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RESEARCH ARTICLE

Effect of signaling molecules on different morphological, physiological, biochemical and yield attributes of groundnut under water stress

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Abstract

In the current era of climate change, water stress has become a serious threat to groundnut and has detrimental effects on crop productivity. A field experiment was conducted with '*Narayani*' variety, where plants were treated with four different chemicals such as ascorbic acid, salicylic acid, hydrogen peroxide and α-tocopherol @ 200 ppm at 40 and 60 days after sowing (DAS) under water stress. Several morphological, physiological and biochemical parameters were studied. Based on the results for proline content, SOD and catalase activity, leaf area, chlorophyll fluorescence, leaf and pod dry weight and various yield attributes, it was observed that plants treated with salicylic acid at 60 DAS (S4) performed best under water stress. Salicylic acid (S3) increased the leaf and root dry weight at 40 DAS, stem dry weight at 60 DAS and total dry weight at 40 and 60 DAS. H_2O_2 (S5) significantly increased stem and pod dry weight, chlorophyll fluorescence at 40 DAS, number of branches and net photosynthetic rate at 40 and 60 DAS. α-tocopherol (S7) increased plant height at 40 DAS and reduced membrane injury index at 40 and 60 DAS. Ascorbic acid (S1) increased the leaf water potential at 40 and 60 DAS. Overall, this study showed that the foliar applications of salicylic acid at 60 DAS (S4) most effectively enhanced the groundnut yield under water stress.

Keywords: alpha-tocopherol; ascorbic acid; hydrogen peroxide; pod yield; salicylic acid; water stress

Introduction

Groundnut (*Arachis hypogaea* L., 2n=20) is an annual, herbaceous legume belonging to the family of Fabaceae cultivated for its edible seed and it is an important food legume in tropical and subtropical regions. India is one of the world's top producers of groundnut, with production of 9.2 million tonnes and productivity of 1893 kg ha^{-1} across 4.8 million hectares of land. Although India ranks first in area and total production, it ranks eighth in productivity, which is about 100 kg ha^{-1} lower than the global average. The low productivity is attributed to inadequate inputs, outdated technology, poor plant protection practices, irregular rainfall and adverse environmental conditions. Among these, various abiotic stresses have a major impact on agricultural yield, with water stress being the most significant, especially in rainfed areas and responsible for a loss of up to two-thirds of crop yield potential (1). Absence of adequate moisture, required for growth and development is known as water stress and it is the most common phenomenon in rainfed areas (2). It increases the generation of various ROS, which are mostly produced in chloroplasts and to a lesser extent in mitochondria. This results in oxidative stress, which damages plant cells and subcellular components, particularly lipids, nucleic acids and proteins. Several studies have reported a significant decline in various physiological processes in groundnut under water stress conditions. However, groundnut has shown some ability to maintain yield stability through the up regulation of metabolic pathways, synthesis of antioxidant enzymes and morphological adaptations under drought. To reduce drought-related risks, different strategies have been adopted, including the development of stress-tolerant varieties and the application of plant growth regulators (ABA, GA, cytokinins and salicylic acid), antioxidants (ascorbic acid and hydrogen peroxide) and osmoprotectants (3). Signaling molecules play a vital role in sensing stress signals and initiating appropriate metabolic responses. Salicylic acid, ascorbic acid, hydrogen

peroxide and alpha-tocopherol act as signaling agents or messengers and are known to help in drought acclimation. In groundnut, the pegging stage (35-40 DAS) and pod formation stage (55–60 DAS) are particularly sensitive to water stress, which can severely impact pod yield. Application of these signaling molecules during these stages helps in mitigating the effects of drought. Numerous studies have demonstrated that signaling molecules significantly enhance growth, biochemical traits, physiological parameters and yield attributes under drought conditions. For instance, foliar application of salicylic acid improved various yield traits during water stress (4), while salicylic acid (4) and hydrogen peroxide (5) increased the number of side branches and yield components. Therefore, the present study was undertaken to evaluate the role of four signaling molecules-ascorbic acid, salicylic acid, hydrogen peroxide and alpha-tocopherol under water stress conditions, with treatments imposed at 40 DAS and 60 DAS.

Materials and Methods

Field preparation, imposition of stress and different treatments

A field experiment was conducted at Agricultural College Farm, Bapatla, Guntur Andhra Pradesh (16.3610668° N 80.4347525° E). The experimental field was prepared in sandy loamy soil and area was divided into the required number of plots as per the split-plot design with 3 replications. Healthy and matured seeds of the '*Narayani*' variety were sown with 22.5 cm x 10 cm spacing and depth of 5 cm and gap-filling was done at 10 DAS, urea and single super phosphate were supplied, respectively during the time of land preparation and calcium and sulphur were applied through gypsum at 40 DAS. Further, water stress was imposed during the reproductive stage for 20 to 25 days, starting from the pegging stage (35-40 DAS) to the pod formation stage (55-60 DAS). The different main treatments were control and water stress. Different signaling molecules were ascorbic acid, salicylic acid, hydrogen peroxide and alpha tocopherol applied at 40 DAS and 60 DAS and different sub treatments were 1. S_0-control, 2. S_1-ascorbic acid @ 200 ppm at 40 DAS, 3. S_2-ascorbic acid @ 200 ppm at 60 DAS, 4. S_3- salicylic acid @ 200 ppm at 40 DAS, 5. S_4- salicylic acid @ 200 ppm at 60 DAS, 6. S_5- hydrogen peroxide @ 200 ppm at 40 DAS, 7. S_6- hydrogen peroxide @ 200 ppm at 60 DAS, 8. S_7- alpha-tocopherol @ 200 ppm at 40 DAS and 9. S_8- alpha-tocopherol @ 200 ppm at 60 DAS.

Evaluation of different morphological, physiological, biochemical and yield parameters

Morphological parameters

Different morphological parameters like plant height and number of branches of five different tagged plants were measured at 40 and 60 DAS respectively and finally, the average value of plant height and number of branches was calculated.

Physiological parameters

Different physiological parameters like net photosynthetic rate, chlorophyll fluorescence, leaf area and leaf water potential was measured in matured young leaf (1st leaf/2nd leaf) and recorded between 10 AM to 12 Noon with the help of Infra-Red Gas Analyser (IRGA model TPS-2), chlorophyll fluorometer (Hudson: model OS 30 p+), leaf area meter (Biovis PSM 2000-L) and Dew Point potentiometer (Meter group: Decagon model: WP4C) at 40 and 60 DAS. The total dry matter was also determined in five adjacent plants sampled and then separated into stems, roots, leaves and pods and these were dried in hot-air oven at 80 °C for two days at 40 and 60 DAS. Membrane Injury Index (MII) was measured and calculated by using this formula at 40 and 60 DAS.

MII= Conductivity at 45 °C/Conductivity at 100 °C x 100 (6)

Biochemical parameters

Proline

The amount of proline can be estimated at 40 and 60 DAS respectively (7). A leaf sample (0.5 g) was homogenized with 10 ml of 3 % sulpho salicylic acid, filtered and added 2 mLof acid ninhydrin and glacial acetic acid to 2 mL of aliquot in a test tube. These test tubes were kept at 100 °C in a hot water bath for 1 hr and placed in an ice bath. The reaction mixture was extracted using 4 mL of toluene, aspirated and then the absorbance was read at 520 nm by UV-VIS spectro photometer (UV 2600, Shimadzu, Japan).

