger number of cultivars for the root architectural response to drought along with above-ground and biochemical responses to drought in the 20 cultivars of soybean studied.

Thus this research was carried out to study the effect of drought stress on 20 soybean cultivars at the seedling stage, by (i) studying the root structure under drought among cultivars (ii) assessing the response of 20 soybean cultivars to drought and identifying cultivars with high drought adaptability characteristics, and (iii) to evaluate relationships between above-ground (AGP), below-ground (BGP) and biochemical (BP) characteristics of the 20 soybean cultivars studied in order to determine genotype(s) with tolerance to drought.

Materials and Methods

Soybean Seed Collection

Twenty different cultivars of soybean seeds were sourced from the seed bank of the International Institute of Tropical Agriculture (IITA), Ibadan, Oyo state, Nigeria for the purpose of this research (Table 1).

Table 1. Accessions of soybeans used in this study

Serial No.	Soybean Accessions	Serial No.	Soybean Accessions
1	TGm-50	11	TGm-3972
2	TGm-95	12	TGm-4004
3	TGm-112	13	TGm-4400
4	TGm-263	14	TGm-4414
5	TGm-422	15	TGm-4144
6	TGm-665	16	TGm-4015
7	TGm-946	17	TGm-4499
8	TGm-951	18	TGm-4500
9	TGm-1326	19	TGm-4502
10	TGm-1678	20	TGm-4022

Planting Location and Experimental Design

The planting for the soybean experiment was conducted in a screen-house located at the College of Agriculture, Engineering and Sciences, Bowen University Iwo, Osun State, Nigeria (7°38'N 4°11'E). This experiment was carried out within 7 weeks. The experiment was arranged in a Factorial Randomized Complete Block Design (RCBD) with 3 replications. Humus topsoil and sawdust mixed in the ratio 2:1 were filled in each experimental bag (of 11 L capacity). The 20 cultivars were planted in 120 experimental bags with 60 in each block (60 drought + 60 control) with 0.5 m spacing between bags. Four seeds were sown in each bag and watered to field capacity daily. Soybean grew at day/night 14/10 h, average temperature 30-33 °C / 24-26 °C, and relative humidity 65%.

Drought Treatments

Twenty-eight (28) days after sowing, the seedlings were thinned to three plants per experimental bags and left for another 7 days before the drought treatment was initiated. Drought treatment was applied i.e., complete withholding of water for 14 days to designated seedlings, while plants designated as control experiment were watered to field capacity at every other day for 14 days. This is to allow for the moderate amount of time for drought period for the seedlings.

Measurements of Above-Ground Parameters (AGP)

Fourteen days after treatments initiation, the following AGP were measured:

- Shoot height (cm): this is the shoot length measured with a meter rule from the shoot-root joining point to the apex of the plant.
- Number of leaves: the amount of fully expanded leaves.
- Leaf width (cm): the widest breadth of the topmost fully expanded leaves.
- Leaf Length (cm): the length of the topmost fully expanded leaves from the petiole to the leaf apex.

Canopy wilting: Fourteen days after drought treatment, seedlings leaves were observed for canopy wilting using a grade system of canopy wilting scale of 0 to 5. With a scale of '5' representing wilting of the whole above-ground (leaves and stem), scale of '4' means wilting of the first three uppermost trifoliate leaves, scale of '3' means wilting of the first two uppermost trifoliate leaves, scale of '2' represents the wilting of the uppermost trifoliate leaf, scale of '1' represents wilting of the uppermost unifoliate leaf and scale of '0' represents no wilting. Canopy wilting index is therefore interpreted as follows (Pathan et al., 2014):

Wilting Index = Σ (Grade × No. of plants of each grade) ⁄ total plants graded)

Grade = canopy wilting scale from 0 to 5

Measurements of Below-Ground Parameters (BGP)

Plants were uprooted from the soil, and debris removed from the roots. The following components of root system architecture were measured manually: root length was measured using a measuring tape, root diameter was measured using a Vizbrite electronic digital vernier caliper and the number of lateral roots were counted and recorded.

Dry Biomass Measurement

Shoot and root samples were oven-dried at 80 °C for 24 hours. The above-ground dry weight (g), below - ground weight (g) were measured.

Measurements of Biochemical Parameters (BP)

Fourteen days after treatments initiation, fresh leaves samples were excised from the drought treatment and control in each block and the following biochemical parameters were measured.

Determination of Photosynthetic Pigment (Chlorophyll and Carotenoids)

The Arnon (1949) methodology was employed to determine the photosynthetic pigments; Chlorophyll *a* (Chlr *a*), Chlorophyll *b* (Chlr *b*), and carotenoids (carotd). Fresh soybean leaves (0.06 g) from drought - and control-treated plants were utilized and homogenized with 10 ml of 80% acetone and a small amount of sodium bicarbonate. The samples were kept for a full day at room temperature in the dark. At 470, 646, and 663 nm, respectively, the absorbances of carotd, Chlr *a*, and Chlr *b* were measured. Porra's (2002) equation was utilized to compute the pigment content on a fresh weight basis and express it as $\mu g\ g^{-1}$ FW.

