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Gas Exchange Responses of Foxtail Millet (*Setaria Italica*l.) Under Drought Stress at Grain Filling Stage

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Abstract

A pot culture experiment was conducted to determine the responses of Foxtail millet (*Setaria italica* L.) varieties FXV 625, SIA 3222, SIA 3085 and SIA 3156 against drought stress at grain filling stage. Pots of 30×30×30 cm were selected for this study and the experiment was done in CRD. All the plants were subjected to drought stress by withholding irrigation for ten days at grain filling stage. On the final day of the treatment data was collected on various morpho-physiological, biochemical parameters and yield parameters. The varieties SIA 3156 and SIA 3085 recorded maximum growth under drought stress whereas the varieties FXV 625 and SIA 3222 were recorded less growth under drought stress. The maximum growth of the SIA 3156 and SIA 3085 is linked with maximum gas exchange characteristics which is further coupled with high yields under drought stress.

Keywords: Photosynthetic rate, Drought, Grain filling, RWC, WUE

1. INTRODUCTION

Water is one of the most important factors which play a prime role in many metabolic activities of the plant body [1,2]. Drought to limited water availability is a permanent barrier to world's food production especially in many developing countries [3]. Sometimes drought stress may leads to great loss of agricultural production even in developed countries [4].

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According to Population Stat the world's total population has hiked to 250% in the past seven decades (https://populationstat.com). To feed this bursting population crop production has to increase significantly in swift by developing efficient methods [5,6].

Reduced soil water results in progressive negativity of the surrounding environment which further drops the leaf relative water content. These circumstances resulted in numerous biochemical and physiological changes to extend the plant survivability [7].

Reduced supply of water mainly acts on stomatal conductance and photosynthesis followed by dry matter accumulation [8,9]. The stomatal reduction in turn negatively influences efficiency of RUBP carboxylase [10, 11]. The photosynthetic decrease due drought further associated with damage to oxygen-evolving complex (OEC) of PSII reaction centre [12]. A direct link between reduced stomatal conductance and transpiration on grain yield was previously recorded [13].

The rate of photosynthesis positively associated with leaf area, specific leaf weight and available chlorophyll content [14]. Lessened leaf area, chlorophyll content under drought stress should be considered as a typical symptom of oxidative stress [15,16]. This condition may be the result of photo-oxidation of chlorophyll pigment and chlorophyll degradation [17]. Further water deficit stress results in increased canopy temperature [18,19] which weakens the membrane stability and destruction of lamellae vesicles [20,21,22]. Use of SPAD chlorophyll meter readings (SCMR) is considered to be a trustable parameter to measure the leaf chlorophyll content [23,24]. Increased root growth under drought stress coupled with enhanced leaf water potential was recorded earlier [25,26]. Water use efficiency (WUE) is also one of the significant indicators to identify the drought tolerant crop species [27]. Impact of drought stress on WUE depends on plant species and phenological stage of water stress. Drought stress induced the accumulation of reactive oxygen species (ROS) which activates the ROS scavenging enzymes such as speroxide dismutase, catalase, peroxisae, proline etc. [28,29].
Water stress may occur at any time during the growing season because of variable climatic changes associated with global warming and this may lead to a profound decrease in yield [30,31]. It is important to identify the critical period and responses to water deficit among crops. Decreases in grain yield following water deficit stress occur during early reproductive and grain filling/heading stages significantly reduce the crop yield [32,33]. Drought spells after flowering results in aborted grains and diminished yield [28]. Understanding of the counter act mechanisms of plants to the drought conditions at critical growth stages will lead to development of drought tolerant crop species [34].
Millets can grow well in awide variety of environmental conditions. Due to its short growing season, it has potential value, especially in semi-arid regions [35]. Foxtail millet (*Setaria italica* [L.] Beauv.) is a minor China originated annual C_4 Gramineae cereal with good nutritional values [36]. Foxtail millet believed to has better adaptability to drought conditions and plays predominant role in agricultural yields of arid and semi-arid regions [37]. However the response of foxtail varieties under drought stress at grain filling stage was less explored. Moreover, it has not been studied as comprehensively as the major crops especially against drought responses. Understanding the combating responses of foxtail millet against water drought stress will provide noteworthy information to develop drought tolerant varieties.

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2. MATERIALS AND METHODS

The drought combating responses of foxtail millet at grain filling stage was studied through pot culture experiment. The seed material for the present investigation comprises four foxtail millet varieties FXV 625 (Prof. J.T.S Agricultural University, Hyderabad), SIA 3223 (Y.V. University, Kadapa), SIA 3085 (RARS, Nandyal) and SIA 3156 (Sathavahana University, Telangana).

Pot culture experiment

Seeds of foxtail millets were sown in pots (30 × 30 × 30 cm) containing 10 kg red soil, FYM and sand in 3:2:1 ratio in each pot during March 2019 to May, 2019. Completely randomized design (CRD) with three replications was followed for this experiment. A total of five seeds per pot were sown and after seedling emergence, plants were thinned to one per pot. Immediately after sowing, irrigation was provided to all the pots. Till the panicle initiation control and drought pots were maintained at field capacity and plants were subjected to drought stress for 10 days at grain filling stage. On the final day of drought the following parameters were measured both in control and drought pots.

