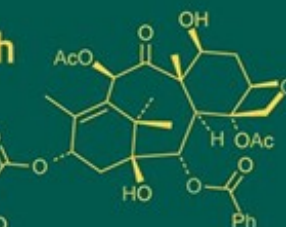


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Morphological and biochemical evaluation of foxtail millet (*Setaria italica*) varieties under moisture stress conditions

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ABSTRACT

The present study was carried out to assess the morphological and biochemical responses of two varieties of foxtail millet (*Setaria italica* (L.) P. Beauv.) viz. AAU GSG CAWN-1 (V_1) and Gossaigaon Local (V_2) under different levels of moisture stress and the mitigating effect of salicylic acid (SA). The experiment was carried out in the greenhouse condition of Assam Agricultural University, Jorhat in five irrigation treatments with three replications. Moisture stress severely affected plant growth and biochemical attributes with most severe effects in the treatment of complete withdrawal of irrigation (T_3). The height of plant under control conditions was 144.80 and 160.60 cm for V_1 and V_2 at 120 DAS respectively, while it decreased to 110.00 and 104.21 cm under T_3 . Similarly, the leaf area at 80 DAS decreased from 487.40 and 401.00 cm² under control to 184.00 and 213.50 cm² under T_3 . Chlorophyll an at 80 DAS was declined from 3.67 and 2.73 to 1.06 and 0.92 mg g⁻¹ FW while proline was increased from 2.49 and 1.45 to 3.87 and 3.56 mg g⁻¹ FW in V_1 and V_2 respectively. Similarly, under T_3 , MDA also increased significantly to 80.30 and 82.29 μ mol g⁻¹ FW compared to 20.20 and 20.86 μ mol g⁻¹ FW in control plants. The plant height was increased to 136.80 and 148.25 cm and leaf area to 241.30 and 296.40 cm² at respective stages by T_3 +SA. These effects were partially alleviated by application of SA. SA promoted growth and biochemical stability and inhibited drought-induced oxidative damage in foxtail millet.

Keywords: Foxtail millet, Moisture stress, Salicylic acid, Biochemical response, Stress mitigation

1. Introduction

Millets are a group of small seeded cereal grasses which do not shatter easily at maturity. The French word "mille," meaning thousand, is the origin of the word "millet" which suggests that a handful of millet contains thousands of grains (Taylor, 2019) [1]. Because of their long history of cultivation and consistent yield, these are frequently referred to as "heritage crops." Often referred to as "coarse cereals" these rainfed crops do best in arid and semi-arid regions of the world and are well-suited to marginal soil fertility and moisture conditions. With their many applications as food, feed, fodder, biofuels, and brewing, millets are the foundation of dryland agriculture. They benefit not only consumers but also farmers and the environment so these are referred to as "smart foods." The Government of India (GoI) took a step forward and submitted a proposal to the United Nations (UN) to declare 2018 as the National Year of Millets in an effort to promote millets and boost domestic production. require little to no purchased inputs. The Food and Agriculture Organization (FAO) declared the year 2023 the "International Year of Millets" after carefully considering India's position. As we face challenges like climate change and rising rates of obesity, millets offer a path toward a more sustainable and nutritious food system. Because of their resilience, millets have been dubbed "the ultimate famine insurance". Some types can remain edible for decades if stored properly.

Foxtail millet (*Setaria italica*) is a widely grown crop in arid and semi-arid regions for its short growth cycle and drought tolerance and is mainly grown as rainfed crop on marginal soils. It is cultivated on about 2.5 million ha worldwide, with 85–90% of the area in Asia, particularly China and India. In India its cultivation is predominantly in Andhra Pradesh, Karnataka and Tamil Nadu with some pockets in north-eastern states under rainfed and shifting cultivation systems (Brunda et al., 2014) [2]. The highest productivity was recorded in the year 2022 with production of 3.6 lakh tons from 1.52 lakh ha at 2363 kg ha⁻¹ in Andhra Pradesh (NABARD, 2023). Foxtail millet is known for nutritional and climate resilient properties, but has always received little attention due to the dominance of rice and wheat, low productivity and processing constraints (Upadhyaya et al., 2018) [3]. Popularly called Koni dhan in Assam. It is grown mainly in the tribal and rainfed upland areas, mainly in the Brahmaputra valley and adjoining hill districts. Its adaptability to subtropical conditions makes it a promising climate resilient crop.