Chlr a ($\mu g\ mL^{-1}$) = $12.25A_{663} - 2.79A_{646}$

Chlr b ($\mu g\ mL^{-1}$) = $21.50A_{646} - 5.10A_{663}$

Total chlorophyll ($\mu g\ mL^{-1}$) = $17.76A_{646} + 7.34A_{663}$

Total carotenoids ($\mu g\ mL^{-1}$) = $(1000A_{470} - 1.82Ca - 85.02Cb) / 198$

where, A_{663}, A_{646}, A_{470} were the absorbance read at 663 nm, 646 nm and absorbance at 470 nm respectively using a 752N UV-VIS Spectrophotometer (BOSCH).

Total Chlorophyll Using SPAD Meter

Chlorophyll content of the three uppermost fully expanded leaves was also measured 14 days after treatment initiation with using chlorophyll SPAD-502Plus meter (KONICA MINOLTA).

Free Proline Measurement

Soybean cultivars under drought and the controlled regimes were measured for free proline contents using Bates et al. (1973) procedure. Soybean leaf sample (0.06 g) was ground with 1.5 ml aliquot of 3% (w/v) sulfosalicylic acid and was centrifuged at 12,000 g for 5 min, after which 400 µL aliquot of the supernatant was transferred to separate test tubes. 800 µL glacial acetic acid and 800 µL of 2.5% acid-ninhydrin mixed with the solution in the test tube. The mixture was boiled in a water bath at 100 °C for 40 min. It was cooled and washed with 2 ml of toluene. The clear liquid at the top was read at 520 nm using a 752N UV-VIS Spectrophotometer (BOSCH) for the estimation of the free proline content.

Statistical Analysis

The AGP, BGP and BP data collected were analyzed by one-way ANOVA using R statistical package version 4.0. Fischer's least significant difference (F-LSD) was used to separate means at probability level of 5 % ($P \leq 0.05$). The relationships among the above-ground, below-ground and physiological parameters were computed using Pearson Correlation matrix. Principal component analysis was carried out and cultivars were exposed to biplot analysis to see association among cultivars and parameters using XLSTAT 2018 version software.

Results

Effect of Genotype and Drought Interactions on the AGP, BGP and BP of 20 Soybean Cultivars

The interaction of genotypes with drought treatment in this study produced a significant effect on the AGP, BGP and BP of soybean cultivars. For the AGP studied there were significant ($P \leq 0.01$) differences among the soybean genotypes for number of leaves and a highly significant ($P \leq 0.001$) difference for shoot height. Drought had significant ($P \leq 0.001$) effects on all the AGP, with the least level of significance for number of leaves. However, for genotype *x* drought interaction, there was a significant effect on the shoot dry weight (Table 2).

For the BGP studied, there were significant differences among genotypes for root length, root diameter and number of lateral roots. Drought had significant effects on all the BGP studied. Genotype x drought interaction had effects on root length and root diameter (Table 2).

There were significant differences among the BP of the 20 soybean genotypes, except for chlorophyll contents measured with SPAD (SPAD). Drought treatment and genotype x drought interaction also had highly significantly effect on all the BP measured except for chlorophyll content (Table 2).

Effect of Drought on the AGP of 20 Soybean Cultivars.

The effect of drought on mean value for the AGP of soybean cultivars studied is presented in Table 3.

Table 2. Effect of genotype, drought and genotype x drought interaction on above ground, below ground and biochemical parameters of 20 soybean cultivars

Parameters	Variables	Genotypes	Drought	Genotypes x Drought	Min	Max
			Above Ground			
	Shoot dry weight	0.0448^{ns}	2.2861^{***}	0.067^{9*}	0.1	1.2
	Leaf length	2.89^{ns}	70.23^{***}	1.85^{ns}	4.70	14.60
	Leaf width	1.41^{ns}	39.22^{***}	1.13^{ns}	4.90	11.50
	No. of leaves	0.563^{**}	1.63^{9*}	0.388^{ns}	2.0	5.0
	Shoot height	14.51^{***}	161.94^{***}	2.84^{ns}	7.60	21.20
	Canopy wilting	1.35^{ns}	310.41^{***}	1.23^{ns}	0.0	5.0
			Below Ground			
	Root dry weight	0.042^{ns}	1.587^{***}	0.021^{ns}	0.1	1.2
	Root length	441.0^{***}	13746^{***}	328.0^{**}	17.00	115.0
	Root diameter	0.33^{***}	8.37^{***}	0.20^{**}	0.50	2.99
	Number of lateral roots	264.0^{**}	6810^{***}	158^{ns}	7.0	65.0
			Biochemical			
	Proline	0.331^{***}	9.79^{***}	0.43^{***}	0.054	1.868
	Chlr *a*	61.3^{***}	474.1^{***}	59.9^{***}	2.51	22.63
	Chlr *b*	29.89^{***}	120.75^{***}	24.06^{***}	0.768	15.077
	Carotd	154.5^{***}	1279.5^{***}	135.3^{***}	2.76	36.40
	SPAD	6.972^{ns}	17.03^{ns}	9.10^{ns}	23.0	35.0

Note: Values specify the mean square. Min: Minimum across genotypes, Max: Maximum across genotypes, Chlr *a*: Chlorophyll *a* content, Chlr *b*: Chlorophyll *b* content, SPAD: Chlorophyll content measured with SPAD meter. *Significant at $P \leq 0.05$; **highly significant at $P \leq 0.01$; ***very highly significant at $P \leq 0.001$, ns = non-significant at $P > 0.05$.