2.1 Morpho-physiological characteristics

2.1.1 Plant height and root length (cm)

Plant height and root length were recorded by measuring it from the ground level to the growing tip and from the base of the soil to root tip respectively.

2.1.2 Total leaf area per plant (cm^2)

The leaves were collected and kept in polythene bags to avoid wilting and immediately brought to the lab. The total leaf area per plant was measured by using *LICOR 3100* leaf area meter. The total leaf area was expressed in terms centimetres per square meter (cm^2).

2.1.3 Specific leaf weight (mg/cm^2)

Specific leaf area of each cultivar was determined by selecting the third leaf starting from the shoot apex of the plant. The fresh weight and leaf area of the sample was taken. The leaf sample was kept in hot air oven for about 96 hours at 80°C until it reaches the constant weight. The specific leaf area was using the following formula [38] and expressed as mg/cm^2 fr.wt.

$$\text{Specific leaf weight} = \frac{\text{Leaf area } (cm^2)}{\text{Dry weight of the same leaf (g)}}$$

2.1.4 Leaf chlorophyll (mg/g)

Total leaf chlorophyll of each variety was calculated by using DMSO method [39]. To the 30 mg of fresh leaf material taken in a test tube 10 ml of dimethyl sulfoxide (DMSO) was added and kept in hot water bath at 60 °C for halften hour. The optical density was recorded at 645 and 663 nm by using UV–VIS spectrophotometer (Elico *SL 159*). The amount of chlorophyll pigment present in the sample was determined using the following formula.

$$\text{Total chlorophyll} = (20.2 \times \text{O.D at } 645 \text{ nm} + 8.02 \times \text{O.D at } 663 \text{ nm}) \times \frac{V}{10} \times W$$

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2.1.5 Chlorophyll stability index (CSI)

Chlorophyll stability index was determined according to Sairam [40] . Thirty milligrams of leaf sample taken in a test tube was subjected to heat treatment 100 °C per 1 hr in hot water bath. Later 10 ml of DMSO was added to the test tubes and was placed in hot air oven at 60 °C for about 30 minutes. A control was run without using leaf sample. The absorbance was recorded at 645 and 663 nm using UV-VIS Spectrophotometer (Elico *SL 159*). The rate of chlorophyll stability was calculated using the following formula.

$$CSI = \frac{\text{Chlorophyll reading with heat treatment}}{\text{Chlorophyll reading without heat treatment}} \times 100$$

2.1.6 SPAD Chlorophyll Meter Reading (SCMR)

The SCMR measurements were taken on five randomly selected plants by selecting third fully matured leaf from the apex of the stem of each plant [41]. SPAD-502 meter (Minolta Konica Co. Ltd., Japan) was used to measure the SCMR values.

2.1.7 Canopy temperature (°C)

Crop canopy temperature was determined with an infrared thermo meter (Raytek Raynger ST80, Burlington) between 13:00 – 15:00 h of the midday.

2.1.8 Gas exchange parameters

The parameters like photosynthetic rate (Pr), stomatal conductance (Gs), transpiration rate (T) and internal CO_2 concentration were measured by using Licor–*Li 6400 XT* portable photosynthetic system. The above were expressed in units viz., µmol/cm^2, mmol/cm^2, mol/m^2/sec and µmol CO_2/mole.

2.2 Biochemical characteristics

2.2.1 Proline (µg/g)

The proline an anti oxidative enzyme was extracted and estimated [42]. Acid Ninhydrin was prepared freshly by mixing ninhydrin (1.25 g), glacial acetic acid (30 ml) and 6 M Phosphoric acid (20 m) followed by agitation until complete dissolution and kept in a refrigerator at 4 °C. Fresh leaf material (500 mg) was homogenized with 3% of aqueous sulfosalicylic acid. The homogenate was filtered by using muslin cloth and the filtrate was collected. To the 2 ml of the filtrate 2 ml of Acid Ninhydrin and 2 ml of Glacial acetic acid was added followed by incubation at 100 ^{o}C for 1 hour in a boiling water bath. The reaction was terminated by placing the test tubes in ice bath. To these contents 4 ml toluene was added and stirred for 15 sec. The upper toluene chromophore was aspirated followed by the absorbance the optical density was measured at 520 nm.

The activities of catalase as well as peroxidase were assayed according to Prathibha Devi [43].

Enzyme Extraction

A 500 mg of plant material was grounded in pre chilled pestle and mortar by adding 30 - 40 ml phosphate buffer (0.02 M). The contents were filtered through cheese cloth followed by centrifugation at 2000 rpm for 10 min. The extract was made up to 100 ml by adding phosphate buffer and preserved for further biochemical analysis.

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2.2.2 Peroxidase activity (u/g)

Reaction mixture was prepared by adding 3 ml of pyrogallol phosphate buffer and 0.1 ml of enzyme extract into a cuvette. To the reaction mixture 0.5 ml of H_2O_2 was added and gently shaken. The absorbance was measured after 3 min at 420 nm. A control was run by using boiled enzyme extract. The enzyme activity was measured by subtracting the absorbance value of the blank from the sample.