Super oxide dismutase (SOD)

The activity of SOD was determined at 40 and 60 DAS respectively (8). A 0.2 g of fresh leaf was homogenized with 10 mL of 0.5 M phosphate buffer containing 1 % NEDD. The homogenate was then centrifuged at 4 °C for 30 min at 10000 rpm. Then 0.1 mL of supernatant was mixed with 1.5 mL buffer, 0.1 mL of sodium carbonate, 0.1 mL of NBT solution, 0.2 mL of methionine solution, 0.1 mL of EDTA solution and 1 mL of double distilled water in test tubes as reaction mixture. At last, 0.1 mL of riboflavin was added before illuminating reaction mixture. Among these test tubes, one set of test tubes *i.e.*, blank 'A' was kept under dark mixed with enzyme extract whereas another set of test tubes *i.e.*, blank 'B' along with sample test tubes were kept under light mixed with-out any enzyme extract for 10 min. The absorbance of sample test tubes and blank 'B' were measured at 560 nm against blank 'A' by UV-VIS spectro photometer (UV 2600, Shimadzu, Japan). The percent reduction in colour between two blank was measured and 50 % reduction in colour was taken as 1 unit of enzymatic activity and the activity was expressed in units of the enzyme per g FW per min (U. g^{-1} FW. min^{-1}).

Estimation of catalase

The activity of catalase was at 40 and 60 DAS, respectively (9). A 500 mg of leaf was homogenized with 2.5 mL of 0.05 M sodium phosphate buffer and 1 mL of 1 % PVP and centrifuged at 10000 rpm for 15 min at 4 °C. Then 2 mL of 50 mM buffer solution, 0.95 mL of 0.03 % hydrogen peroxide and 0.05 mL of enzyme extract were taken into a test tube. The absorbance was read at 240 nm by UV-VIS spectro photometer (UV 2600, Shimadzu, Japan) and expressed in unit's $min^{-1}g^{-1}$.

Enzyme activity = (Maximum Absorbance - Minimum Absorbance) × 60 × 2

Yield parameters

Different yield parameters like test weight, shelling percentage, pod yield, harvest index, number of pods and pod weight were measured and calculated at the harvesting of crop. Test weight

was measured by weighing 100 kernels. Shelling percentage was calculated by dividing weight of kernels to weight of pods and multiplied with 100. Pod yield was calculated by weighing sun dried pods collected from the different plots. Shelling percentage was calculated by dividing economic yield to biological yield and multiplied by 100. Number of pods and pod weight per plant were calculated by counting number and weight of pods per plant.

Stastistical analysis

The experiment was conducted in split plot design and the data were subjected to two-way factorial ANOVA. Inferential statistics performed using the library field hub for split plot analysis (10). A post hoc analysis for pair-wise comparison of treatment × genotype combination was performed by Tukey's range test using Graph pad prism (version 9.5.1) software. The charts were also prepared using a licensed version of Graphpad Prism 9.5.1. Further, principal component analysis was performed by using the PAST software (version 4.03) and pearson-correlation analysis was performed through ORIGIN PRO software.

Results

Morphological parameters

Plant height and number of branches

Under water stress conditions, the application of various signaling molecules significantly influenced morphological and physiological parameters of plants. Plant height measured at 40 and 60 DAS showed 13.75 % and 11.17 % increase with the application of alpha-tocopherol @ 200 ppm at 40 DAS (S7), effectively mitigating the negative effects of water stress. In contrast, ascorbic acid @ 200 ppm at 60 DAS (S2) did not produce any significant change and showed 14.07 % reduction in plant height compared to the control and other treatments (Supplementary Table 1, 6, 7).

Different signaling molecules were applied exogenously and it was found that hydrogen peroxide @ 200 ppm at 40 DAS (S_5) increased the number of branches whereas, ascorbic acid @ 200 ppm at 60 DAS (S_2) reduced the number of branches at 40 and 60 DAS respectively under water stress (Supplementary Table 2, 6, 7).

Physiological parameters

Leaf area, net photosynthetic rate and chlorophyll fluorescence

The leaf area is reduced under water stress condition as compared to the control plants. At 40 DAS, when plants were treated with alpha-tocopherol @ 200 ppm at 40 DAS (S7) increased the leaf area whereas, ascorbic acid @ 200 ppm at 40 DAS (S1) reduced the leaf area at 40 DAS respectively as compared to the other treatments. At 60 DAS, leaf area was increased when plants were treated with salicylic acid @ 200 ppm at 60 DAS (S4) whereas, it was reduced when plants were treated with hydrogen peroxide @ 200 ppm at 60 DAS (S6) as compared to the control and other treatments (Supplementary Table 1, 6, 7).

The photosynthetic rate is reduced under water stress condition as compared to the control plants. At 40 DAS, hydrogen peroxide @ 200 ppm at 40 DAS (S5) had improved net photosynthetic rate. Similarly, it was found that foliar application of hydrogen peroxide @ 200 ppm (S5) at 60 DAS increased the net photosynthetic rate. However, alpha-tocopherol @ 200 ppm (S8) and salicylic acid @ 200 ppm at 60 DAS (S4) did not show any significant effect on photosynthetic rate as compared to the control and other treatments (Supplementary Table 2, 6, 7).

The chlorophyll fluorescence is reduced under water stress as compared to the control plants. At 40 DAS, salicylic acid @ 200 ppm at 40 DAS (S3) increased the chlorophyll fluorescence as compared to the control and other treatments. At 60 DAS, salicylic acid @ 200 ppm at 40 DAS and 60 DAS (S3 and S4) increased the chlorophyll fluorescence and alpha-tocopherol @ 200 ppm at 60 DAS (S8) reduced the chlorophyll fluorescence under water stress when it is compared with control and other treatments (Supplementary Table 2, 6, 7) .

Leaf water potential was considerably lower under stress than in irrigated plants. Nonetheless, ascorbic acid @ 200 ppm at 40 DAS (S1) improved water potential (-1.87 MPa) by 41 % and 38.07 % compared to hydrogen peroxide (S5) (-3.17 MPa) and salicylic acid (S3) (-3.02 MPa) treatments, respectively. This effect remained consistent at 60 DAS, where ascorbic acid @ 200 ppm at 40 DAS (S1) (-2.05 MPa) improved leaf water potential by 17 % as compared to control (-2.47MPa) (Supplementary Table 2, 6, 7).

Total dry matter partitioning

Leaf dry weight, stem dry weight, pod dry weight, root dry weight and total dry weight

The leaf dry weight was reduced under water stress condition as compared to the control. At 40 DAS, treating the plants with salicylic acid @ 200 ppm at 40 DAS (S3) enhanced the leaf dry weight under water stress as compared to the control and other treatments. Similarly, at 60 DAS, salicylic acid @ 200 ppm at 40 and 60 DAS (S3 and S4) increased the leaf dry weight under water stress as compared to the control and other treatments (Table 1, 3-6); At 60 DAS, treating plants with salicylic acid @ 200 ppm at 40 DAS (S3) increased the stem dry weight under water stress when it is compared with the control and other treatments (Supplementary Table 3, 6, 7).