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Millet is often referred to as “nutri-cereals” or “miracle grains” because of their higher nutritional and functional values compared to the major cereals (FAO, 2021; Saini *et al.*, 2021) [4]. Foxtail millet is a good source of protein, dietary fiber, carbohydrates, minerals, vitamins and bioactive compounds such as phenolic and phytic acids (Kumar *et al.*, 2016; Gowda *et al.*, 2022) [6, 5]. Its grains have 12–16% protein and 4–8% fat and appreciable quantities of iron, zinc, calcium and essential amino acids (Sachdev *et al.*, 2021; Yang *et al.*, 2022) [7, 8]. Foxtail millet is a high-fibre, low-glycemic index, gluten-free grain with antioxidant activities and is useful for diabetes, cardiovascular health, digestive system, and weight management (Mohammed *et al.*, 2009; Zhang *et al.*, 2024) [9, 10]. Its extensive nutritional profile also highlights its potential as a biofortification and climate resilient food crop (Hariprasanna, 2023) [11].

Climate change is increasing temperature variability, changing rainfall patterns, and intensifying water scarcity and extreme weather, which are major challenges to agricultural production (IPCC, 2021; Hoekstra *et al.*, 2012) [12]. Drought stress causes loss in yield by causing stomatal closure, reduced CO₂ assimilation, oxidative stress and disruption of photosynthetic and metabolic processes. These effects are alleviated by plants through the production of osmolytes such as proline, glycine betaine and trehalose that help in osmotic adjustment and cell protection. In addition, high temperature stress (>32–35 °C) disrupts physiological processes and may lower crop productivity by 10–40% during sensitive stages (Chakraborty *et al.*, 2025) [13]. The climate-resilient nature of foxtail millet growth, yield and grain quality is under threat due to drought and unpredictable rainfall patterns especially in rainfed systems. These stresses are of concern to the rainfed and tribal farming communities in Assam and could be exacerbated under combined stress conditions (Swain *et al.*, 2024; Terfa *et al.*, 2025) [14, 15]. Water stress during vegetative growth reduces the tillering, but drought at reproductive phase increases the number of unfilled grains and significantly reduces the yield (Terfa *et al.*, 2025) [15]. Therefore, understanding these responses is important for developing climate-resilient foxtail millet production systems.

Foxtail millet is generally cultivated under rainfed circumstances by marginal farmers and can incur large yield losses under drought stress. Although it demonstrates C₄ metabolism, deep root system and antioxidant and osmolyte defenses provide great climate tolerance. Its biochemical reactions to drought particularly in local Assam landraces are little characterized. Therefore, the present study was undertaken to examine the physiological and biochemical responses of foxtail millet to drought stress addressing an essential research need under changing climatic conditions along with application of Salicylic Acid for its mitigation.

2. Material and methods

2.1 Plant material, experimental site and drought stress

Two varieties of foxtail millet (*Setaria italica* (L.) P. Beauv.) namely AAU GSG CAWN-1 (white seeded) and Gossaigaon Local (red seeded) procured from Assam Agricultural University, Zonal Research Station, Gossaigaon were tested under drought stress conditions. The experiment was carried out at the ICR Farm, Assam Agricultural University, Jorhat (26°41'N, 94°19'E; 86.6 m amsl) in 2024 in a greenhouse. In the experiment temperature and relative humidity varied between 12.5–36.5 °C and 69.84–94.36 %, respectively. Irrigation was scheduled based on crop evapotranspiration (ET_c) calculated as $ET_c = K_c \times ET_o$, where K_c is the crop coefficient and ET_o is reference evapotranspiration.

2.2 Details of treatment

Five treatments were applied: T_1 , normal irrigation (ET_c); T_2 , 50% irrigation; T_3 , no irrigation; T_4 , 50% irrigation + SA; and T_5 , no irrigation + SA, with two varieties and three replications.

2.3 Seed priming and application of SA

Seeds were primed in 1 mM salicylic acid (SA) and control seeds were soaked in distilled water for same duration and shade dried before sowing. Foliar application of 1 mM SA was performed at 40 and 60 DAS as per Yadav *et al.* (2020) [16].

2.4 Morphological and germination characteristics

Plant height was measured at 40, 80 and 120 days after sowing (DAS), while tillers and panicles plant⁻¹ were recorded at 40 and 80 DAS. Leaf area was calculated as length x maximum width x 0.75.

2.5 Chemical analysis

Chlorophyll a and b were determined by the DMSO method of Hiscox *et al.* (1979) [17]. Leaf samples were incubated at 65 °C for 4 h in DMSO and absorbance was measured at 645 and 663 nm. Contents were calculated according to Arnon (1949) [18] and expressed as mg g⁻¹ FW.