2.2.3 Catalase activity (u/g)

One gram of leaf material was macerated into thin paste using pH 7 phosphate buffer and the enzyme extract was filtered through muslin cloth. A 2 ml of the enzyme extract was taken in a conical flask and added with 1 ml of 0.45 molar H_2O_2. After 5 minutes of incubation the enzyme activity was inhibited with 1 ml of 12% H_2SO_4. The extract was titrated against 0.05 N of $KMnO_4$ taken in a burette, appearance of pink color which remains constant for about 30 seconds was considered as the end point. The amount of H_2O_2 destroyed by catalase is calculated by the formula given hereunder.

$$\text{Catalase activity} = \frac{25 \times 0.85}{2} \times \frac{V}{W}$$

Where, W = Weight of material used; V = Volume of $KMnO_4$ utilized (Blank sample value)

2.2.4 Superoxide dismutase (µu/g)

Superoixde dismutase activity was measured using standard protocols [44,45]. A 500 mg of leaf sample was homogenized in pre-chilled pestle and mortar with ice cold 50 mM potassium phosphate buffer (pH 7.8). Homogenates were centrifuged at 10, 000 rpm using ice cold centrifuge (4 °C) (Eppendorf – 5415 R). A reaction cocktail of 33 ml was prepared by adding 60 µl Phosphate buffer (50 mM), 390 µl methionine (13 mM), 0.6 µl Riboflavin (02 µM), 60 µl EDTA (0.1 mM), 300 µl NBT (75 mM) and 50 µl of Enzyme extract. A blank was set without enzyme and NBT to calibrate the spectrophotometer. Another control was set having NBT but no enzyme as reference control. All the tubes were exposed to 400 W bulbs (4×100 W bulbs) for 15 min. The percentage inhibition of the reaction between riboflavin and NBT in the presence of methionine was measured at 560 nm.

2.3 Water relation characteristics

2.3.1 Relative Water Content (%)

Relative water content was estimated in present study [46,47]. Fresh leaf material was collected and weighed (FW). Then the leaf material was dipped in distilled water for four hours and the turgid weight (TW) was taken. Leaf material was dried in an oven at 96 °C for four days and the dry weight (DW) was recorded.

$$\text{RWC} = \frac{\text{Fresh weight - Dry weight}}{\text{Turgid weight - Dry weight}} \times 100$$

2.3.2 Leaf water potential (MPa)

Midday leaf water potential was measured by using Psypro meter (WESCOR). From the 3rd or 4th leaf disks were prepared and placed in leaf chamber of Psypro meter. The relative water potential readings were directly appeared in MPa.

2.3.3 Water use efficiency (WUE)

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Water use efficiency is the ratio between two bio-physical parameters and it is determined by the formula given by Blum [48] and was expressed in mmol H_2O/µmol CO_2.

$$\text{Water use efficiency (WUE)} = \frac{\text{Rate of transpiration (T)}}{\text{Photosynthetic rate (Pr)}}$$

2.3.4 Soil water content (%)

The soil moisture content was calculated [49,50]. The soil water content was measured gravimetrically, by oven drying the soil sample at 80 °C for about 3 days.

$$\text{\% water by weight} = \frac{\text{(Wet weight – Dry weight)}}{\text{Wet weight}} \times 100$$

2.4 Yield Characteristics

2.4.1 Panicles per plant

Total number of grain bearing panicles on each plant was counted at maturity and the average was recorded.

2.4.2 Grains per panicle

The total number of grains per panicles was counted at the time of harvest.

2.4.3 1000 seed weight (g)

One thousand seeds were counted randomly from each variety and the weight was recorded in grams.

2.4.4 Yield/plant (g)

The grain yield per plant was weighed in grams.

3. RESULTS

3.1 Morpho- physiological parameters

3.1.1 Plant Height (cm)

Growth of the plants in terms of height was measured (Figure 1A). The plant height in control plants was ranged from 100 cm to 140.30 cm with an average value of 126.44 cm. In case of treated plants it was varied between 68.00 cm to 112.64 cm with a mean value of 89.03 cm. Of all the varieties maximum plant height was observed in FXV 625 (140.30 cm) and SIA 3156 (135.12 cm) in control plants whereas in treated plants the highest plant height was reported in SIA 3085 (112.64 cm) and SIA 3156 (100.30 cm).

3.1.2 Root length (cm)

The root length is considered as one the basic biomarker to identify the drought tolerance among the plants. In present study the root length of the foxtail millets differed significantly (Figure 1B). It was ranged from 5.72 cm (FXV 625) to 12.86 cm (SIA 3156) in untreated plants whereas in case of treated plants root length was varied between 6.70 cm (FXV 625) to 18.06 cm (SIA 3156). In control plant highest root length was observed in variety SIA 3156 (12.86 cm). Plants treated with water stress recorded increased root length when compared to controls. The maximum root length was reported with SIA 3156 (18.06 cm) followed by SIA 3085 (16.82 cm) in drought treated foxtail millet varieties.

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3.1.3 Total leaf area (cm^2/plant)

Leaf area is one of the primitive characters to evaluate the drought tolerant varieties. The total leaf area in present study was varied between 226.21 cm^2/plant to 525.16 cm^2/plant with an average value of 369.97 cm^2/plant and in case of water stressed plants leaf area was varied between 209.68 cm^2/plant to 500.16 cm^2/plant with an average mean of 339.98 cm^2/plant. In control plants maximum total leaf area was observed in SIA 3156 (525.16 cm^2/plant) (Figure 1C) and SIA 3085 (428.41 cm^2/plant). When plants were treated with water stress at grain filling stage highest leaf area was recorded with SIA 3156 (500.16 cm^2/plant) and SIA 3085 (384.27 cm^2/plant).