Pod dry weight decreased significantly under stress but was enhanced at 40 DAS by hydrogen peroxide (S5) and salicylic acid (S3). At 60 DAS, salicylic acid @ 200 ppm (S4) it increased pod dry weight, while alpha-tocopherol @ 200 ppm at 40 DAS (S7) decreased it under stress (Table 1, 3-6; Fig. 1).

The total dry weight was reduced under water stress as compared to the control. At 40 DAS, total dry weight was increased when plants were treated with salicylic acid @ 200 ppm at 40 DAS (S3) and hydrogen peroxide @ 200 ppm at 40 DAS (S5) as compared to the control and other treatments. At 60 DAS, foliar application of salicylic acid @ 200 ppm at 40 and 60 DAS (S3 and S4) increased the total dry weight and alpha-tocopherol @ 200 ppm at 60 DAS (S8) reduced the total dry weight under water stress as compared to the control and other treatments (Supplementary Table 3, 6, 7).

Membrane Injury Index (MII)

MII indicated by electrolyte leakage, was higher under stress but significantly reduced when treated with hydrogen peroxide @ 200 ppm at 40 DAS (S5) and alpha-tocopherol @ 200 ppm at 40 DAS (S7). At 60 DAS, treatments with ascorbic acid @ 200 ppm

Table 1. Effect of signaling molecules on leaf dry weight and pod dry weight of groundnut under water stress

	Treatments	Leaf dry weight (g plant^{-1})		Pod dry weight (g plant^{-1})	
		40 DAS	60 DAS	40 DAS	60 DAS
Control	**S_0- Control**	2.96	6.00^{b}	1.33	4.01^{b}
	S_1- Ascorbic acid (40 DAS) @ 200 ppm	3.18	6.22^{b}	2.40	4.99^{ab}
	S_2- Ascorbic acid (60 DAS) @ 200 ppm	3.02	6.49^{ab}	2.12	4.83^{ab}
	S_3- Salicylic acid (40 DAS) @ 200 ppm	4.13	7.31^{ab}	2.50	3.93^{b}
	S_4- Salicylic acid (60 DAS) @ 200 ppm	3.23	9.3^{a}	1.92	7.25^{a}
	S_5- Hydrogen peroxide (40 DAS) @ 200 ppm	3.22	5.49^{b}	2.44	5.54^{ab}
	S_6- Hydrogen peroxide (60 DAS) @ 200 ppm	3.48	6.44^{b}	2.19	4.70^{ab}
	S_7- α-tocopherol (40 DAS) @ 200 ppm	3.22	6.35^{ab}	2.49	3.72^{b}
	S_8- α-tocopherol (60 DAS) @ 200 ppm	3.19	5.56^{b}	1.57	4.60^{ab}
Drought	**S_0- Control**	2.93	4.17^{b}	2.09	3.60^{b}
	S_1- Ascorbic acid (40 DAS) @ 200 ppm	2.58	5.01^{b}	1.43	3.76^{b}
	S_2- Ascorbic acid (60 DAS) @ 200 ppm	2.81	5.79^{ab}	1.86	2.56^{c}
	S_3- Salicylic acid (40 DAS) @ 200 ppm	2.89	5.18^{ab}	1.87	3.80^{b}
	S_4- Salicylic acid (60 DAS) @ 200 ppm	2.65	9.02^{a}	1.82	6.86^{a}
	S_5- Hydrogen peroxide (40 DAS) @ 200 ppm	2.94	4.95^{b}	2.40	2.81^{c}
	S_6- Hydrogen peroxide (60 DAS) @ 200 ppm	2.38	4.80^{b}	1.83	3.32^{b}
	S_7- α-tocopherol (40 DAS) @ 200 ppm	3.28	5.60^{ab}	1.35	3.34^{b}
	S_8- α-tocopherol (60 DAS) @ 200 ppm	2.57	4.96^{b}	1.84	3.48^{b}

(S2) and alpha-tocopherol @ 200 ppm at 40 DAS (S7) continued to reduce leakage under stress conditions (Supplementary Table 4, 6, 7).

Biochemical parameters

Proline content

Water stress significantly increased proline accumulation in groundnut plants compared to the control. Foliar application of salicylic acid @ 200 ppm at 60 DAS (S4) and hydrogen peroxide @ 200 ppm at 40 DAS (S5) led to a marked increase in proline content by 240.44 % and 12.35 % at 60 DAS respectively, suggesting an osmo protective role. In contrast, ascorbic acid @ 200 ppm at 40 DAS (S1) did not significantly influence proline content and increased by 1.69 % at 40 DAS and decreased by 4.49 % at 60 DAS. Other treatments also lacked significant impact under stress conditions (Table 2-6; Fig. 2).

Antioxidant enzymes: Superoxide dismutase (SOD) and catalase activity (CAT)

Under water stress, SOD and CAT activities were elevated relative to control plants. Application of salicylic acid at 60 DAS (S4) and hydrogen peroxide at 40 DAS (S5) significantly enhanced SOD activity and scavenged higher concentration of hydrogen peroxide and other different types of ROS. It ultimately reduced the oxidative stress and stabilized the endomembrane present in the cell. However, ascorbic acid at 40 DAS (S1) did not cause any measurable change (Table 2-6; Fig. 3). Similarly, catalase activity was significantly boosted by S4, while salicylic acid at 40 DAS (S3) showed no impact.

Yield parameters and productivity

Test Weight was improved with salicylic acid @ 200 ppm at 60 DAS (S4) but reduced with hydrogen peroxide at 40 DAS (S5) (Fig. 1). Shelling Percentage dropped under stress but was increased by ascorbic acid (S2) and salicylic acid (S4) at 60 DAS. In contrast, salicylic acid at 40 DAS (S3) decreased shelling percentage. Pod Yield declined sharply under water stress, but was improved by S4 and S5, indicating a yield-conserving effect (Fig. 1). Harvest Index fell significantly under stress, but foliar application of salicylic acid at 40 and 60 DAS (S3, S4) increased it. However, hydrogen peroxide at 40 DAS (S5) reduced harvest index. Number of pods per plant was highest under S4 and lowest under hydrogen peroxide at 60 DAS (S6). Pod weight per plant was enhanced by ascorbic acid (S2) and salicylic acid (S4) but reduced by alpha-tocopherol at 40 DAS (S7) (Supplementary Table 5-7).

