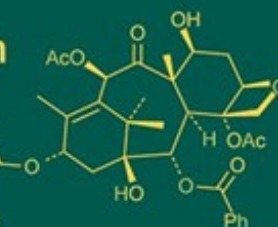
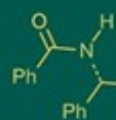


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Assessment of heat stress responses and salicylic acid mediated mitigation in foxtail millet (*Setaria italica*)

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ABSTRACT

High temperature stress is a major constraint to crop productivity in changing climatic conditions. Foxtail millet (*Setaria italica* (L.) P. Beauv.) is a climate-resilient C4 cereal. There might be varietal differences in tolerance to high temperature. The present investigation was carried out to evaluate the morphological and biochemical responses of two varieties of foxtail millet, AAU GSG CAWN-1 (white seeded) and Gossaigaon Local (red seeded) under elevated temperature stress and salicylic acid (SA) treatment. The experiment was carried out in a greenhouse at Assam Agricultural University, Jorhat during 2024 with three treatments namely ambient temperature (T_1), ambient temperature + 2 °C (T_2) and ambient temperature + 2 °C with SA application (T_3). At different stages of plant growth, the growth of the plants, photosynthetic pigments, proline, malondialdehyde (MDA), crude fat, total carbohydrates and crude protein were evaluated. Higher temperature negatively affected the growth and biochemical attributes of plants. At 80 DAS, chlorophyll a decreased from 3.18 to 1.55 mg g⁻¹ fresh weight (FW) and 3.29 to 1.55 mg g⁻¹ FW in AAU GSG CAWN-1 and Gossaigaon Local respectively. The proline content in white-seeded variety was 1.85 mg g⁻¹ FW at 40 DAS under elevated temperature. MDA increased from 19.30 to 50.33 μmol g⁻¹ FW at 80 DAS in AAU GSG CAWN-1 and from 29.21 to 67.30 μmol g⁻¹ FW in Gossaigaon Local. SA treatment decreased MDA to 35.84 μmol g⁻¹ FW and 45.96 μmol g⁻¹ FW, respectively. The crude protein decreased to 10.88% and 10.61% in the two varieties, respectively, under elevated temperature, and SA treatment partially recovered it. In general SA partially alleviated heat associated biochemical damage, although responses were variety and growth stage dependent.

Keywords: Foxtail millet, Elevated temperature, Salicylic acid, Chlorophyll, Proline, Malondialdehyde, Biochemical responses

Introduction

Climate change poses a serious challenge to agricultural productivity, as rising temperatures increasingly affect crop growth, development and yield. High temperature stress is a condition when the environmental temperature is outside the optimum range for normal plant growth and physiological functioning. Photosynthesis, respiration, membrane stability, enzyme activity and reproductive development can be disrupted by heat stress, eventually resulting in reduced crop productivity. Its effects depend on the intensity and duration of exposure, crop species, developmental stage and prevailing environmental condition. Temperature extremes during flowering and grain filling are of particular concern as they can impair reproductive success and reduce the time available for grain development (IPCC, 2021; Chakraborty *et al.*, 2025) [1].

Foxtail millet (*Setaria italica* (L.) P. Beauv.) is an important C4 cereal crop with a short growing duration, nutritional value and adaptability to diverse agro-ecological conditions. Its C4 photosynthetic pathway confers an advantage under warm environments by concentrating CO₂ around the enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) and thus reducing photorespiratory losses under suitable conditions. But this adaptation does not fully protect against severe or prolonged heat stress. Cardinal temperatures for foxtail millet are reported to be ~9.3 °C (base), 37 °C (optimum) and 46 °C (ceiling), but responses may vary depending on genotype and growth stage (Choudhary *et al.*, 2023) [2]. The high temperatures for a long time, especially when daily temperatures are above 35–38 °C and night temperatures are high, can affect the vegetative growth, reproductive development and grain production.

Physiologically high temperature stress can affect the photosynthetic efficiency by disrupting the chloroplast function, altering the photosynthetic enzymes and encouraging the degradation of chlorophyll. Heat-induced damage to RuBisCO activase can inhibit RuBisCO activation and regeneration and thus limit carbon fixation. Interference with cellular metabolism and higher respiratory activity may further limit the availability of assimilates for growth and grain development. Heat stress may also induce the generation of reactive oxygen species (ROS) that result in oxidative damage to membranes, proteins and other cellular components.

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Plants respond by antioxidant defense systems and accumulation or regulation of protective metabolites such as proline and phenolic compounds. The degree to which these mechanisms maintain cellular integrity under high temperature conditions may underlay differences in heat tolerance between genotypes ((Hariprasanna, 2023) [3].