Table 3. Effect of drought on above-ground parameters of 20 soybean cultivars

Genotype	No of leaves		Leaf length (cm)		Leaf width (cm)		Shoot height (cm)		Shoot dry weight (g)	
	Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought
TGm-50	3.33^{bcd}	3.0^{bcd}	10.83	7.96	0.4	0.43	10.06	7.83	14.93	10.96^{cde}
TGm-95	3^{cd}	3.33^{abc}	9.8^{d}	10.33	0.57	0.57	8.76	9.46	13.46	11.9^{bcde}
TGm-112	3.33^{bcd}	3.0^{bcd}	11.13	10.3	0.73	0.37	9.4	8.63	14.8	12.0^{bcde}
TGm-263	3.66^{abc}	4.00^{a}	8.733	8.16	0.5	0.4	8.56	7.33	16.13	13.53^{bcd}
TGm-422	3.0^{cd}	2.33^{d}	10.76	8.4	0.57	0.3	9.06	7.76	13.6	10.36^{de}
TGm-665	3.33^{bcd}	3.66^{ab}	11.03	10.46	0.77	0.27	9.36	9.43	16.7	12.9^{bcde}
TGm-946	3.33^{bcd}	3.0^{bcd}	10.73	9.3	0.7	0.33	9.03	8.63	12.33	12.16^{bcde}
TGm-951	3.66^{abc}	3.0^{bcd}	11.06	10.1	0.90	0.37	9.7	8.93	14.56	13.96^{abcd}
TGm-1326	3.33^{bcd}	3.0^{bcd}	10.66	10.36	0.67	0.57	10.4	9.0	17.23	17.4^{a}
TGm-1678	4.00^{ab}	3.0^{bcd}	11.43	10.4	0.67	0.53	10.06	9.56	17.96	15.06^{ab}
TGm-3972	4.33^{a}	3.33^{abc}	12.3	9.43	1.0	0.4	10.16	8.13	14.6	11.53^{bcde}
TGm-4004	2.66^{d}	3.0^{bcd}	11.53	9.2	0.87	0.47	9.73	8.53	12.93	9.76^{e}
TGm-4400	3.33^{bcd}	3.0^{bcd}	11.3	9.5	0.93	0.5	10.36	8.6	12.63	10.93^{cde}
TGm-4414	3.0^{cd}	3.66^{ab}	10.33	10.83	0.83	0.53	8.93	9.1	15.53	14.43^{abc}
TGm-4144	3.0^{cd}	2.66^{cd}	10.5	8.96	0.8	0.5	9.33	8.03	13.2	10.6^{de}
TGm-4015	3.66^{abc}	3.0^{bcd}	12.13	9.26	0.93	0.3	9.96	8.2	15.26	11.06^{dce}
TGm-4499	4.00^{ab}	3.33^{abc}	11.43	9.6	0.6	0.63	10.46	8.96	13.96	13.33^{bcde}
TGm-4500	3.0^{cd}	3.66^{ab}	11.13	9.4	0.5	0.5	8.9	8.03	13.36	12.3^{bcde}
TGm-4502	3.66^{abc}	3.33^{abc}	12.76	10.13	0.8	0.4	11.16	8.36	15.33	11.7^{bcde}
TGm-4022	3.33^{bcd}	3.00^{bcd}	12.96	9.83	0.77	0.47	10.23	8.26	14.86	11.03
Grand mean	0.5123	0.4386	2.835	1.912	0.72	0.44	1.433	1.113	7.098	2.003
LSD	0.87	0.802	2.20	2.25	0.35	0.24	1.74	2.07	3.30	3.73
CV	15.50	15.33	11.97	14.18	29.33	22.72	10.90	14.72	13.63	18.32
Pr (<F)	0.05	0.05	0.108^{ns}	0.451^{ns}	0.055^{ns}	0.15^{ns}	0.248^{ns}	0.793^{ns}	0.065	0.0338*

Note: Numbers with the same letters are not significantly different within the same column at ($P \leq 0.05$). *Significant at $P \leq 0.05$; **highly significant at $P \leq 0.01$; ***very highly significant at $P \leq 0.001$, ns = non-significant at $P > 0.05$. CV is Coefficient of variation.

Drought had a significant effect on the number of leaves of soybeans, with genotype TGm-263, TGm-665, TGm-4414, and TGm-4500 having relatively higher number of leaves under drought, whereas genotype TGm-422 recorded the lowest number. of leaves under drought.

Drought treatment had a significant ($P \leq 0.05$) effect on the shoot dry weight of soybean cultivars, with genotypes TGm-1326, TGm-1678, and TGm-4414 having the highest shoot dry weight under drought. Genotype TGm-4004 had the lowest shoot dry weight under drought. There was no significant effect of drought on the leaf length, leaf width and shoot height of the 20 soybean cultivars (Table 3).

Effect of Drought on the BGP of 20 Soybean Cultivars

The effect of drought on the mean performances for the BGP of 20 soybean cultivars is presented in Table 4. Drought had a significant effect on the root length of soybean with genotype TGm-665, TGm-4004, and TGm-422 having more elongated roots under drought. Drought significantly increased the root diameter of some soybean genotypes. The widest diameter was observed in genotypes TGm-665, TGm-50, TGm-4414, and TGm-422. Drought had also a significant effect on the number of lateral roots with genotypes TGm-1326 and TGm-4144 having the highest lateral roots. Drought had no significant ($P > 0.05$) effect on dry root biomass.