Pearson correlation analysis

At 60 DAS, proline content (r = 0.99), SOD activity (r = 0.98), test weight (r = 0.95), pod dry weight (r = 0.88), number of pods per plant (r = 0.88), catalase activity (r = 0.80) and harvest index (r =

Table 2. Effect of signaling molecules on SOD and CAT activity and proline content of groundnut under water stress

	Treatments	SOD (U g^{-1} FW min^{-1})		Catalase (units min^{-1} g^{-1} FW)		Proline (µg g^{-1} FW)	
		40 DAS	60 DAS	40 DAS	60 DAS	40 DAS	60 DAS
Control	**S_0- Control**	0.51	0.43d	3.62	6.29^{a}	0.22	0.52^{a}
	S_1- Ascorbic acid (40 DAS) @ 200 ppm	0.47	0.65b	4.09	5.40^{a}	0.20	0.51^{a}
	S_2- Ascorbic acid (60 DAS) @ 200 ppm	0.58	0.78a	5.56	5.44^{a}	0.22	0.48^{ab}
	S_3- Salicylic acid (40 DAS) @ 200 ppm	0.66	0.76ab	4.07	4.63^{a}	0.15	0.44^{b}
	S_4- Salicylic acid (60 DAS) @ 200 ppm	0.62	0.84a	3.92	7.01^{a}	0.19	0.44^{b}
	S_5- Hydrogen peroxide (40 DAS) @ 200 ppm	0.33	0.50c	5.23	5.42^{a}	0.22	0.51^{a}
	S_6- Hydrogen peroxide (60 DAS) @ 200 ppm	0.62	0.89a	3.29	5.40^{a}	0.21	0.51^{a}
	S_7- α-tocopherol (40 DAS) @ 200 ppm	0.55	0.72ab	4.78	5.48^{a}	0.15	0.41^{bc}
	S_8- α-tocopherol (60 DAS) @ 200 ppm	0.38	0.66b	4.77	5.68^{a}	0.17	0.46^{b}
Drought	**S_0- Control**	1.15	1.25^{b}	4.97	7.11^{b}	0.59	0.89^{c}
	S_1- Ascorbic acid (40 DAS) @ 200 ppm	0.83	1.02^{c}	4.09	6.79^{b}	0.60	0.85^{c}
	S_2- Ascorbic acid (60 DAS) @ 200 ppm	1.06	1.30^{b}	3.93	6.29^{b}	0.57	0.89^{c}
	S_3- Salicylic acid (40 DAS) @ 200 ppm	1.25	1.24^{b}	4.74	5.73^{b}	0.73	0.87^{c}
	S_4- Salicylic acid (60 DAS) @ 200 ppm	1.05	4.46^{a}	4.56	12.25^{a}	0.53	3.03^{a}
	S_5- Hydrogen peroxide (40 DAS) @ 200 ppm	0.74	1.17^{bc}	6.41	10.66^{a}	0.71	1.00^{b}
	S_6- Hydrogen peroxide (60 DAS) @ 200 ppm	1.16	1.16^{bc}	5.11	7.51^{b}	0.59	0.78^{d}
	S_7- α-tocopherol (40 DAS) @ 200 ppm	1.24	1.24^{b}	6.07	6.64^{b}	0.71	0.95^{b}
	S_8- α-tocopherol (60 DAS) @ 200 ppm	1.16	1.22^{b}	5.23	7.21^{b}	0.54	0.93^{b}

Table 3. Descriptive statistical analysis of different parameters of groundnut under different conditions

		Mean	Standard deviation	Standard Error of mean
Proline	Control	0.48	0.03	0.01
	Drought	1.13	0.71	0.23
SOD	Control	0.69	0.15	0.05
	Drought	1.56	1.08	0.36
CAT	Control	5.63	0.66	0.22
	Drought	7.79	2.17	0.72
LDW	Control	6.57	1.15	0.38
	Drought	5.49	1.4	0.46
PDW	Control	4.46	0.63	0.21
	Drought	3.54	0.67	0.22
Pod yield	Control	2456.27	420.331	140.11
	Drought	1412.51	530.16	176.72
Test weight	Control	43.37	3.43	1.14
	Drought	40.32	4.04	1.34

Table 4. ANOVA of different parameters of groundnut under different conditions

		Degree of Freedom (DF)	Sum of squares	Mean square	F value	Prob>F
Proline	Model	1	1.94	1.94	7.58	0.014
	Error	16	4.09	0.25		
	Total	17	6.03			
SOD	Model	1	3.40	3.40	5.62	0.03
	Error	16	9.68	0.60		
	Total	17	13.08			
CAT	Model	1	20.99	20.99	8.11	0.011
	Error	16	41.37	2.58		
	Total	17	62.36			
Leaf dry weight	Model	1	5.20	5.20	3.15	0.094
	Error	16	26.38	1.64		
	Total	17	31.59			
Pod dry weight	Model	1	3.7	3.75	8.65	0.009
	Error	16	6.93	0.43		
	Total	17	10.69			
Pod yield	Model	1	4902509.41	4902509.41	**21.42**	**2.8**
	Error	16	3661997.84	228874.87		
	Total	17	8564507.25			
Test weight	Model	1	41.80	41.80	**2.96**	**0.10**
	Error	16	225.39	14.08		
	Total	17	267.19			

Table 5. Descriptive statistical analysis of different parameters of groundnut in different treatments

	Treatments	Mean	Standard deviation	Standard error of mean
Proline	S0	0.71	0.26	0.18
	S1	0.68	0.24	0.17
	S2	0.69	0.29	0.21
	S3	0.66	0.30	0.22
	S4	1.73	1.83	1.30
	S5	0.75	0.34	0.25
	S6	0.65	0.19	0.14
	S7	0.68	0.38	0.27
	S8	0.70	0.33	0.24
SOD	S0	0.84	0.58	0.41
	S1	0.84	0.26	0.19
	S2	1.04	0.36	0.26
	S3	1	0.34	0.24
	S4	2.65	2.56	1.81
	S5	0.84	0.47	0.34
	S6	1.02	0.19	0.14
	S7	0.98	0.37	0.26
	S8	0.94	0.40	0.28
CAT	S0	6.7	0.58	0.41
	S1	6.1	0.98	0.70
	S2	5.86	0.60	0.43
	S3	5.18	0.77	0.55
	S4	9.63	3.70	2.62
	S5	8.04	3.70	2.62
	S6	6.45	1.49	1.05
	S7	6.06	0.82	0.58
	S8	6.45	1.08	0.77
Leaf dry weight	S0	5.08	1.29	0.91
	S1	5.61	0.85	0.60
	S2	6.14	0.49	0.35
	S3	6.25	1.50	1.06
	S4	9.16	0.19	0.14
	S5	5.22	0.38	0.27
	S6	5.62	1.15	0.82
	S7	5.97	0.53	0.37
	S8	5.26	0.42	0.3

	S0	3.81	0.28	0.21
	S1	4.37	0.86	0.62
	S2	3.70	1.60	1.13
	S3	3.87	0.09	0.07
Pod dry weight	S4	4.56	0.43	0.31
	S5	4.17	1.93	1.37
	S6	4.01	0.97	0.69
	S7	3.53	0.26	0.19
	S8	4.04	0.79	0.56
	S0	1614.416	817.45	578.02
	S1	1814.801	737.85	521.74
	S2	1770.86	751.54	531.42
	S3	1791.77	741.51	524.33
Pod yield	S4	3179.82	535.18	378.43
	S5	1937.50	766.04	541.67
	S6	1707.77	769.56	544.16
	S7	1813.02	733.38	518.58
	S8	1779.57	789.94	558.57
	S0	38.49	3.86	2.73
	S1	42.16	2.48	1.76
	S2	40.99	0.72	0.51
	S3	41.90	1.66	1.17
Test weight	S4	51.08	1.52	0.81
	S5	39.63	0.38	0.27
	S6	40.49	2.67	1.89
	S7	40.73	4.10	2.9
	S8	41.16	2.35	1.66