3.1.4 Specific leaf weight (mg/cm^2)

Specific leaf weight is one of the major factors that may directly link with the leaf chlorophyll and it was found to be significant (Figure 1D). In present study the specific leaf weight was varied between 8.19 mg/cm^2 to 25.58 mg/cm^2 in controls and from 5.42 mg/cm^2 to 19.59 mg/cm^2 in drought stressed plant with an average value of 17.14 mg/cm^2 and 11.82 mg/cm^2 respectively. Of all the varieties the maximum specific leaf weight was reported with SIA 3156 mg/cm^2 both in controls 25.58 mg/$cm^2$and 19.59 mg/cm^2 in drought treated plants.

3.1.5 Total chlorophyll (mg/g)

Chlorophyll is the one of the basic factors needed for the photosynthetic process. The total chlorophyll content of the foxtail millets varied significantly in the present study (Figure 1E). The mean chlorophyll content was ranged from 10.96 mg/g to 18.21 mg/g with an average mean of 14.34 mg/g in controls and during grain filling stress the chlorophyll content was varied between 7.16 mg/g to 17.33 mg/g with a mean of 11.73 mg/g. Of all the varieties maximum chlorophyll content 18.21 mg/g was found in SIA 3156 and minimum chlorophyll content was reported with FXV 625 (10.96 mg/g) in case of controls. Under water stress conditions highest chlorophyll content was observed in SIA 3156 (17.33 mg/g) whereas the minimum chlorophyll content was recorded with FXV 625 (7.16 mg/g).

3.1.6 Chlorophyll stability index

Membrane leakage is the major problem during drought stress. This membrane leakage was determined by chlorophyll stability index (CSI). In present study the CSI was varied significantly both in controls and treatments (Figure 1F). The CSI was ranged from 42.98% to 65.27% in controls and 27.75% to 52.99% in treatments with an average mean of 54.59 and 40.72. Both in controls and stress plants the maximum CSI was observed in SIA 3156.

3.1.7 SCMR

In present study the SCMR values varied significantly (Figure 1G). The SCMR values were differed from 25.43 to 56.62 with an average mean 40.22 in untreated plants. In case of drought treated plants the SCMR values are ranged from 12.16 to 52.76 with an average of 32.77. The maximum SCMR was reported with SIA 3156 (56.62) whereas the minimum SCMR was recorded in FXV 625 (25.43) in case of controls. In drought treated plant samples maximum SCMR values were observed in SIA 3156 (52.76) followed by SIA 3085 (48.27) however the lower SCMR values were reported with FXV 625 (12.16).

3.1.8 Canopy temperature (^oC)

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Drought prone conditions leads to the decrease in soil water availability and plant water content thereby increased soil and plant temperature. In present study the canopy temperature was ranged from 20.76 ^{o}C to 22.10 ^{o}C with an average mean of 21.36 ^{o}C in controls. In case of water stressed plants the canopy temperature was varied between 22.70 ^{o}C to 26.16 ^{o}C with a mean of 24.51 ^{o}C. In controls lower canopy temperature was observed in SIA 3156 (20.76 ^{o}C) and SIA 3085 (21.00 ^{o}C) (Figure 1H). Under water stressed conditions the minimum canopy temperature was recorded with SIA 3156 (22.70 ^{o}C) followed by SIA 3085 (23.19 ^{o}C).

3.1.9 Photosynthetic rate (µmol/cm^2)

The mean photosynthetic rate was varied between 20.32 µmol/cm^2 to 32.91 µmol/cm^2 in control plants and from 7.00 µmol/cm^2 to 21.78 µmol/cm^2 in drought treated plants with a grand mean of 26.48 µmol/cm^2 and 13.85 µmol/cm^2 (Figure 1I). The maximum photosynthetic rate of 32.91 µmol/cm^2 and 21.78 µmol/cm^2 was reported in both controls and drought treated foxtail millet varieties (SIA 3156). The decreased photosynthetic rate of 20.32 µmol/cm^2 and 7.00 µmol/cm^2 was reported with the variety FXV 625 in both untreated and treated plant samples.

3.1.10 Stomatal conductance (mmol/cm^2)

During drought stress conditions the stomatal conductance was reduced and the entry of CO_2 will be limited. The stomatal conductance was varied between 0.24 mmol/cm^2 to 0.27 mmol/cm^2 with a mean of 0.25 mmol/cm^2 in control whereas in case of drought treated varieties stomatal conductance was differed between 0.08 mmol/cm^2 to 0.22 mmol/cm^2 with an average mean of 0.15 mmol/cm^2 (Figure 1J)). In present study significant decrease in stomtal conductance was reported. In present study maximum stomatal conductance of 0.27 mmol/cm^2 and 0.22 mmol/cm^2 was reported with SIA 3156 both in control and drought stress respectively.

3.1.11 Transpiration rate (mol/m^2/sec)

In present study the rate of transpiration was varied significantly (Figure 1K). Under controlled conditions all plants were transpired well and it was ranged from 9.80 mol/m^2/sec to 11.41 mol/m^2/sec with an average mean of 10.48 mol/m^2/sec whereas in case of drought treated plants it was varied between 5.20 mol/m^2/sec to 6.60 mol/m^2/sec with a mean value of 6.03 mol/m^2/sec. Of all the foxtail millet varieties highest transpiration rate was observed in SIA 3156 both in control (11.41 mol/m^2/sec) and drought (6.60 mol/m^2/sec) treatments. However the low transpiration rates were reported with FXV 625 (9.80 mol/m^2/sec) in controls and SIA 3222 (5.20 mol/m^2/sec) in drought treated varieties.