Proline was estimated by method of Bates *et al.* (1973) [19] using 3% sulfosalicylic acid, acid ninhydrin and glacial acetic acid. Absorbance was read at 520 nm after extraction with toluene and content was expressed as μmol g⁻¹ FW.

MDA was measured as an index of lipid peroxidation according to Heath *et al.* (1968) [20]. Leaf extracts were treated with TCA–TBA and heated at 95 °C for 30 min and absorbance was measured at 532 nm corrected at 600 nm. MDA content expressed as μmol g⁻¹ FW.

Crude fat was determined by Soxhlet extraction with petroleum ether (40–60 °C) for 6–8 h (AOAC 920.39). After extraction the solvent was removed and the extracted lipid in the flask was dried at 100–105 °C for 30 min, cooled in a desiccator and weighed. The crude fat content was calculated from the increase in flask weight and expressed as a percentage of the sample weight.

Total carbohydrate was determined by the anthrone method of Hedge *et al.* (1962) [21]. The finely ground sample (100 mg) was hydrolyzed with 5 mL 2.5 N HCl in boiling water bath for 3 h, cooled, neutralized with sodium carbonate, made up to 100 mL and centrifuged at 10,000 rpm for 15 min. An aliquot (0.5 mL) was mixed with 4 mL of anthrone reagent (200 mg anthrone in 100 mL ice-cold 95% H₂SO₄) and heated in a boiling water bath for 5 min. Absorbance was measured at 630 nm with glucose standards (10–100 μg) and carbohydrate content was expressed as percentage on dry weight.

Crude protein was analyzed by Kjeldahl method (AOAC 979.09) 0.5–1.0 g sample was digested with concentrated H₂SO₄ and Kjeldahl catalyst at 380–420 °C until clear, followed by dilution and distillation with 40% NaOH. The liberated ammonia was absorbed in 4% boric acid containing mixed indicator and titrated against 0.1 N HCl. Nitrogen content was calculated from sample and blank titre values. Crude protein was calculated by multiplying the nitrogen content by 6.25 and expressed in percentage on dry-weight basis.

3. Result and discussion morphological characteristics under moisture stress

Moisture stress significantly decreased the growth and yield related morphological traits of both the foxtail millet varieties while salicylic acid (SA) alleviated these effects to a certain degree. Maximum plant height was recorded in T_1 (normal irrigation) at 40, 80 and 120 DAS (52.72, 142.80 and 144.80 cm in V_1 ; 66.30, 156.60 and 160.60 cm in V_2 , respectively). Maximum reduction in plant height was observed in T_3 (complete withdrawal of irrigation) (37.83, 106.00 and 110.00 cm in V_1 ; 27.21, 95.60 and 104.21 cm in V_2). The application of SA improved the plant height under stress, particularly at later stages, where T_3 +SA achieved 136.80 cm in V_1 and 148.25 cm in V_2 at 120 DAS. Similar trend was observed in the production of tiller and panicle

which was decreased under moisture stress and lowest values were obtained in T_3 . The application of SA improved their formation especially at 80 DAS. At 80 DAS, control plants recorded 6.10 and 6.24 tillers and 9.07 and 8.32 panicles plant⁻¹ in V_1 and V_2 , respectively, as against 4.12 and 4.85 tillers and 5.02 and 4.75 panicles plant⁻¹ under T_3 . SA increased these values to 5.64 and 5.26 tillers and 5.72 and 6.29 panicles plant⁻¹, respectively. Leaf area was also significantly reduced by moisture stress, particularly under T_3 , from 487.40 and 401.00 cm² in control plants to 184.00 and 213.50 cm² at 80 DAS in V_1 and V_2 , respectively. SA application partially recovered the leaf expansion; T_3 +SA had 241.30 and 296.40 cm². In general, water stress affected cell growth, photosynthetic assimilation and vegetative/reproductive development, while SA was involved in plant growth and leaf development under water deficit in agreement with previous reports (Yadav *et al.*, 2020; Rehman *et al.*, 2021; Li *et al.*, 2021; Jamode *et al.*, 2024) [16, 22].