Table 6. ANOVA of different parameters of groundnut in different treatments

		Degree of Freedom (DF)	Sum of squares	Mean square	F value	Prob>F
	Model	8	1.96	0.24	0.54	0.79
Proline	Error	9	4.06	0.45		
	Total	17	6.03			
	Model	8	5.32	0.66	0.77	0.63
SOD	Error	9	7.76	0.86		
	Total	17	13.08			
	Model	8	28.57	3.57	0.95	0.52
CAT	Error	9	33.79	3.75		
	Total	17	62.36			
	Model	8	24.68	3.08	4.017	0.026
Leaf dry weight	Error	9	6.91	0.76		
	Total	17	31.59			
	Model	8	1.70	0.21	0.21	0.97
Pod dry weight	Error	9	8.98	0.99		
	Total	17	10.69			
	Model	8	3609851.9038	451231.487	**0.81**	**0.61**
Pod yield	Error	9	4954655.34813	550517.2609		
	Total	17	856450.25194			
	Model	8	211.82	26.47	**4.30**	**0.02**
Test weight	Error	9	55.37	6.15		
	Total	17	267.19			

Table 7. Summary row to highlight top-performing treatments for each parameter

Parameters	40 DAS	60 DAS
Plant height	α-tocopherol @ 200 ppm at 40 DAS (S7)	α-tocopherol @ 200 ppm at 40 DAS (S7)
Number of branches	H_2O_2 @ 200 ppm at 40DAS(S_5)	H_2O_2 @ 200 ppm at 40DAS(S_5)
Leaf area	α-tocopherol @ 200 ppm at 40 DAS (S7)	Salicylic acid @ 200 ppm at 60 DAS (S4)
Chlorophyll fluorescence	Salicylic acid @ 200 ppm at 40 DAS (S3)	Salicylic acid @ 200 ppm at 40 DAS (S3)
Net photosynthetic rate	H_2O_2 @ 200 ppm at 40 DAS (S5)	H_2O_2@ 200 ppm (S5)at 40 DAS
Leaf water potential	Ascorbic acid @ 200 ppm at 40 DAS (S1)	Ascorbic acid @ 200 ppm at 40 DAS (S1)
Membrane injury index	H_2O_2 @ 200 ppm at 40 DAS (S5)	α-tocopherol @ 200 ppm at 40 DAS (S7)
Proline	Salicylic acid @ 200 ppm at 40 DAS (S3)	Salicylic acid @ 200 ppm at 60 DAS (S4)
SOD	Salicylic acid @ 200 ppm at 40 DAS (S3)	Salicylic acid @ 200 ppm at 60 DAS (S4)
CAT	H_2O_2 @ 200 ppm at 40 DAS (S5)	Salicylic acid @ 200 ppm at 60 DAS (S4)
Leaf dry weight	Salicylic acid @ 200 ppm at 40 DAS (S3)	Salicylic acid @ 200 ppm at 60 DAS (S4)
Stem dry weight	Salicylic acid @ 200 ppm at 40 DAS (S3)	Salicylic acid @ 200 ppm at 40 DAS (S3)
Pod dry weight	H_2O_2 @ 200 ppm at 40 DAS (S5)	Salicylic acid @ 200 ppm at 60 DAS (S4)
Root dry weight	H_2O_2 @ 200 ppm at 40 DAS (S5)	H_2O_2 @ 200 ppm at 60 DAS (S6)
Total dry weight	H_2O_2 @ 200 ppm at 40 DAS (S5)	Salicylic acid @ 200 ppm at 40 DAS (S3)
	Yield parameters	
Pod yield	Salicylic acid @ 200 ppm at 60 DAS (S4)	
Harvest index	Salicylic acid @ 200 ppm at 60 DAS (S4)	
Test weight	Salicylic acid @ 200 ppm at 60 DAS (S4)	
Number of pods per plant	Salicylic acid @ 200 ppm at 60 DAS (S4)	
Pod weight per plant	Ascorbic acid @ 200 ppm at 60 DAS (S2)	
Shelling percentage	H_2O_2 @ 200 ppm at 40 DAS (S5)	