Table 4. Effect of drought on below-ground parameters of 20 soybean cultivars

Genotype	Root length (cm)		Root diameter (cm)		Number of lateral roots (cm)		Root dry weight (g	
	Control	Drought	Control	Drought	Control	Drought	Control	Drought
TGm-50	35.43^{de}	52.2^{jkl}	1.85	2.81^{ab}	24.33	39.0^{defg}	0.37	0.17
TGm-95	38.5^{bcde}	45.7m	1.92	2.30^{efg}	26.67	49.67^{abcd}	0.5	0.27
TGm-112	42.77^{bcde}	54.0^{ijk}	1.68	2.37^{cdef}	27.33	41.0^{bcdefg}	0.6	0.2
TGm-263	37.0^{cde}	38.67^{n}	1.53	2.29^{efg}	15.0	47.67^{abcde}	0.57	0.17
TGm-422	47.83^{bcde}	71.0^{b}	1.54	2.72^{abcd}	32.67	38.33^{defgh}	0.4	0.17
TGm-665	67.33^{a}	78.3^{a}	2.23	2.96^{a}	38.33	54.0^{abc}	0.5	0.17
TGm-946	36.1^{cde}	49.3^{l}	1.63	2.013^{fg}	29.0	25.0^{h}	0.53	0.27
TGm-951	50.0^{abcde}	60.0^{ef}	1.79	2.25^{efg}	20.0	37^{defgh}	0.57	0.53
TGm-1326	45.0^{bcde}	51.67^{kl}	1.9	2.17^{efg}	28.67	56.0^{a}	0.43	0.3
TGm-1678	49.0^{bcde}	64.2^{d}	1.85	2.47^{bcde}	45.0	48.67^{abcd}	0.47	0.17
TGm-3972	38.23^{bcde}	55.0^{hij}	2.08	2.83^{ab}	15.0	40.33^{cdefg}	0.4	0.2
TGm-4004	48.57^{bcde}	73.87^{b}	1.84	1.91^{gh}	22.67	46.33^{abcdef}	0.53	0.43
TGm-4400	36.57^{cde}	58.33^{fg}	1.30	2.11^{efg}	30.0	25.0^{h}	0.63	0.4
TGm-4414	34.43^{e}	60.73^{ef}	1.84	2.77^{abc}	20.33	32.67^{fgh}	0.43	0.23
TGm-4144	39.1^{bcde}	56.2^{ghi}	1.72	2.11^{efg}	23.67	54.33^{ab}	0.53	0.23
TGm-4015	53.33^{abcd}	62.0^{de}	1.65	2.03^{fg}	23.0	34.33^{efgh}	0.57	0.2
TGm-4499	35.33^{de}	58.0^{fgh}	1.73	1.95^{fgh}	28.67	38.0^{defgh}	0.33	0.2
TGm-4500	35.17^{de}	67.3^{c}	2.05	1.55^{h}	16.0	31.67^{gh}	0.73	0.33
TGm-4502	54.0^{abc}	52.5^{jk}	1.75	2.35^{def}	27.33	32.67^{fgh}	0.43	0.3
TGm-4022	55.33^{ab}	58.7^{fg}	1.68	2.11^{efg}	15.67	31.0^{gh}	0.4	0.4
Grand mean	43.95	58.38	1.78	2.30	25.47	40.13	0.50	0.26
LSD	18.23	3.00	0.52	0.42	17.72	13.83	0.37	0.26
CV	25.09	3.11	17.81	11.03	30.10	20.85	26.55	28.21
Pr (<F)	0.03531*	0.000307***	0.24^{ns}	9.68e-07***	0.118^{ns}	0.00022***	0.88^{ns}	0.193^{ns}

Note: Numbers with the same letters are not significantly different within the same column at ($P \leq 0.05$). *Significant at $P \leq 0.05$; **highly significant at $P \leq 0.01$; ***very highly significant at $P \leq 0.001$, ns = non-significant at $P > 0.05$. CV is Coefficient of variation.