2. Biochemical characteristics under moisture stress

The contents of chlorophyll a and b were decreased under moisture stress in both the varieties of foxtail millet, and the maximum reduction was observed under complete irrigation withdrawal (T_3). These effects were somewhat alleviated by salicylic acid (SA). Chlorophyll a decreased from 1.61 and 1.54 mg g⁻¹ FW under control to 1.41 and 1.28 mg g⁻¹ FW under T_3 in V_1 and V_2 , respectively, while chlorophyll b decreased from 0.74 and 0.71 to 0.51 and 0.59 mg g⁻¹ FW at 40 DAS, respectively. The control plants at 80 DAS had 3.67 and 2.73 mg g⁻¹ FW chlorophyll a and 1.74 and 1.71 mg g⁻¹ FW chlorophyll b, respectively, which were reduced to 1.06 and 0.92 and 0.51 and 0.59 mg g⁻¹ FW, respectively, in T_3 . SA application enhanced pigment retention under stress, T_3 +SA led to increase in chlorophyll a to 2.30 and 2.36 mg g⁻¹ FW and chlorophyll b to 1.48 and 1.60 mg g⁻¹ FW at 80 DAS in V_1 and V_2 respectively. The reduction in chlorophyll due to moisture stress could be either due to reduced biosynthesis or enhanced degradation of chlorophyll or oxidative damages to chloroplasts. SA may regulate the biosynthesis of chlorophyll as well as help protect the photosynthetic machinery through improved antioxidant defense and reduced ROS induced damages. Similar responses were also observed in foxtail millet and other cereals under drought stress (Yadav *et al.*, 2020; Li *et al.*, 2021; Rehman *et al.*, 2021; Khan *et al.*, 2023) [16, 22].

The proline and malondialdehyde (MDA) contents were significantly affected by moisture stress in both foxtail millet varieties, and the

most significant effects were observed under complete irrigation withdrawal (T_3), whereas the effects were mitigated by salicylic acid (SA). Proline increased from 1.00 and 0.74 mg g⁻¹ FW under control to 1.76 and 1.16 mg g⁻¹ FW under T_3 in V_1 and V_2 respectively at 40 DAS and further increased at 80 DAS to 3.87 and 3.56 mg g⁻¹ FW compared to 2.49 and 1.45 mg g⁻¹ FW in controls. SA reduced the accumulation of proline due to stress. T_3 +SA recorded 2.14 and 2.24 mg g⁻¹ FW at 80 DAS. In contrast, MDA was increased significantly under drought from 20.20 and 20.86 μ mol g⁻¹ FW in control to 80.30 and 82.29 μ mol g⁻¹ FW under T_3 at 40 and 80 DAS, respectively. SA application reduced MDA accumulation especially in severe stress condition, where T_3 +SA showed 54.30 and 50.19 μ mol g⁻¹ FW at 40 and 80 DAS respectively. The increase in proline indicates osmotic adjustment and stress adaptation while the increase in MDA indicates increased ROS induced lipid peroxidation and membrane damage. The SA-induced reduction in MDA and proline accumulation regulation might be associated with better water status and antioxidant defense, thus contributing to the maintenance of membrane integrity under drought stress. Similar responses to water deficit have been reported in cereal crops (Farooq *et al.*, 2022; Hafez, 2022; Urmi *et al.*, 2023; Kaur *et al.*, 2024).

Moisture stress decreased crude fat, total carbohydrate and crude protein contents of leaves of both foxtail millet varieties, while salicylic acid (SA) partially alleviated these reductions. The control plants at 40 DAS showed the highest crude fat (4.87 and 4.43 %), total carbohydrate (64.50 and 68.02 %) and crude protein (10.91 and 11.15 %) in V_1 and V_2 , respectively, whereas complete irrigation withdrawal (T_3) decreased these values to 3.98 and 3.80 %, 45.85 and 60.66 %, and 3.80 and 9.50 %, respectively. Reductions were more severe at 80 DAS, particularly under T_3 , where crude fat was reduced to 1.21 and 2.12 %, carbohydrate to 48.45 and 48.15 % and protein to 10.56 and 10.25 % in V_1 and V_2 , respectively as compared with higher values under control conditions. SA application partially restored these biochemical constituents. At 80 DAS, T_3 +SA increased crude fat to 3.55 and 2.22, carbohydrate to 38.15 and 50.12 and protein to 11.25 and 11.98 % in V_1 and V_2 respectively. Under moisture stress the reductions may be due to impaired photosynthetic carbon assimilation, reduced nutrient uptake and disruption of lipid and protein metabolism. SA may help to maintain metabolic activity through improved stress tolerance. Similar effects of drought stress on nutritional and metabolic constituents have been reported in millets and cereals (Harish *et al.*, 2024).