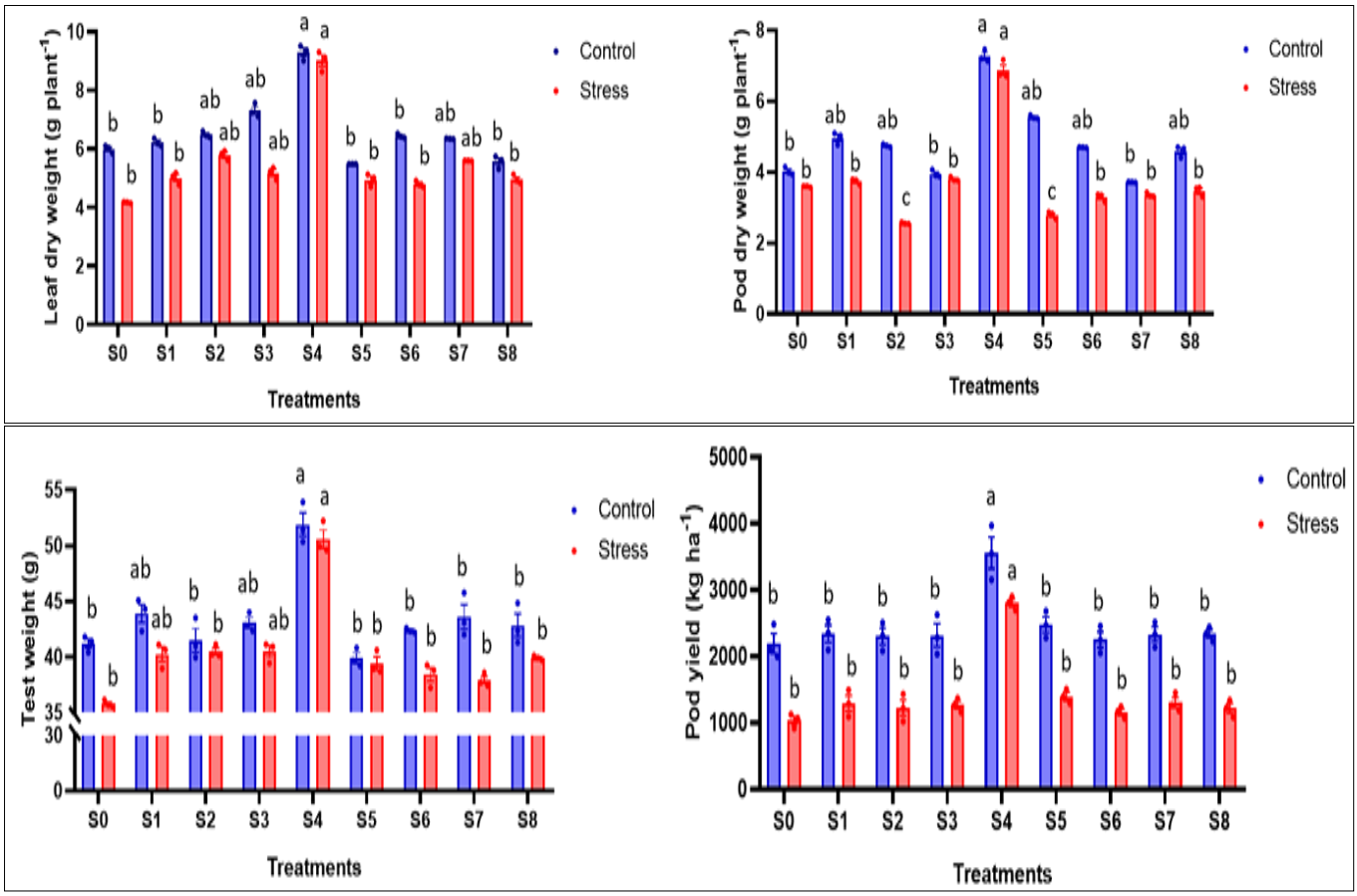

Fig. 1. Effect of signaling molecules on biomass partitioning in groundnut under water stress at 60 DAS (a) leaf dry weight (b) pod dry weight (c) test weight (d) pod yield. Here S0- Control, S1- ascorbic acid at 40 DAS, S2-ascorbisc acid at 60 DAS, S3-salicylic acid at 40 DAS, S4-Salicylic acid at 60 DAS, S5-H2O2 at 40 DAS, S6-H2O2 at 60 DAS, S7- α-tocopherol at 40 DAS, S8- α-tocopherol at 60 DAS and DAS refers to Days after sowing. M1-Control, M2-Stress. This figures depicts the mean of three biological replicates and the statistical significance was tested using two -way ANOVA for split-plot design.

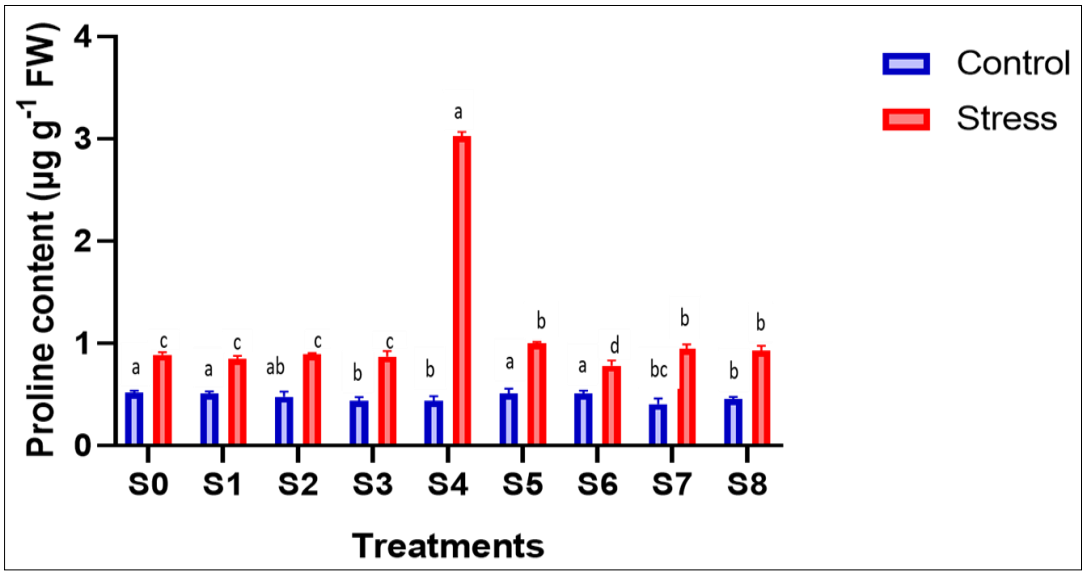

Fig. 2. Effect of signaling molecules on proline content of groundnut under water stress at 60 DAS. Here S0- Control, S1- ascorbic acid at 40 DAS, S2-ascorbisc acid at 60 DAS, S3-salicylic acid at 40 DAS, S4-Salicylic acid at 60 DAS, S5-H2O2 at 40 DAS, S6-H2O2 at 60 DAS, S7- α-tocopherol at 40 DAS, S8- α-tocopherol at 60 DAS and DAS refers to Days after sowing. M1- Control, M2- Stress. This figure depicts the mean of three biological replicates and the statistical significance was tested using two way ANOVA for split-plot design.

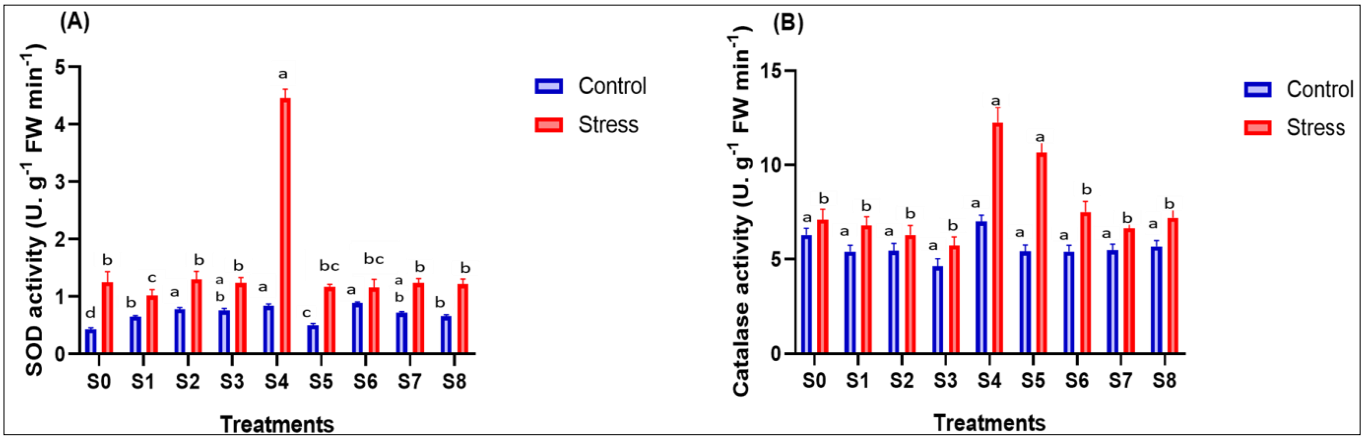

Fig. 3. Effect of signaling molecules on antioxidant activity of groundnut under water stress at 60 DAS (a) SOD activity. (b) Catalase activity. Here S0- Control, S1- ascorbic acid at 40 DAS, S2-ascorbic acid at 60 DAS, S3-salicylic acid at 40 DAS, S4-Salicylic acid at 60 DAS, S5-H2O2 at 40 DAS, S6-H2O2 at 60 DAS, S7- α-tocopherol at 40 DAS, S8- α-tocopherol at 60 DAS and DAS refers to Days after sowing. M1-Control, M2-Stress. This figure depicts the mean of three biological replicates and the statistical significance was tested using two way ANOVA for split plot design.