3.1.12 Internal CO_2 concentration (µmol CO_2/mole)

The internal CO_2 concentration differed significantly both in controls and treatments in present study (Figure 1L). It was ranged between 219.00 µmol CO_2/mole to 278.12 µmol CO_2/mole in untreated plant samples and from 106.27 µmol CO_2/mole to 266.06 µmol CO_2/mole in treated plants with a mean value of 250.88 µmol CO_2/mole 191.27 µmol CO_2/mole. The high internal CO2 concentration was observed in SIA 3156 (278.12 µmol CO_2/mole) followed by SIA 3085 (269.42 µmol CO_2/mole) whereas the lowest CO_2 concentration found with FXV 625 (219.00 µmol CO_2/mole) in controls. When plants were subjected to drought stress the availability of CO_2 in inner mesophylls was decreased due to

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stomatal conductance and in present study the more CO_2 concentration was recorded with SIA 3156 (266.06 µmol CO_2/mole) followed by SIA 3085 (220.10 µmol CO_2/mole).

3.2 Biochemical characteristics

3.2.1 Proline (µg/mg)

The proline activity of the foxtail millets varied significantly in present study and the increased proline activity was observed in drought treated plants (Figure 2A). In present study proline activity in controls was ranged between 64.80 µg/mg to 86.10 µg/mg with a mean value of 76.37 µg/mg whereas in water stressed conditions its activity increased and it was varied between 76.17 µg/mg to 97.27 µg/mg with an average value of 87.34 µg/mg. Both in controls and stressed plants the highest proline activity was recorded with SIA 3156 (C: 86.10 µg/mg; S: 97.27 µg/mg) and the minimum proline activity was recorded with FXV 625 (C: 64.80 µg/mg; S: 76.17 µg/mg).

3.2.2 Peroxidase activity (u/g)

The POX activity was ranged from 0.09 u/g to 0.18 u/g with a mean value of 0.09 u/g in controls (Figure 2B). The peroxidase activity was reported to be high and low in foxtail varieties SIA 3156 (0.18 u/g) and FXV 625 (0.09 u/g) in control conditions. The relatively highest POX activity of 0.18 u/g was found with SIA 3156 foxtail variety. The variety FXV 625 (0.67 u/g) was showed less POX activity in stressed conditions.

3.2.3 Catalase (u/g)

The available sugar levels were found to be reduced with the increased drought stress conditions (Figure 2C). The CAT activity was ranged from 5.00 u/g to 8.84 u/g in controls with an average mean of 6.84 u/g and in case of stress the CAT activity was varied between 3.21 u/g to 5.56 u/g with an average mean of 5.16 u/g. The variety SIA 3156 was showed maximum CAT content when compared to other varieties both in controlled (8.84 u/g) and stress (5.56 u/g) conditions.

3.2.4 Super oxide dismutase (u/mg)

Superoxide dismutase activity was found to be increased with enhanced water stress (Figure 2D). Among the controls the SOD activity was less and it was ranged from 21.44 u/mg to 34.62 u/mg. The maximum SOD activity was observed at stress among all the varieties. Among all the genotypes the maximum SOD activity was noticed in SIA 3156 (C: 34.62 u/mg; S: 56.87 u/mg) whereas the lower SOD activity was observed in FXV 625 (C: 21.44 u/mg; S: 32.14 u/mg).

3.3 Water related characteristics

3.3.1 Relative water content (%)

Leaf relative water content is considered to be the best marker to evaluate the drought sensitive and drought tolerant varieties. The relative water content of the leaves was ranged from 67.00% to 86.94% with a mean value of 77.39% in controls whereas in drought treated plants it was differed between 49.36% to 75.36% with an average mean of 63.53%. The highest leaf water content was recorded with SIA 3156 (86.94%) in control plants. In water stress plants the maximum RWC was found with SIA 3156 (74.27%) whereas the minimum RWC was observed in FXV 625 (49.36%) (Figure 3A) .

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3.3.2 Leaf water potential (MPa)

In present study the leaf water potential was ranged from -0.70 Mpa to -1.14 MPa with an average mean of -0.93 Mpa in controls (Figure 3B). In case of water stressed plants the water potential was varied between -1.14 Mpa to -1.64 Mpa with a mean of -1.43 Mpa. In controls lower water potential was observed in SIA 3156 (-0.70 Mpa) followed by SIA 3085 (-0.76 Mpa). Under water stressed conditions the minimum water potential was recorded with SIA 3156 (-1.14 Mpa) and SIA 3085 (-1.20).