High temperatures and low temperatures are especially damaging to reproductive development. High temperatures may affect pollen viability, pollen germination, fertilization and grain setting, and faster crop development may shorten the duration of grain filling. Such effects can cause a reduction in the number of successfully developed grains and finally a yield decrease. Foxtail millet is generally considered tolerant to heat compared to many cereal grains, however, its response to prolonged high temperature and associated biochemical changes are still important areas of investigation, particularly in field conditions where temperature fluctuations can be quite large (Mohammed *et al.*, 2009; Zhang *et al.*, 2024) [4, 5].

The increasing variability of temperature may pose a challenge to crop productivity in Assam where foxtail millet is grown in rainfed and upland farming systems. Local varieties may vary in their ability to maintain growth, photosynthetic pigments and metabolic stability under heat stress. However, physiological and biochemical responses of locally relevant foxtail millet varieties to elevated temperature are not well characterized (Swain *et al.*, 2024; Terfa *et al.*, 2025) [6, 7]. The present study was aimed to evaluate the morphological and biochemical responses of two foxtail millet varieties under high-temperature stress. Special emphasis was given on plant growth, photosynthetic pigments and stress-associated metabolic changes. The findings may contribute to a better understanding of varietal responses and support the development of heat-resilient foxtail millet production strategies under changing climatic conditions.

2. Materials and method 2.1 Cultivars, site of the experiment and Temperature stress

Two varieties of foxtail millet (*Setaria italica* (L.) P. Beauv.), AAU GSG CAWN-1 (white seeded) and Gossaigaon Local (red seeded) collected from the Zonal Research Station, Assam Agricultural University, Gossaigaon were evaluated under high temperature stress conditions. The experiment was conducted in a greenhouse at the Instructional-Cum-Research Farm, Assam Agricultural University, Jorhat (26°41'N, 94°19'E; 86.6 m above mean sea level) during the year 2024. The temperature and relative humidity during the experimental period ranged from 12.5 to 36.5 °C and 69.84 to 94.36%, respectively. Temperature stress analysis specimens were housed in a temporary polyhouse inside the main greenhouse. The temperature inside this makeshift greenhouse was always 2° higher than the outside air temperature.

2.2 Treatments used for the experiment

Two varieties of foxtail millet were subjected to three high temperature and salicylic acid (SA) treatments and three replications per treatment. The treatments were T_1 , Ambient temperature; T_2 , Ambient temperature + 2 °C; T_3 , Ambient temperature + 2 °C + Salicylic acid

2.3 Method for application of salicylic acid Seeds were primed in 1 mM salicylic acid (SA) solution before sowing, while control seeds were soaked in distilled water for the same duration. Seeds were shade-dried to original moisture content after priming before sowing. The foliar application of 1 mM SA was carried out at 40 and 60 DAS as per the procedure described by Yadav *et al.* (2020) [8].

2.4 Characteristics of morphology and germination Plant height was assessed at 40, 80, and 120 days post-sowing (DAS), whilst tillers and panicles per plant were documented at 40 and 80 DAS. The leaf area was determined by multiplying the length by the maximum width and then by 0.75. **2.5 Biochemical analysis** Chlorophyll 'a' and 'b' were quantified using the DMSO technique established by Hiscox *et al.* (1979) [9]. Leaf samples were incubated at 65 °C for 4 h in DMSO and absorbance was measured at 645 and 663 nm. The contents were determined following Arnon (1949) [10] and shown as mg g⁻¹ FW. Proline was quantified by the technique established by Bates *et al.* (1973) [11], which involved 3% sulfosalicylic acid, acid ninhydrin, and glacial acetic acid. Absorbance was read at 520 nm following extraction with toluene and concentration was reported as μmol g⁻¹ FW. MDA was tested as an indicator of lipid peroxidation according to

Heath *et al.* (1968) [12]. Leaf extracts were treated with TCA–TBA and heated at 95 °C for 30 min and absorbance was measured at 532 nm adjusted at 600 nm. MDA content reported as μmol g⁻¹ FW. Crude fat was evaluated by Soxhlet extraction with petroleum ether (40–60 °C) for 6–8 h (AOAC 920.39). After extraction the solvent was withdrawn 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 estimated from the increase in flask weight and reported as a percentage of the sample weight. Total carbohydrate was assessed by the anthrone technique of Hedge *et al.* (1962) [13]. The finely ground material (100 mg) was hydrolyzed with 5 mL 2.5 N HCl in boiling water bath for 3h, 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 combined with 4 mL of anthrone reagent (200 mg anthrone in 100 mL ice-cold 95% H₂SO₄) and cooked in a boiling water bath for 5 min. Absorbance was measured at 630 nm with glucose standards (10–100 μg) and carbohydrate content was given as percentage on dry weight. Crude protein was evaluated by Kjeldahl technique (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 released ammonia was absorbed in 4% boric acid containing mixed indicator and titrated against 0.1 N HCl. Nitrogen content was determined from sample and blank titre readings. Crude protein was estimated by multiplying the nitrogen concentration by 6.25 and expressed in percentage on dry-weight basis.