0.80) were strongly and positively correlated with pod yield. During this period, different enzymes like SOD and catalase scavenged various reactive oxygen species, reduced the damage and oxidative stress in the cell. Proline contents were increased at a higher rate, which enhanced the relative water content and turgidity of cell. Altogether, they maintained a redox homeostasis in the cell during pod development stage and enhanced pod yield under this stress condition. On the other hand, net photosynthetic rate was (r = –0.74) was negatively correlated with pod yield. As stomata remains close during this period of time, gaseous exchange between leaves to atmosphere was reduced, which ultimately affected net photosynthetic rate negatively. No significant correlations were observed at 40 DAS. These findings highlight that key biochemical and morphological traits at 60 DAS play a critical role in mitigating yield loss under drought stress (Fig. 4).

Discussion

In this experiment we studied the responses of different signaling molecules *i.e.*, ascorbic acid, salicylic acid, hydrogen peroxide and alpha-tocopherol on different growth and yield parameters of groundnut under water stress. Different signaling molecules were applied exogenously at 40 and 60 DAS, respectively and it was found that proline content, enzymatic activity of SOD and catalase, leaf and pod dry weight at 60 DAS, test weight, harvest index and number of pods per plant was found to be highly correlated with pod yield as compared to other parameters.

Increase in the proline content and antioxidant enzymatic activity enhanced the pod yield under stress

Hydrogen peroxide acts as both reactive oxygen species and signaling molecule under different circumstances in the cell. When it is present in optimum concentration in the cell, it can participate in different signal transduction pathways, whereas it acts as an oxidizing agent, when the concentration is increased in the cell. Hydrogen peroxide at 40 DAS (S5) and hydrogen peroxide at 60 DAS (S6) enhanced the concentration of proline and increased the activity of SOD and CAT at 60 DAS, which reduced the endogenous hydrogen peroxide and malondialdehyde content in the cell (11). Among these treatments (S5 and S6), S5 (hydrogen peroxide at 40 DAS)

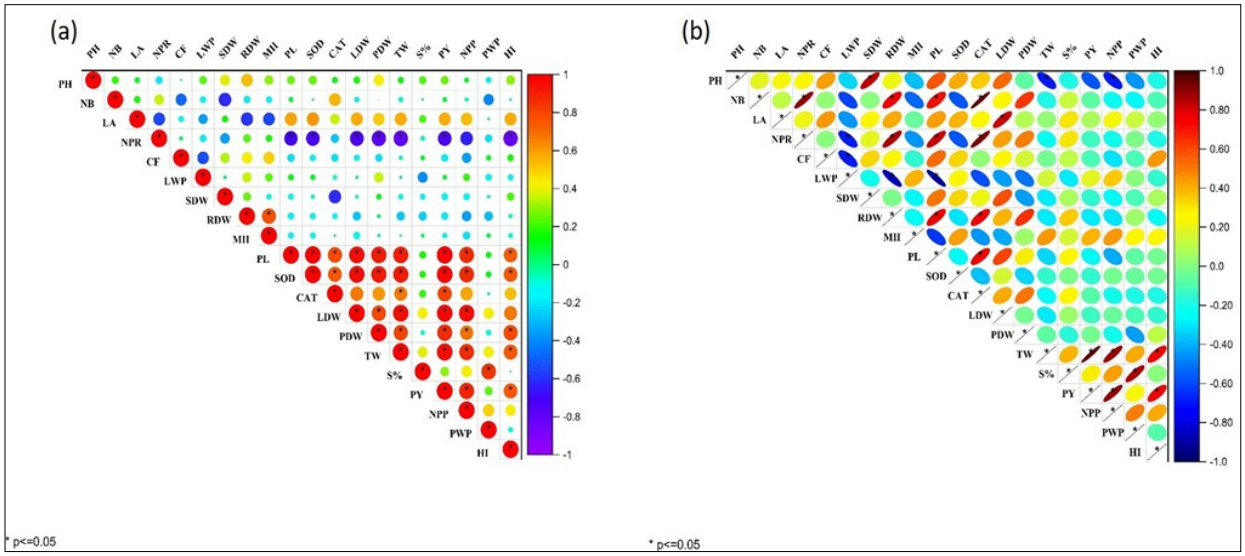

Fig. 4. Pearson correlation analysis of different parameters at both 40 and 60 DAS. (a) 60 DAS and (b) 40 DAS. Here PH refers to plant height, NB -Number of branches, LA-Leaf area, NPR-Net Photosynthetic rate, CF-Chlorophyll fluorescence, LWP-Leaf water potential, SDW-Shot dry weight, RDW-Root dry weight, MII-Membrane Injury Index, PL-Proline, SOD-Super oxide dismutase, CAT-Catalse, LDW-Leaf dry weight, PDW-Pod dry weight, TW-Test weight, S %-Shelling percentage, PY-Pod yield, NPP-Number of pods per plant, PWP-Pod weight per plant and HI-Harvest index.

treatment produced higher yield as compared to S6 (hydrogen peroxide at 60 DAS) treatment. This result was found similar with earlier studies who found that foliar application of hydrogen peroxide increased the grain yield significantly in rice under water stress (12).

Exogenous application of ascorbic acid (S1 and S2) and alpha-tocopherol (S7 and S8) also increased the proline concentration, antioxidant activity of SOD and catalase at 60 DAS, however it did not show significant impact on pod yield under water stress condition.

In our present study, it was found that foliar application of salicylic acid at 60 DAS (S4) enhanced the proline content, antioxidant activities of SOD and catalase enzymes and leaf area at 60 DAS under water stress. This result was found similar with other findings, where foliar application of salicylic acid increased the endogenous salicylic acid content, which also increased the proline content, maintained turgidity of cell and increased the leaf area (13-15). It also enhanced the gene expression of different antioxidant enzymes, which elevated the activity of these enzymes and reduced the oxidative stress in the cell (16). Through different signal transduction pathways, it interacted with abscisic acid and calcium ions in the cell and enhanced the gene expression of different antioxidant enzymes (17). SOD and other antioxidant enzymes play a crucial protective role in scavenging Reactive Oxygen Species (ROS) and shielding plant tissues from oxidative damage (13, 15, 18). This is found similar with the findings of previous works who found that salicylic acid reduced the MDA content by increasing the antioxidant activity of SOD under water stress (19). Salicylic acid enhanced the activity of SOD and catalase enzymes, which reduced the extent of lipid peroxidation and malon dialdehyde content in the leaves (20). Similarly, catalase activity in different strawberry cultivars was found to be positively correlated with salicylic acid @ 0.1 mM (18). All together enhanced different yield parameters like pod yield, test weight, harvest index and total number of pods per plant significantly when plants were treated with salicylic acid at pod development stage of groundnut under water stress.

However, treating plants with salicylic acid at 40 DAS (S3) could not increase the proline content, SOD and catalase activity significantly at 60 DAS as compared to other treatments. So, it did not produce more yield under water stress.

Increase in the leaf dry weight and pod dry weight enhanced the pod yield under water stress

Leaf dry weight and pod dry weight play major role in regulating pod yield in groundnut under water stress condition. Increase in the leaf dry weight could also enhanced the pod dry weight, which ultimately enhanced the pod yield under different stress conditions.