3.3.3 Water use efficiency (mmol H_2O/µmol CO_2)

The efficient use of water in drought conditions is prime character to evaluate the drought tolerant varieties. In present study WUE was ranged from 2.07 mmol H_2O/µmol CO_2 to 2.89 mmol H_2O/µmol CO_2 in controls and from 1.21 mmol H_2O/µmol CO_2 to 3.30 mmol H_2O/µmol CO_2 with a mean of 2.36 mmol H_2O/µmol CO_2 and 3.30 mmol H_2O/µmol CO_2 (Figure 3C). In case of drought stress plants the WUE was found to be more in SIA 3156 (3.30 mmol H_2O/µmol CO_2) and in controls the WUE was recorded with SIA 3156 (2.89 mmol H_2O/µmol CO_2). The minimum water use efficiency was reported with FXV 625 (C: 2.07 mmol H_2O/µmol CO_2; S: 1.21 mmol H_2O/µmol CO_2).

3.3.4 Soil water content

The soil water content is the important medium which controls the transport of water and minerals to the plant body. In present study the soil water content of the pots varied with the varieties. In control pots maximum soil water content was reported with SIA 3156 (29.20%) whereas the less SWC was recorded in FXV 625 (22.30%). In case of drought treated plants also the maximum soil water availability was observed in SIA 3156 (18.60%) and the minimum SWC was reported in FXV 625 (7.02%) (Figure 3D).

3.4 Yield characteristics

3.4.1 Panicles per plant

The rate of panicle emergence was studied in present study and was presented in Figure 4A. The panicle number was ranged from 8.10 to 10.10 in controlled conditions with an average mean of 8.90 whereas in case of water stress treatment the panicle number was varied between 5.00 to 9.82 with a mean of 7.38. The highest number of panicles were observed in the variety SIA 3156 (10.10) in controls followed by SIA 3085 (9.64). Under water stress treatment its number varied significantly and the maximum number of panicles were reported with SIA 3156 (9.82). Both in controls and treatments the panicle number was found to be low in FXV 625 (C: 8.10; S: 5.00).

3.4.2 Number of grains per panicle

The grain number per panicle was differed significantly both in controls and treatments in all the varieties (Figure 4B). In present study the grain number was ranged from 1004 to 7800 grains with an average mean of 4127.25. In drought treated foxtail millets the grain number per panicle was reduced when compared to controls and it was varied between 481 to 6489 grains per panicle with mean value of 3392.00. In both controls and drought treatments the maximum and minimum grain number per panicle was reported with varieties SIA 3156 (C: 7800; S: 6489) and (C: 1004; S: 481).

3.4.3 1000 seed weight (g)

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The seed weight was ranged from 1.87 g to 4.65 g with a grand mean of 3.04 g whereas in case of drought treated samples the 1000 seed weight was ranged from 0.90 g to 3.75 g with a mean value of 2.07 g (Figure 4C). The maximum seed weight of 4.65 g was observed in SIA 3156 g followed by SIA 3085 (3.56 g) in controls. In case of drought treated plants the seed weight of the samples found to be high in SIA 3156 (3.75 g), SIA 3085 (2.70 g).

3.4.4 Seed yield per plant (g)

Seed yield per plant was recorded and presented in Figure 4D. In present study seed yield per plant was ranged from 8.10 g to 11.00 g in controls and from 3.14 g to 6.83 g in drought treated plants with an average mean of 9.36 g and 5.08 g both in controls and stressed plants. With 11.00 g and 6.83 g the foxtail variety SIA 3156 recorded highest yield per plant on the other side the variety FXV 625 recorded in lowest per plant yield in stress (3.14 g) and control (8.10 g).

4. DISCUSSION

In the present study significant decrease in plant height was in all the varieties. For the cell expansion process turgor pressure acts as a driving force [51]. Due to lack of necessary turgor pressure a decrease in cell wall extensibility was observed in present study. In the present study relatively less decrease in plant height observed in SIA 3156 and SIA 3085 this may be due to their ability to maintain proper turgor pressure. Similar trend of results observed in maize, *Phaseolus vulgaris,* common bean [52,53,54]. Increased root length under reduced water availability is a peculiar feature of plants [55]. Increased root length during dry spells may lead to the root efficiency to draw water from deep soils. By maintain the proper turgor pressure foxtail varieties SIA 3156 and SIA 3085 increased their root length and efficiently uptake the water [56,57].

Under drought stress conditions the total leaf area and specific leaf weight were highly influenced. Declined photosynthetic rate may be the reason for the decreased total leaf area and SLW [58]. On the other side cell division inhibition is the reason for the reduced LA and SLW under drought stress [59]. Blackgram and common bean also showed the similar type of responses [14,54].

The best index for the photosynthetic potentiality is Chlorophyll content [60]. The ability of varieties to maintain maximum chlorophyll density during drought stress is drought tolerance character which was observed in SIA 3156 and SIA 3085 of the present study.This type of report was observed ealrlier in potato and barley [61,62]. The reduction in chlorophyll and CSI under drought stress is may be due to the damaged caused by reactive oxygen species (ROS) to the chloroplast thylakoid membranes [63,64]. In present study foxtail varieties SIA 3156 and SIA 3085 showed maximum chlorophyll content by maintaining their cell membrane stability. Canola and cowpea also exhibited the decreased chlorophyll under drought stress [65,66]. In order to estimate the chlorophyll pigment and nitrogen content SCMR is widely used [67]. Varieties recording high SCMR i.e SIA 3156 and SIA 3085 had maximum photosynthetic rate and assimilated more carbon/unit leaf area. The reduction in SCMR in FXV 625 and SIA 3222 in drought stress may be due to their inefficiency to uptake the nutrients from the dry soil. The genotypes of peanut and groundnut noticed the reduced photosynthetic rate under drought stress [24,6].