3. Result and discussion Morphological changes associated with high temperature stress

The effect of growth stages and varieties on plant height, tiller number, panicle number and leaf area of foxtail millet under elevated temperature was different. Plant height varied from 56.20 to 66.00 cm at 40 DAS, with V_2 showing maximum height under normal temperature (T_1) and decreased height under elevated temperature (T_2 ; normal temperature + 2 °C) in both varieties. The application of salicylic acid (SA) (T_3) partially improved early plant growth. Plant height was ranged from 123.60 to 159.30 cm at 80 DAS. V_2 gave maximum plant height at T_3 and V_1 gave minimum plant height at T_2 . However, the plant height under elevated temperature was still lesser than normal at 120 DAS indicating the adverse effect of prolonged heat exposure. Tiller number ranged from 4.89 to 9.78 plant⁻¹ at 40 DAS and 2.41 to 4.66 plant⁻¹ at 80 DAS. In some treatment-variety combinations the tillering increased at the early stage with the elevated temperature, but the response was not consistent at the later stage. The number of panicles also differed among treatments and varieties, with significant varietal or interaction effects at certain growth stages. These changes may be related to a temperature-induced change in meristematic activity, assimilate availability and the change from vegetative to reproductive growth (Zenda *et al.*, 2022) [14]. The differential response of the two varieties indicates that there is genotypic variation in growth and reproductive development under elevated temperature (Chen *et al.*, 2023; He *et al.*, 2022) [15, 16]. In both varieties, leaf area increased from 40 to 80 DAS, which is in agreement with the progressive leaf expansion and canopy development. At 40 DAS leaf area was between 133.30–218.00 cm² with maximum in V_1 at T_2 and minimum in V_1 at T_3 . The leaf area ranged from 466.90 to 663.90 cm² at 80 DAS with maximum leaf area obtained in V_1 under normal temperature and the minimum leaf area under elevated-temperature treatments. The reduction in leaf area in some treatments could be due to limited cell expansion, altered plant water relations, impaired photosynthesis and accelerated leaf senescence. High temperature can also increase respiratory demand and oxidative stress possibly limiting assimilate availability for shoot and reproductive development. SA application had varying impact on different traits, varieties, and growth stages indicating that the protective effect of SA was dependent on stress duration and plant developmental stage. The positive effects of SA can be related to the enhanced antioxidant defense, membrane stability and photosynthetic functioning (Altaf *et al.*, 2023; Chen *et al.*, 2023) [17, 15]. Overall, vegetative growth, tillering, panicle development and leaf expansion were influ

enced by high temperature. Varietal differences showed differential responses to heat stress. The differential response to SA suggests that the efficacy of SA needs to be tested at development stages and genotypes. **Biochemical changes associated with high temperature stress** The contents of chlorophyll 'a' and 'b' in foxtail millet were affected by the temperature treatment, variety and growth stage. At 80 DAS, generally both the pigments were higher in normal temperature condition and decreased in elevated temperature condition indicating possible impairment of photosynthetic apparatus. Salicylic acid (SA) partially improved pigment retention under heat stress suggesting a protective effect. High temperature can accelerate chlorophyll degradation by damaging chloroplasts and increasing the production of reactive oxygen species (ROS) (Sun *et al.*, 2023; Malaweera *et al.*, 2024) [18, 19]. The positive effect of SA could be related to enhanced antioxidant defense and protection of chloroplast membranes (Sangwan *et al.*, 2022; Hilal *et al.*, 2024) [21, 20]. The differences in responses to prolonged heat stress among the varieties and growth stages indicate that chlorophyll retention is a useful physiological indicator to assess temperature tolerance in foxtail millet. The content of proline and malondialdehyde (MDA) in foxtail millet leaves was different under the treatment of elevated temperature and salicylic acid (SA). Proline (mg g⁻¹ FW, 40 DAS) ranged from 0.59 to 1.85, with the maximum in V₁ under T₂, while (mg g⁻¹ FW, 80 DAS) ranged from 0.88 to 1.38. MDA increased significantly under high temperature at 80 DAS from 19.30 to 50.33 μmol g⁻¹ FW in V₁ and from 29.21 to 67.30 μmol g⁻¹ FW in V₂. Application of SA decreased MDA to 35.84 and 45.96 μmol g⁻¹ FW in V₁ and V₂, respectively. The increase in proline accumulation indicates an osmotic and protective response to heat stress, while the increase in MDA indicates increased lipid peroxidation and membrane damage (Hasanuzzaman *et al.*, 2020; Tokić *et al.*, 2023) [22, 23]. The decreased MDA content after SA treatment indicates that SA may reduce oxidative damage by enhancing antioxidant defense and preserving membrane stability (Sangwan *et al.*, 2022; Eswaran *et al.*, 2024) [21, 24]. Overall, the combined responses of proline and MDA suggested that high temperature induced both protective biochemical responses and oxidative stress, and SA relieved heat-induced membrane damage to a certain