Treating with salicylic acid at 60 DAS (S4) enhanced the leaf area, which also increased leaf dry weight and pod dry weight at 60 DAS. It ultimately enhanced the pod yield under water stress condition as compared to other treatments. Similarly, sink strength and pod yield was enhanced through cell division and translocation of different metabolites into the developing grains in presence of salicylic acid (21). Additionally, it was noted that reduction in the abortion of ovaries lead to increase the total number of pods per plant and number of seeds in soybean plants (22).

However, salicylic acid at 40 DAS (S3), hydrogen peroxide at 40 DAS (S5), hydrogen peroxide at 60 DAS (S6), ascorbic acid at 40 DAS (S1), ascorbic acid at 60 DAS (S2), alpha tocopherol at 40 DAS (S7) and alpha tocopherol at 60 DAS (S8) could not produce higher leaf and pod dry weight at 60 DAS under water stress condition.

These findings were found to be like those of different researchers who discovered that treating plants with salicylic acid at the pod filling stage (60 DAS) had significant effects on groundnut pod yield, compared to the pod initiation stage (40 DAS). When it is applied exogenously to the plants, it is absorbed at a particular place and translocated to the different plant parts, activates different secondary messengers through different signal transduction pathway and finally enhances the growth, biochemical and physiological parameters. Finally, it was found that foliar application of salicylic acid had significantly greater impact on different biochemical, physiological and yield parameters at pod filling stage.

Principal Component Analysis (PCA) in groundnut under water stress condition

PCA was performed with twenty different traits and nine different treatments at 60 DAS under water stress condition. In this PCA, Principal component 1 (PC1) and PC2 individually constitute 44.44 and 14.63 % of total variability among traits and individuals, respectively, representing total variance of 59.07 %. Among different treatments, salicylic acid @ 200 ppm at 60 DAS (S4) was found to be highly correlated with proline content, leaf dry weight, test weight, superoxide dismutase activity, harvest index, pod dry weight and pod yield, whereas ascorbic acid @ 200 ppm at 40 DAS (S1), ascorbic acid @ 200 ppm at 60 DAS, hydrogen peroxide @ 200 ppm at 40 DAS (S5), hydrogen peroxide @ 200 ppm at 60 DAS (S6), alpha tocopherol @ 200 ppm at 40 DAS (S7) and alpha-tocopherol @ 200 ppm at 60 DAS (S8) was not found to be correlated with pod yield and other morpho-physiological, biochemical and yield parameters. Finally, it was concluded that, foliar application of salicylic acid @ 200 ppm at 60 DAS enhanced the proline content, enzymatic activity of SOD and catalase, which increased the leaf dry weight and pod dry weight at 60 DAS, which ultimately improved the pod yield under water stress condition as compared to other treatments (Fig. 5).

Conclusion

In today's era, due to climate change several problems were raised, which have drastic effect on the survival of crops. Drought stress is one of the stresses, has major effect on groundnut and takes the attention of different scientists throughout the world. In case of groundnut, pegging and pod formation are two most critical stages for irrigation as compared to the other developmental stages. Water stress during this period reduces the rate of cell division in the ovary position, which ultimately affects pod yield. To cope with climate change and enhance the survival ability, several methods were attempted to enhance productivity of groundnut, out of these methods foliar application has become

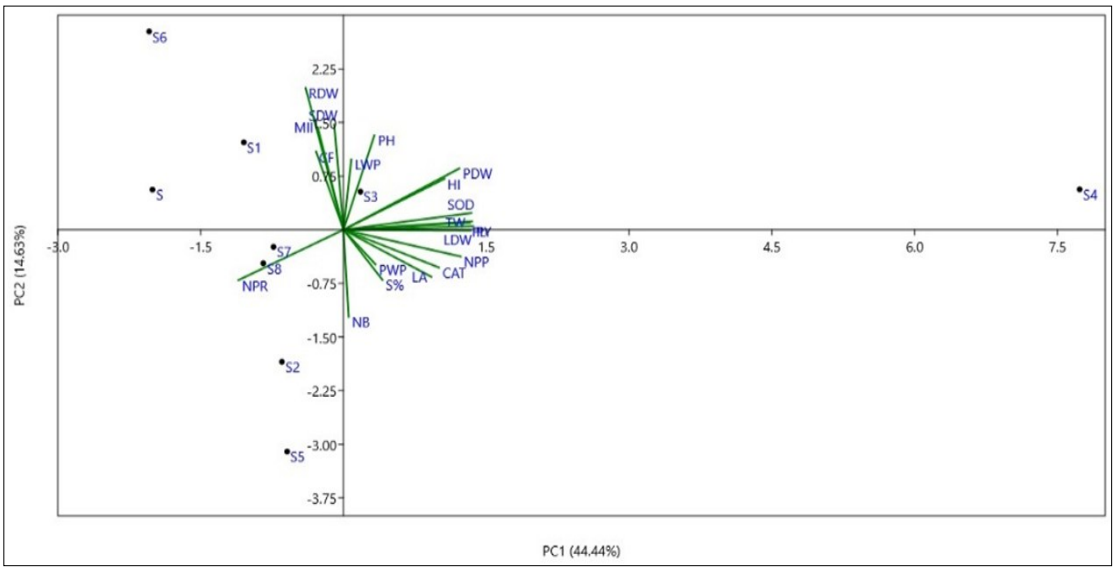

Fig. 5. Principal Component Analysis was performed between different parameters and treatments under water stress at 60 DAS. Here PH refers to plant height, NB-Number of branches, LA-Leaf area, NPR-Net Photosynthetic Rate, CF-Chlorophyll Fluorescence, LWP-Leaf Water Potential, SDW-Shot dry weight, RDW-Root dry weight, MII-Membrane Injury Index, PL-Proline, SOD-Super oxide dismutase, CAT-Catalse, LDW-Leaf dry weight, PDW-Pod dry weight, TW-Test weight, S %-Shelling percentage, PY-Pod yield, NPP-Number of pods per plant, PWP-Pod weight per plant and HI-Harvest index.

the most feasible method and accepted by different crop physiologists. Through this method, different signaling molecules will be absorbed through the leaf surface, transmitted to the required plant parts and transduce different signaling pathways within a small span of time and induce different morphological and physiological responses. In this experiment, different signaling molecules like ascorbic acid, salicylic acid, hydrogen peroxide and alpha-tocopherol were applied through foliar method at both pegging and pod formation stage and it was found that salicylic acid at 60 DAS @ 200 ppm (S4) increased the leaf area and chlorophyll fluorescence which also improved the leaf dry weight. It also increased the concentration of proline and antioxidant activity of catalase and super oxide dismutase which reduced the oxidative damage and drastic effect of different reactive oxygen species in plant cells. All these together enhanced the pod dry weight, which ultimately increased different yield attributes. Finally, it was concluded that treating plants with salicylic acid @ 200 ppm at 60 DAS (S_4) showed higher yield, whereas hydrogen peroxide @ 200 ppm at 60 DAS (S6) showed lesser yield as compared to other treatments.

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Authors' contributions

DM and BS conceptualized the manuscript. DM conducted the experiments. DM, SM, TV and AM wrote the manuscript. JKN, BP, SM and MS performed the analysis of data. BS, MS, SM and JKN edited and finalized the manuscript with the help of DM and JKN.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

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