Table 5. Effect of drought on biochemical parameters of the 20 soybean cultivars

Genotype	Carotd (µg mL^{-1})		Chlr *a* (µg mL^{-1})		Chlr *b* (µg mL^{-1})		SPAD		Proline (µg mL^{-1})	
	Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought
TGm-50	10.71^{efg}	16.60^{fghi}	10.79^{fgh}	15.95^{e}	0.4219^{hi}	0.7355^{fgh}	29.46	29.93	1.034^{a}	0.63^{ij}
TGm-95	4.86^{h}	11.81^{hi}	6.129^{j}	11.32^{i}	1.304^{efghi}	0.5391^{gh}	32.56	34.23	0.341^{cd}	0.688^{h}
TGm-112	12.23^{de}	14.01^{ghi}	12.79^{ef}	13.03^{h}	0.5544^{ghi}	1.052^{fgh}	30.8	31.16	0.756^{b}	0.66^{hi}
TGm-263	18.23^{c}	18.08^{efgh}	15.12^{cd}	14.97^{fg}	3.308^{bc}	3.298^{de}	28.33	31.03	0.082^{hi}	0.53^{k}
TGm-422	10.67^{efg}	15.69^{fghi}	12.14^{fg}	2.53^{k}	1.504^{efgh}	1.352^{fgh}	33.53	29.53	0.215^{efg}	0.763^{g}
TGm-665	18.07^{c}	26.16^{bcd}	14.62^{de}	20.59^{b}	3.646^{b}	5.896^{c}	31.3	30.83	0.218^{ef}	0.177^{n}
TGm-946	2.76^{h}	24.59^{bcde}	3.52^{k}	20.14^{bc}	0.7912^{ghi}	4.710^{cd}	30.66	35.4	0.371^{c}	0.789^{g}
TGm-951	4.33^{h}	31.37^{a}b	6.17^{j}	20.84^{b}	1.912^{def}	11.08^{b}	28.16	33.66	0.096^{hi}	0.221^{mn}
TGm-1326	13.80^{d}	10.63^{i}	11.61^{fg}	11.84^{i}	2.323^{cde}	0.9328^{fgh}	28.43	33.36	0.11^{ghi}	0.395^{l}
TGm-1678	9.74^{fg}	19.03^{defg}	8.96h^{i}	17.45^{d}	0.8442^{fghi}	2.101^{efgh}	26.93	32.53	0.14^{efghi}	0.767^{g}
TGm-3972	11.83^{def}	20.81^{cdefg}	11.66^{fg}	19.71^{c}	0.2164^{i}	5.115^{c}	27.33	29.0	0.063^{i}	0.601^{j}
TGm-4004	9.10^{g}	16.85^{fghi}	10.27^{gh}	15.67^{ef}	1.20^{fghi}	1.431^{fgh}	32.43	31.96	0.165^{efghi}	0.785^{g}
TGm-4400	20.65^{b}	27.84^{abc}	17.78^{ab}	21.97^{a}	3.07^{bc}	13.12^{a}	27.03	28.66	0.063^{i}	1.30^{d}
TGm-4414	8.89^{g}	14.32^{gh}i	7.01^{ij}	12.77^{h}	1.153^{fghi}	0.377^{h}	28.5	29.9	0.071^{hi}	0.246^{m}
TGm-4144	16.20^{c}	17.32^{fghi}	16.20^{bcd}	14.31^{g}	0.703^{ghi}	1.823^{efg}h	30.2	32.83	0.123^{fghi}	0.804^{g}
TGm-4015	12.68^{de}	34.07^{a}	11.14^{fg}	20.91^{b}	1.643^{efg}	12.62^{ab}	28.26	26.5	0.125^{fghi}	1.593^{b}
TGm-4499	16.20^{c}	24.97^{bcde}	16.92^{abc}	20.45^{bc}	1.432^{efgh}	4.152^{cd}	27.9	30.5	0.175^{efgh}	1.011^{e}
TGm-4500	17.48^{c}	10.80^{i}	15.37^{cd}	9.79^{j}	2.833^{bcd}	0.456^{h}	29.9	31.3	0.243^{ef}	0.881^{f}
TGm-4502	12.56^{de}	22.85^{cdef}	11.43^{fg}	17.37^{d}	1.212^{fghi}	2.469^{ef}	26.63	28.46	0.133^{fghi}	1.36^{c}
TGm-4022	23.92^{a}	19.85^{defg}	18.48^{a}	15.99^{e}	5.747^{a}	2.303^{efg}	29.4	34.13	0.078^{hi}	1.817^{a}
Grand mean	12.78	19.88	51.46	69.65	5.514	48.44	11.99	15.59	0.183	0.578
LSD	2.23	7.20	2.15	0.78	1.09	1.77	6.09	6.84	0.105	0.052
CV	10.55	21.91	10.92	3.00	26.93	28.33	12.55	13.25	27.72	3.96
Pr (<F)	<2e-16***	2.07e-07***	<2e-16***	<2e-16***	4.78e-11***	<2e-16***	0.607^{ns}	0.575^{ns}	<2e-16***	< 2e-16***

Note: Numbers with the same letters are not significantly within the same column different at ($P \leq 0.05$). *Significant at P ≤ 0.05; **highly significant at P ≤ 0.01; ***very highly significant at P ≤ 0.001, ns = non-significant at P > 0.05. CV is Coefficient of variation, Chlr *a*: Chlorophyll *a* content, Chlr *b*: Chlorophyll *b* content, Chlr SPAD: Chlorophyll content measured with SPAD meter

Drought Effect on the BP of 20 Soybean Cultivars

Drought effect on the mean performances for the BP of 20 soybean cultivars are presented in Table 5. Drought significantly increased the level of carotenoids contents in soybean among genotypes. Genotypes TGm-4015, TGm-951, and TGm-4400 had a significantly high level of carotenoids under drought treatment compared to the rest of the genotypes. Drought increased the Chlr *a* content of soybean bean cultivars. Genotypes TGm-4400, TGm-4015, TGm-951, and TGm-665 produced the highest amount of Chlr *a* under drought compared to the rest of the genotypes. Drought significantly increased the Chlr *b* content of some of the soybean cultivars. Genotypes TGm-4400, TGm-4015, and TGm-951 had the highest amount of Chlr *b* under drought. Proline contents were significantly low in genotypes TGm-665, TGm-951 and TGm-4414. Proline accumulation was observed in genotypes TGm-4022 and TGm-4015 under drought stress.

Relationship between AGP, BG and BP under Drought Stress

For AGP, there was a positive correlation between shoot height and leaf width (r = 0.492), between shoot height and leaf length (r = 0.518), between leaf width and number of lateral roots (r = 0.583) and a strong correlation between leaf width and leaf length (r = 0.844). A positive correlation existed between number of lateral root and root length (r = 0.494), whereas a negative and significant correlation was observed between root length and shoot dry weight (r = -0.494). Among the BP, there was a positive correlation between Chlr *a* and Chlr *b* (r = 0.697), between Chlr *a* and carotd (r = 0.791), and a strong positive correlation between Chlr *b* and carotd (r = 0.896). For the relationship between AGP and BGP under drought, there was a negative correlation between SDW and RL (r = -0.494), and a positive correlation between leaf width and number of lateral roots (r = 0.583) (Table 6).