degree. Crude fat, total carbohydrate and crude protein contents of foxtail millet leaves varied with temperature treatment, variety and growth stage. Crude fat ranged from 3.99 to 4.83% at 40 DAS and from 2.77 to 5.24% at 80 DAS with higher values generally found at normal temperature. Elevated temperature reduced total carbohydrate content (48.19 to 62.55% at 40 DAS and 36.93 to 71.81% at 80 DAS). The crude protein content also decreased with increased temperature at 80 DAS from 14.14 and 15.51 % under normal conditions to 10.88 and 10.61% in V₁ and V₂ respectively. Application of Salicylic acid (SA) partially restored the carbohydrate and protein contents by increasing to 56.62 and 54.26 % for carbohydrate and 12.09 and 13.46 % for protein in V₁ and V₂, respectively. These decreases under heat stress may be attributed to impaired photosynthesis, increased respiratory demand, altered membrane lipid metabolism and disruption of protein synthesis and turnover (Hancock *et al.*, 2014; Seydel *et al.*, 2022; Choudhary *et al.*, 2024) [26, 27, 25]. The partial improvement after SA treatment could be related to its role in preserving the photosynthetic activity, membrane stability and stress-responsive metabolism (Sangwan *et al.*, 2022) [21]. Varietal differences reflect genotypic variation in the ability to maintain metabolic stability under elevated temperature. To summarize, heat stress had negative effects on the metabolism of carbohydrates, lipids and proteins, and SA was able to mitigate this effect to a certain degree, especially in the accumulation of carbohydrates and proteins. **Conclusion** Results of the study showed that elevated temperature (+2 °C) negatively affected the morphological and biochemical traits of both varieties of foxtail millet. Heat stress reduced the content of chlorophyll, crude fat, carbohydrates and protein, while increased proline accumulation and MDA content, indicating physiological stress and oxidative membrane damage. Application of salicylic acid (SA) ameliorated these effects somewhat by improving pigment retention, biochemical attributes and decreasing MDA accumulation. The protective potential of MDA was observed in the decline of the MDA from 50.33 to 35.84 μmol g⁻¹ FW in AAU GSG CAWN-1 and 67.30 to 45.96 μmol g⁻¹ FW in Gossaigaon Local. In general, SA may be beneficial for foxtail millet heat stress management. Table 3.1. Change in height of the plant under different treatments

Treatment	40 DAS		80 DAS		120 DAS	
	V1	V2	V1	V2	V1	V2
T ₁ (normal temp.)	65.60	66.00	135.60	158.70	144.80	160.60
T ₂ (normal temp. + 2 °C)	60.30	56.20	123.60	142.70	130.60	115.00
T ₃ (T ₂ + S.A.)	61.60	62.60	151.20	159.30	110.00	104.21
CD _{0.05} (A)	3.15		9.686		0.068	
SEm (±) (A)	1.012		3.109		0.022	
CD _{0.05} (B)	NS		NS		0.056	
SEm (±) (B)	0.826		2.539		0.018	
CD _{0.05} (A x B)	4.46		NS		0.096	
SEm (±) (A x B)	1.432		4.397		0.031	

NB: A=Treatment B=Variety

Table 3.2. Tiller number and number of panicles under different treatment

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 (±) (A)	0.479		0.141		0.193		0.821	

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CD _{0.05} (B)	NS	0.266	0.823	NS
SEm (±) (B)	0.303	0.089	0.122	0.862
CD _{0.05} (A x B)	2.014	0.594	0.809	NS
SEm (±) (A x B)	0.678	0.2	0.272	1.162