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Regular drought spells resulted in reduced stomatal conductance and photosynthesis followed by less accumulation of dry matter [8] . This decreased photosynthesis is may be due to non availability of RUBP carboxylase [9]. The reduction in photosynthesis due to drought is also be associated with damage occurred to OEC of PSII [12,13] . By protecting their thylakoid membranes from the photo-oxidation foxtail varieties i.e. SIA 3156 and SIA 3085 were maintained high photosynthetic yield. Under drought prone conditions the transpiration will curtail and results in enhanced canopy temperature, which is further associated with high negative water potential in drought sensitive varieties [68, 69]. Similar kind of results was observed in foxtail varieties FXV 625 and SIA 3222 of the present study. Foxtail varieties such as SIA 3156 and SIA 3085 showed lower canopy temperature in present study. Cooler canopy of these varieties is may be due to their better water uptake. The genotypes of wheat also reported enhanced canopy temperature under water deficit conditions [70,60].
A reduction in relative leaf water content was observed in present study under drought stress. In present study the foxtail varieties SIA 3156 and SIA 3085 tried to organize their RWC even under drought stress. This ability helped them to normal functioning of gas exchange process. Decreased RWC under drought stress previously reported in wheat [71,72,73]. Drought stress significantly reduced the leaf water potential in present study in all the foxtail varieties. This may be due to dry atmosphere at the soil and root surrounding environment [74]. Similar type of reaction was recorded in number of plant species [75,76]. In the present investigation, WUE found to be varied significantly both in controls and drought treated plants. Among drought stressed foxtail varieties SIA 3156 and SIA 3085 showed more WUE when compared to the other foxtail varieties. Better WUE of these varieties was due to their higher photosynthetic rate coupled with transpiration. The groundnut and chickpea varieties exhibited the reduced RWC under drought stress [77,78].

To identify the drought tolerant varieties measuring proline accumulation is better option [79,80]. Proline accumulation during low water potentials may help the plants to regulate the compatible osmolytes [81]. Similar results were observed in foxtail varieties SIA 3156 and SIA 3085. The cowpea and maize genotypes reported the increased proline concentration during maximum drought stress [82,83]. The foxtail varieties SIA 3156 and SIA 3085 thrive to maintain catalase levels during drought stress. The maximum decline in catalase activity was reported with FXV 625 and SIA 3222 in present study, indicating their susceptibility towards drought stress conditions. In kodomillet cultivars increased catalase content under water limited stress was noticed [84]. Enhanced SOD activities under drought stress are indicative of increased O_{2-} production and tolerance to oxidative stress [85]. Among the four foxtail varieties tested for SOD activity varieties SIA 3156 and SIA 3085 exhibited maximum SOD activity to withstand to the free radical production under drought stress. Increased peroxidase (POX) activity during drought stress linked with oxidative damage protection [86]. In present study all the foxtail varieties were showed significant increase in peroxidase activity under drought stress. Similar kind of results was observed in various plant species [87,15].

Yield components were differed significantly in response to drought stress. In present investigation all the foxtail varieties reported decreased grain yield under drought stress. The reduction in grain yield is due to reduction in panicle number [88]. These results are in agree with reduced yield in bean, French bean and kodomilet [89,90].

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5. CONCLUSION

Grain filling stage is the very critical in plants life cycle as it determines the crop yield. In present study all the foxtail varieties affected by the drought stress. The reduced plant height and increased root length was coupled with more RWC and less negative water potential was observed in foxtail varieties in SIA 3156 and SIA 3085. Further increased chlorophyll content, CSI is associated with RWC, LWP which enhanced the photosynthetic process in present study was observed. The increased ROS enzymes suppress the activity of oxygen free radicles and thereby increased gas exchange factors which coupled with enhanced plant yield was recorded in SIA 3156 and SIA 3085 foxtail varieties of the present study.