Eigenvalues, Proportion or Variance, Cumulative Variance and Variables Contribution to the First Five Principal Component Axes for AGP, BGP and BP

The contribution of AGP, BGP and BP characters to the first five principal components is presented in Table 7. A total of 15 principle components (PCs) were generated by the analysis but only six PCs were used to explain the proportionality, cumulativeness and variable contributions due to the fact that six among the 15 PCs divulged eigenvalues ≥ 1 under drought conditions. The eigenvalues range from the highest value of 3.341 for F1 to the lowest value of 1.245 for F6. Six axes (PCs) under drought stress interpolated cumulative variance of 83.14%, among the soybean cultivars for drought related characters. The other 9 components revealed only 16.86% of the total variation under drought

Table 6. Pearson Correlation matrix among the above ground, below ground and biochemical parameters of 20 soybean genotypes under drought stress

Variable	Prol	LeafN	SH	LeafW	LeafL	SPAD	Chlr *b*	Chlr *a*	C.Wilt	Carotd	RL	SDW	RDW	NLR	RootD
Prol	1														
LeafN	-0.038	1													
SH	-0.247	0.335	1												
LeafW	-0.180	0.082	0.492*	1											
LeafL	0.052	0.213	0.518*	0.844**	1										
SPAD	-0.181	-0.101	0.277	0.330	0.212	1									
Chlrb	-0.160	-0.074	-0.105	0.041	-0.011	-0.341	1								
Chlra	-0.073	0.208	0.026	0.253	0.157	-0.112	0.697**	1							
C.Wilt	0.156	-0.331	-0.251	0.212	0.091	-0.077	0.227	0.287	1						
Carotd	0.035	-0.071	-0.160	0.064	-0.017	-0.309	0.896**	0.791**	0.189	1					
RL	0.105	-0.119	-0.025	0.252	0.312	-0.058	0.213	0.169	-0.044	0.376	1				
SDW	0.079	0.127	0.346	0.323	0.258	0.262	-0.339	-0.099	0.087	-0.439	-0.494*	1			
RDW	-0.043	-0.133	-0.065	0.118	0.212	0.343	0.305	0.196	0.216	0.191	0.111	0.150	1		
NLR	-0.285	-0.306	0.223	0.583*	0.291	0.036	0.018	0.052	0.202	0.103	0.344	-0.035	-0.323	1	
RootD	-0.142	0.379	0.259	0.375	0.377	0.138	-0.342	-0.012	-0.264	-0.257	0.253	0.038	-0.135	0.019	1

Note: **Highly significant ($P < 0.001$), *Significant ($P < 0.05$) Values in bold are different from 0 with a significance level alpha=0.05. Prol (Proline), Number of leaves (LeafN), Shoot Height (SH), Leaf Width (LeafW), Leaf Length (LeafL), Chlorophyll *b* (Chlr *b*), Chlorophyll *a* (Chlr *a*), Canopy Wilt (C.Wilt), Carotenoid (Carotd), Root Length (RL), Shoot Dry Weight (SDW), Root Dry Weight (RDW), Number of lateral roots (NLR), Root diameter (RD) stress. Chlr *b*, Chlr *a*, wilt, carotenoid, root length and root dry weight contributed to the formation of F1 (PC1), while no AGP contributed to the formation of F1 under drought (Table 7 and Fig. 1). All the traits of AGP, BGP and BP positively contributed to the formation of F2 except for proline content. Proline, leaf width, leaf length, chlorophyll content, wilting, shoot dry weight and root dry weight are responsible for the formation of F3 axis. Leaf width, wilting, root length and number of lateral roots showed positive contribution in F4, whereas F5 was positively associated with proline content, leaf length, chlorophyll content, wilting, root length, root dry weight and root diameter (Table 7).

Table 7. Eigenvalues, proportion of variance, cumulative variance and variables contribution to the first five principal component axes for above ground, below ground and biochemical parameters of the soybean cultivars

	F1	F2	F3	F4	F5
Eigenvalue	3.341	3.094	1.809	1.688	1.294
Proportion of variability (%)	22.273	20.629	12.060	11.253	8.626
Cumulative variability (%)	22.273	42.902	54.963	66.216	74.842
Shoot DW	-0.573	0.064	0.510	-0.322	-0.132
Shoot Height	-0.542	0.491	-0.133	-0.191	-0.284
Leaf Width	-0.347	0.877	0.149	0.126	-0.001
Leaf Length	-0.373	0.778	0.057	-0.044	0.294
No. of leaves	-0.279	0.123	-0.518	-0.651	-0.007
Canopy Wilting	0.329	0.210	0.621	0.173	0.051
Root DW	0.171	0.243	0.552	-0.396	0.310
Root length	0.258	0.472	-0.350	0.400	0.510
No. of lateral root	-0.065	0.523	-0.005	0.725	-0.327
Root diameter	-0.499	0.308	-0.485	-0.049	0.277
Proline	0.106	-0.231	0.127	-0.036	0.713
Chlr *a*	0.552	0.574	-0.039	-0.393	-0.120
Chlr *b*	0.813	0.397	-0.003	-0.236	-0.202
SPAD	-0.486	0.193	0.399	-0.028	0.046
Carotd	0.843	0.434	-0.117	-0.135	-0.036