NB: A=Treatment B=Variety

Table 3.3. Leaf area under different treatments

Treatment	Leaf area (cm ²)			
	40 DAS		80 DAS	
	V1	V2	V1	V2
T ₁ (normal temp.)	173.40	141.40	663.90	566.50
T ₂ (normal temp. + 2 °C)	218.00	214.50	466.90	513.00
T ₃ (T ₂ + S.A.)	133.30	178.00	486.40	521.20
CD _{0.05} (A)	0.122		0.57	
SEm (±) (A)	0.039		0.183	
CD _{0.05} (B)	0.1		0.466	
SEm (±) (B)	0.032		0.149	
CD _{0.05} (A x B)	0.173		0.807	
SEm (±) (A x B)	0.055		0.259	

NB: A=Treatment B=Variety

Table 3.4. Chlorophyll 'a' and 'b' content in different treatment under temperature stress

Treatment	Chlorophyll 'a'				Chlorophyll 'b'			
	40DAS		80DAS		40 DAS		80DAS	
	V1	V2	V1	V2	V1	V2	V1	V2
T ₁ (normal temp.)	1.65	1.57	3.18	3.29	0.85	0.75	0.64	0.64
T ₂ (normal temp. + 2 °C)	3.28	2.92	1.55	1.55	0.64	0.60	0.37	0.31
T ₃ (T ₂ + S.A.)	2.91	1.96	2.17	2.61	0.55	0.56	0.48	0.50
CD _{0.05} (A)	0.121		0.271		0.101		0.051	
SEm (±) (A)	0.039		0.087		0.032		0.015	
CD _{0.05} (B)	0.099		0.221		NS		0.051	
SEm (±) (B)	0.032		0.071		0.026		0.015	
CD _{0.05} (A x B)	0.171		0.383		NS		0.69	
SEm (±) (A x B)	0.055		0.123		0.143		0.208	

NB: A=Treatment B=Variety

Table 3.5. Content of Proline (mg/g fw) and Melonaldehyde (MDA) (μ mole/g fw) for membrane stability in foxtail millet plants under different treatments

Treatment	Proline (mg/g fw)				Melonaldehyde (μ mole/g fw)			
	40DAS		80DAS		80DAS			
	V1	V2	V1	V2	V1	Fold change	V2	Fold change
T ₁ (normal temp.)	1.46	0.59	0.96	0.96	19.30		29.21	
T ₂ (normal temp. + 2 °C)	1.85	1.17	1.28	1.38	50.33	2.60	67.30	2.30
T ₃ (T ₂ + S.A.)	0.67	1.14	1.15	0.88	35.84	1.85	45.96	1.57
CD _{0.05} (A)	0.457		0.168		NS			
SEm (±) (A)	0.147		0.042		0.947			
CD _{0.05} (B)	NS		NS		3.136			
SEm (±) (B)	0.12		0.042		0.947			
CD _{0.05} (A x B)	NS		0.237		4.435			
SEm (±) (A x B)	0.027		0.059		1.339			

NB: A=Treatment B=Variety

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Table 3.6. Content of Crude fat (% dw), total carbohydrate (% dw) and crude protein (% dw) content of foxtail millet varieties at 40 and 80 DAS under different treatments

Treatment	Crude fat				Total carbohydrate				Crude protein			
	40DAS		80DAS		40 DAS		80DAS		40 DAS		80DAS	
	V1	V2	V1	V2	V1	V2	V1	V2	V1	V2	V1	V2
T ₁ (normal temp.)	4.83	4.48	5.01	5.24	53.25	62.55	70.54	71.81	6.52	9.93	14.14	15.51
T ₂ (normal temp. + 2 °C)	4.38	4.42	2.77	3.06	48.19	58.99	36.93	41.81	7.98	8.24	10.88	10.61
T ₃ (T ₂ + S.A.)	4.25	3.99	3.89	4.69	50.25	60.48	56.62	54.26	8.17	9.95	12.09	13.46
CD _{0.05} (A)	0.316		0.488		0.326		0.078		0.142		1.554	
SEm (±) (A)	0.101		0.147		0.105		0.026		0.046		0.469	
CD _{0.05} (B)	NS		NS		0.266		0.05		0.116		NS	
SEm (±) (B)	0.083		0.147		0.085		0.017		0.037		0.469	
CD _{0.05} (A x B)	NS		0.69		0.461		0.111		0.201		2.198	
SEm (±) (A x B)	0.143		0.208		0.148		0.037		0.064		0.664	

NB: A=Treatment B=Variety

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