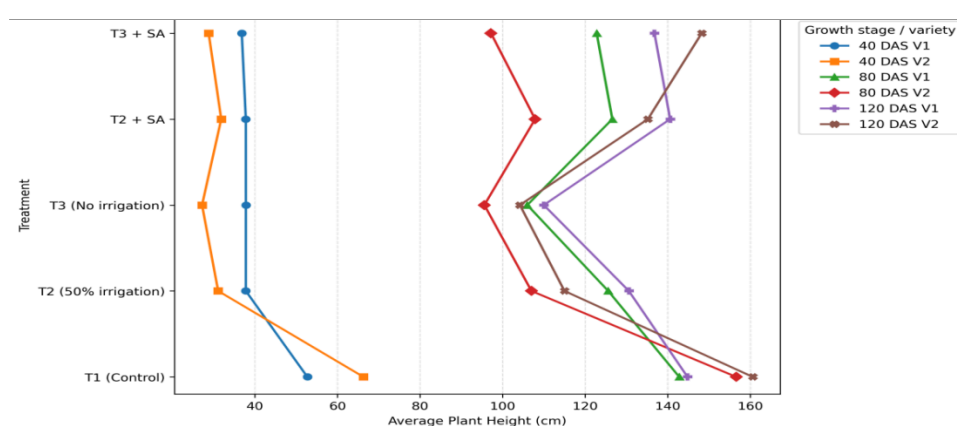


Figure 3.1. Plant height under different treatments

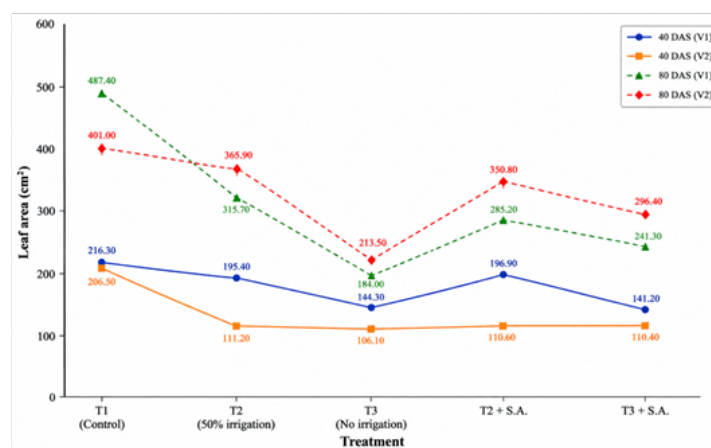


Figure 3.2. Leaf area under different treatments

Table 3.1. Number of tillers and panicles under different treatments

Treatment	40 DAS		80 DAS		40 DAS		80 DAS	
	Average number of tillers/plant				Average number of panicles/plant			
	V1	V2	V1	V2	V1	V2	V1	V2
T_1 (Control)	5.72	6.32	6.10	6.24	6.19	6.98	9.07	8.32
T_2 (50% irrigation)	3.83	3.11	4.76	5.00	3.25	3.59	5.22	7.16
T_3 (no irrigation)	3.82	2.21	4.12	4.85	3.32	2.45	5.02	4.75
T_2 + S.A.	3.81	3.86	5.55	5.65	4.75	4.39	6.94	7.43
T_3 + S.A.	3.83	2.81	5.64	5.26	3.76	3.72	5.72	6.29
CD $_{0.05}$ (A)	1.424		0.42		0.572		NS	
SEm ($\pm$) (A)	0.479		0.141		0.193		0.821	
CD $_{0.05}$ (B)	NS		0.266		0.823		NS	
SEm ($\pm$) (B)	0.303		0.089		0.122		0.862	
CD $_{0.05}$ (A x B)	2.014		0.594		0.809		NS	
SEm ($\pm$) (A x B)	0.678		0.2		0.272		1.162	