Biplot Analysis for Comparing Relationships between AGP, BGP and BP of the Soybean Cultivars under Drought

PCA1 revealed the maximum variability of 22.27 followed by PC 2, 20.67, and the two PCs (PC1 and PC2) accounted for 42.90% of the total variability under water deficit stress. A biplot between PC1 and PC2 illustrated relationship between the characters and soybean cultivars. Genotypes TGm-4015, TGm-4400, TGm-95 and TGm-1326 are positively and significantly associated with F1, therefore associated with Chlr *b*, Chlr *a*, wilt, carotenoid, root length and root dry weight under drought conditions. Soybean genotypes TGm-665, TGm-422, TGm-1678, TGm-263, and TGm-951 combined AGP and BGP such as shoot DW, shoot height, number. of leaves, leaf width, leaf L, N lateral roots, and root D and BP traits except for proline under drought (Fig. 1).

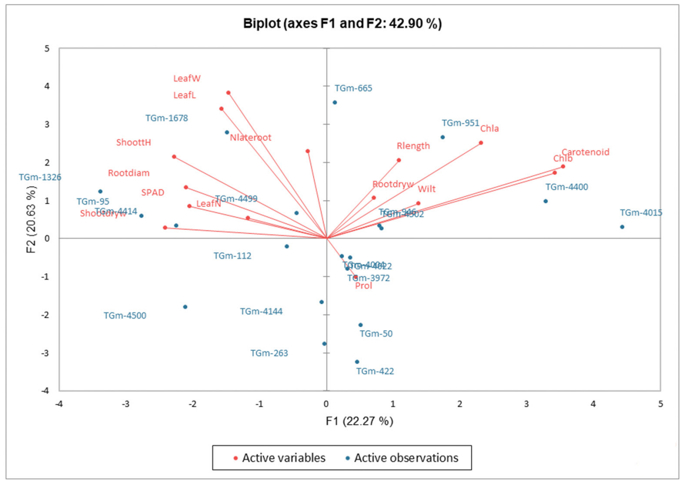

Figure 1. F1 and F2 Biplot using above ground, below ground and biochemical parameters of the 20 soybean genotypes

Discussion

The genetic makeup of a genotype confers adaptation, acclimation or escape to plant species under abiotic and biotic stress. It allows plants to externalize various phenotypic traits when subjected to different environmental conditions, giving room for suitable phenotypic plasticity essential for survival, growth and reproduction (Valladares et al., 2007; Awosanmi et al., 2022). Thus, phenotypic characters such above-ground, below-ground and biochemical parameters were assessed in this study to better the understanding of drought stress tolerance in soybean accessions.

Root System Architectural Responses to Drought among Cultivars

Root systems are the primary organs to experience decline and lack of water in soils, indicating its key roles in the life of plants. A deep and expansive root system, which will supply sufficient water and nutrient extraction from the soils, is one of the most important developmental structures under drought conditions. Under water deficit conditions, root systems play important functions in the survival of the plants, as well as in keeping biochemical and physiological reactions for growth, development and reproduction (da Silva et al., 2013). With the increase in climate change effects, plants will often be exposed to many environmental conditions, which will require adequate root systems for their survival, durability and productivity. Leguminous crops like soybean require a favourable root system to support the microorganisms that live in the root nodules. Legume roots feature nitrogen-fixing nodules for symbiotic interactions with soil bacteria. The symbiotic interaction as well as soil circumstances influence the design of the root system in several ways (Oldroyd & Downie, 2004; Ye, 2018). In this study, drought had an impact on the BGP of soybean genotypes studied. Significant effects of drought were observed on the root length, root diameter and number of lateral roots. Some of the soybean genotypes used in this study, such as TGm-665, TGm-4414 and TGm-422 combined two BGP competitive advantages under drought, adjusting its root structural system to drought, indicating drought tolerance. Root depth allows the plant to explore the moisture deeper in soil layers for its survival and reproduction (Franco et al., 2005). There is the need for root adjustments under drought because the amount of soil that is examined during this condition depends on some below-ground factors, such as lateral root count, root depth, root length and diameter. As crucial component of plant performance and its adaptability to a wide range of abiotic environments is its capacity to modify the root architecture (Smith & De Smet, 2012). Water deficit stress caused reduction in root length, root volume root biomass, total root length, and root surface area of soybean varieties (Mejia et al., 2000). This study demonstrated how useful was the root system architecture in the tolerant soybean genotypes. The genotypes with deeper roots in the soil were able to extract water and keep the genotypes green and ensure the availability of metabolites for growth and development of the tolerant soybean genotypes. This is consistent with an earlier study (Wang et al, 2020).

Above-Ground Parameters of Soybean Cultivars under Drought

Water deficit in the soil can impede the plant growth and development, causing a decrease in above- ground parameters. Many studies have been conducted to identify resistant crops to drought conditions. It is henceforth vital to gain a deeper insight into the impact of consistent drought stress on above-ground parameters of plants. In this study, no significant differences were observed in the shoot height, leaf length and leaf width among genotypes. This might mean that the soybean genotypes in this study could withstand the period of drought with these three parameters. The significant differences in number of leaves and shoot dry weight among genotypes under drought stress show that some genotypes (TGm-1326 and TGm-1678) can maintain stable above-ground biomass under drought, while the shoot dry weight of other genotypes was affected by drought stress after 14 days. This could be due to low production of phyto-assimilates because of stomata closure caused by drought stress conditions. Zahid et al. (2021) report that the rate of photosynthetic activities is usually decreased under water deficit condition. The reduction in photosynthetic rate could also be due to the damage of photosynthetic apparatus, causing rapid aging of the leaves, which results in reduced leaf areas and decline in food production in drought (Lonbani & Arzani, 2011; Zahid et al., 2021). Wang et al. (2004) affirm that the adjustments in morphological characters are often an efficient way used by plants to avoid water deficit stress. Among the 20 accessions TGm-263, TGm-665, TGm-4414, and TGm-4500 had the highest values for number of leaves, whereas TGm-422, and TGm-4144 recorded the lowest values of leaf number. We also identified TGm-1326, TGm-1678, and TGm-4414 as accessions with the highest shoot dry weights, while TGm-4004, TGm-422, and TGm-4144 had the lowest shoot dry weight. These discrepancies pinpoint the genetic makeup of the accessions resulting in phenotypic plasticity observed in this study. Thus, the 20 soybean accessions expressed various responses under drought stress according to their genetic constitution. Esan et al. (2021) observed that above-ground parameters of cowpea were affected by drought. Drought stress declines total biomass, yield, stomatal conductance and morphological traits in soybean varieties (Basal and Szabó, 2020a). There was a decline in plant height, leaf area index, biological yield and shoot biomass (Mejia et al., 2000).

Biochemical Parameters of Soybean Cultivars under Drought

The decline in soil moisture contents lead to alteration in the environmental conditions, which eventually disrupt biochemical and physiological processes in crops (Sarker et al., 2005; Prysiazhniuk et al. 2023). The accession with the highest values of Chlorophyll *a* were TGm-4400, TGm-4015, TGm-951, and TGm-665, whereas for Chlorophyll *b* were TGm-4400, TGm-4015, and TGm-951. The highest carotenoid levels were found in TGm-4015, TGm-951, and TGm-4400, while the highest accumulations of proline were found in TGm-4015, TGm-4400, TGm-4022, TGm-4502, and TGm-4499, and the lowest was recorded with TGm-665, TGm-951 and TGm-4414. Genotype and drought interaction had no significant difference on chlorophyll content measured with a SPAD meter in this research. This might be due to the fact that light absorbance range of SPAD meter is between 650 and 940 nm (Naus et al., 2010). But the optimum wavelengths for chlorophyll measurement in plants were reported to be around 430 nm and 660 nm for blue and red-light absorption respectively (Chen et al., 2021), which falls within the range used for the spectrophotometry method showing significant differences among genotypes and drought treatment in this research.

The accumulation of solutes such as proline, carotenoids, glycine, and betaine in plant cells allows plants to keep the turgidity of cells under drought stress, and it is considered as osmotic adjustment (Manavalan et al., 2009; Prysiazhniuk et al. 2023). Silvente et al. (2012) in their study on soybean under drought stress, observed that susceptible soybean cultivars did not show an increase in proline content, whereas tolerant cultivars had their proline contents increased. There was up-regulation of P5CS gene expression in soybean, encoding for enzyme responsible for the biosynthesis of proline under drought stress (Porcel et al., 2004). A knock down of P5CS gene expression hindered the survival of soybean plants under water deficit stress (de Ronde et al., 2000), indicating that the accumulation of proline conferred resistance to plants under drought stress. Ezin et al. (2021) showed that there was high accumulation of proline in cowpea under water deficit stress, especially in the tolerant cowpea varieties.

Three main adaptation measures including above-ground, below-ground and biochemical characters were assessed in this study. The most tolerant soybean accessions combined the three features. TGm-665 accession had the highest number of leaves, shoot height, root length, root diameter, number of roots, Chlorophyll *a*. TGm-951 had the highest values of photosynthetic pigments (Chlr *a*, Chlr *b* and carotd), root length, and shoot height. TGm-4400 also recorded the highest values in proline content, photosynthetic pigments, leaf width and root dry weight. TGm-4414 was among the accessions with the highest values of root diameter, number of lateral roots, number of leaves, shoot dry weight.

Conclusion

The mechanisms of plants resistance to drought stress have been assessed at above- and below- ground and biochemical levels in this study. The key parameters are biomass yield, root architecture systems, proline content, carotenoids, chlorophyll content, Chlorophyll *a* and Chlorophyll *b*. The above- and below-ground, and biochemical parameters have permitted to identify tolerant and sensitive soybean varieties under drought stress. TGm-665, TGm-951, TGm-4414, TGm-4400, TGm-4400, TGm-4015 varieties are the most drought tolerant accessions under drought stress at seedling stage. Although useful pieces of information were obtained in the course of this study under drought stress at seedling stage, a further study on yield, yield components and in-depth analysis of biochemical and physiological adjustments will give a great insight on drought tolerance mechanisms in soybean genotypes.

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CRediT Authorship Contribution Statement

Idowu Obisesan: Conceptualization, methodology, data curation and writing-original draft. **Vincent Esan:** Conceptualization, methodology, data curation, formal analysis and writing of manuscripts. **Timothy Ogunbode:** Conceptualization, methodology and data curation. **Olayinka Oluranti:** Editing and review of final manuscript. All authors read and have agreed to the published version of this manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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