NB: A=Treatment B=Variety

Table 3.2. Chlorophyll 'a' and Chlorophyll 'b' content

Treatment	40 DAS		80 DAS		40 DAS		80 DAS	
	Chlorophyll 'a' (mg/g fw)				Chlorophyll 'b' (mg/g fw)			
	V1	V2	V1	V2	V1	V2	V1	V2
T_1 (Control)	1.61	1.54	3.67	2.73	0.74	0.71	1.74	1.71
T_2 (50% irrigation)	1.52	1.42	1.26	1.91	0.58	0.61	0.58	0.61
T_3 (no irrigation)	1.41	1.28	1.06	0.92	0.51	0.59	0.51	0.59
T_2 + S.A.	1.55	1.48	2.48	2.87	0.53	0.62	1.53	1.62
T_3 + S.A.	1.50	1.30	2.30	2.36	0.48	0.61	1.48	1.60
CD _{0.05} (A)	0.258		NS		0.079		0.078	
SEm (±) (A)	0.087		0.082		0.026		0.019	
CD _{0.05} (B)	0.163		NS		NS		NS	
SEm (±) (B)	0.055		0.082		0.017		0.019	
CD _{0.05} (A x B)	0.365		0.382		0.111		NS	
SEm (±) (A x B)	0.123		0.115		0.037		0.027	

NB: A=Treatment B=Variety

(continued on next page)

Table 3.3. Change in proline and Melonaldehyde content under different treatments

Treatment	Proline content (mg/g fw)				Melonaldehyde content (μ mole/g fw)			
	40 DAS		80 DAS		80 DAS		Fold change	Fold change
	V1	V2	V1	V2	V1	Fold change		
T_1 (Control)	1.00	0.74	2.49	1.45	20.20		20.86	
T_2 (50% irrigation)	1.26	0.78	3.24	3.21	35.28	1.74	49.26	2.36
T_3 (no irrigation)	1.76	1.16	3.87	3.56	80.30	3.97	82.29	1.67
T_2 + S.A.	0.67	0.98	1.65	1.25	31.93	1.58	48.62	0.59
T_3 + S.A.	0.37	1.22	2.14	2.24	54.30	2.68	50.19	1.03
CD _{0.05} (A)	0.418		NS				7.12	
SEm (±) (A)	0.141		0.163				2.216	
CD _{0.05} (B)	0.537		0.541				7.66	
SEm (±) (B)	0.089		0.163				2.274	
CD _{0.05} (A x B)	0.592		0.765				10.51	
SEm (±) (A x B)	0.199		0.231				3.194	

NB: A=Treatment B=Variety

Table 3.4. Crude fat, Total carbohydrate and Crude protein content

Treatment	Crude fat (% dw)				Total carbohydrate (% dw)				Crude protein (% dw)			
	40 DAS		80 DAS		40 DAS		80 DAS		40 DAS		80 DAS	
	V1	V2	V1	V2	V1	V2	V1	V2	V1	V2	V1	V2
T_1 (Control)	4.87	4.43	5.60	4.98	64.50	68.02	50.41	58.36	10.91	11.15	13.30	12.47
T_2 (50% irrigation)	4.33	4.40	2.41	3.14	50.45	62.13	35.16	41.20	6.45	9.96	12.52	10.65
T_3 (no irrigation)	3.98	3.80	1.21	2.12	45.85	60.66	48.45	48.15	3.80	9.50	10.56	10.25
T_2 + S.A.	4.65	4.46	4.58	4.11	51.23	62.50	44.14	56.11	9.50	11.15	12.68	11.58
T_3 + S.A.	4.12	4.18	3.55	2.22	50.07	62.60	38.15	50.12	8.30	11.10	11.25	11.98
CD _{0.05} (A)	0.081		1.297		0.061		0.097		0.133		0.067	
SEm ($\pm$) (A)	0.027		0.392		0.021		0.029		0.044		0.02	
CD _{0.05} (B)	0.051		1.293		0.039		0.097		0.082		0.067	
SEm ($\pm$) (B)	0.017		0.392		0.013		0.026		0.028		0.02	
CD _{0.05} (A x B)	0.114		NS		0.087		0.134		0.184		0.094	
SEm ($\pm$) (A x B)	0.038		0.554		0.029		0.041		0.062		0.028	

NB: A=Treatment B=Variety

Conclusion

The study revealed significant effect of moisture stress on morphological and biochemical performance of two foxtail millet varieties. Complete withdrawal of irrigation resulted in highest reductions of plant height, tillering, panicle formation, leaf area, chlorophyll, carbohydrate, crude fat and protein contents. Conversely, proline and MDA increased under severe moisture stress indicating osmotic adjustment and oxidative membrane damage. Application of salicylic acid partially alleviated these detrimental effects by improving plant growth, leaf expansion and chlorophyll retention and reducing MDA accumulation. The responses observed in AAU GSG CAWN-1 and Gossagaon Local suggest that SA can help in the maintenance of physiological and biochemical stability of foxtail millet under moisture-deficit conditions.

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