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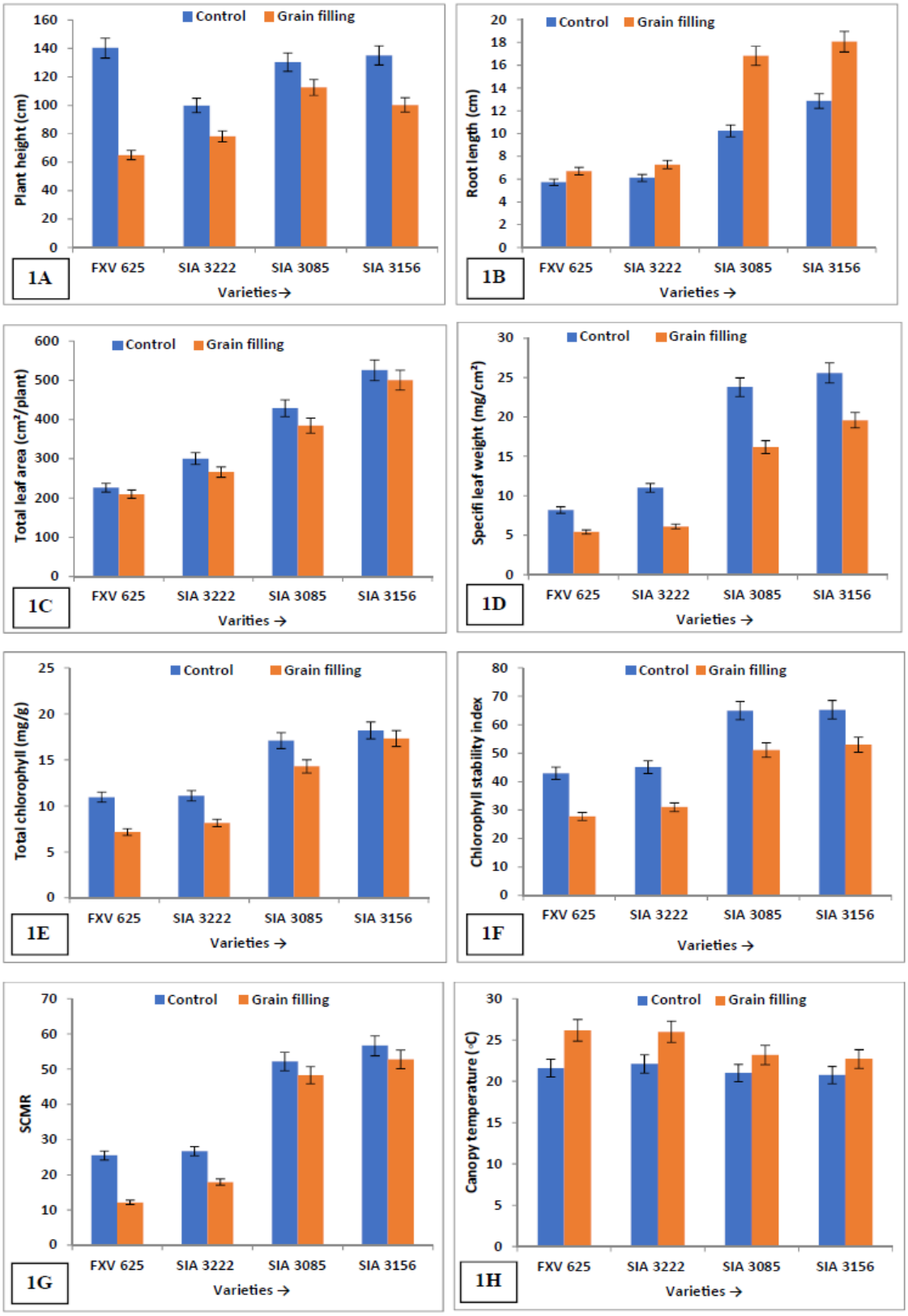

Figure 1A-1H. Morpho-physiological traits under drought stress in foxtail millet at grain filling stage

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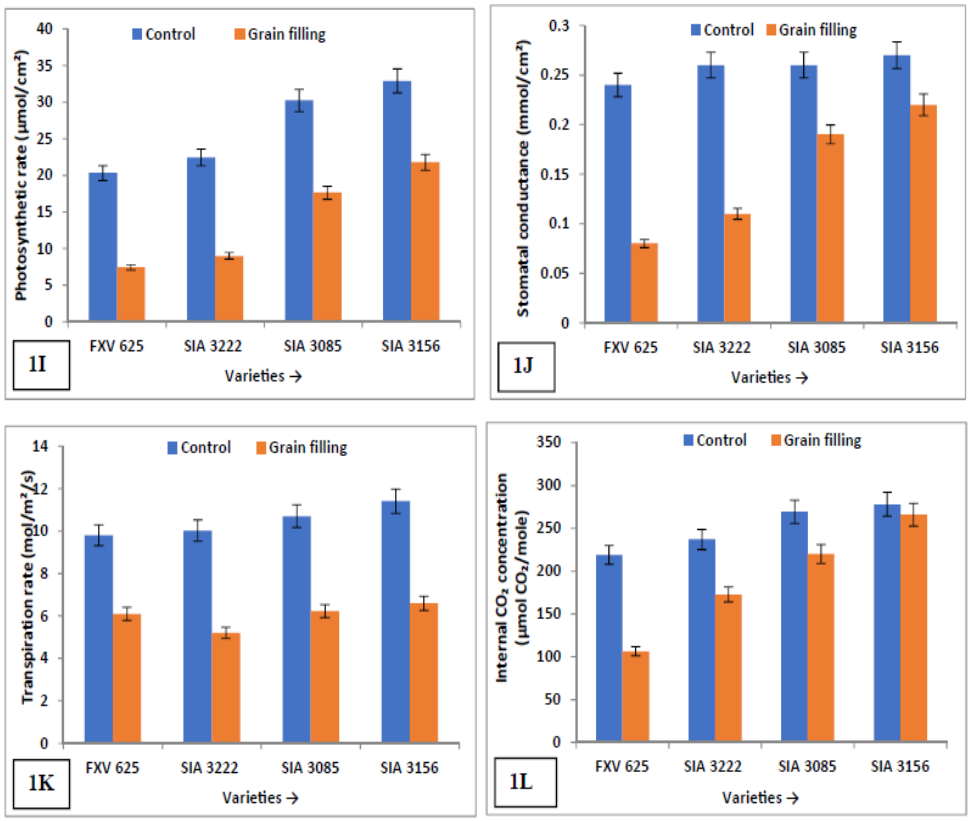

Figure 1I – 1L. Gas exchange parameters under drought stress in foxtail millets at grain filling stage

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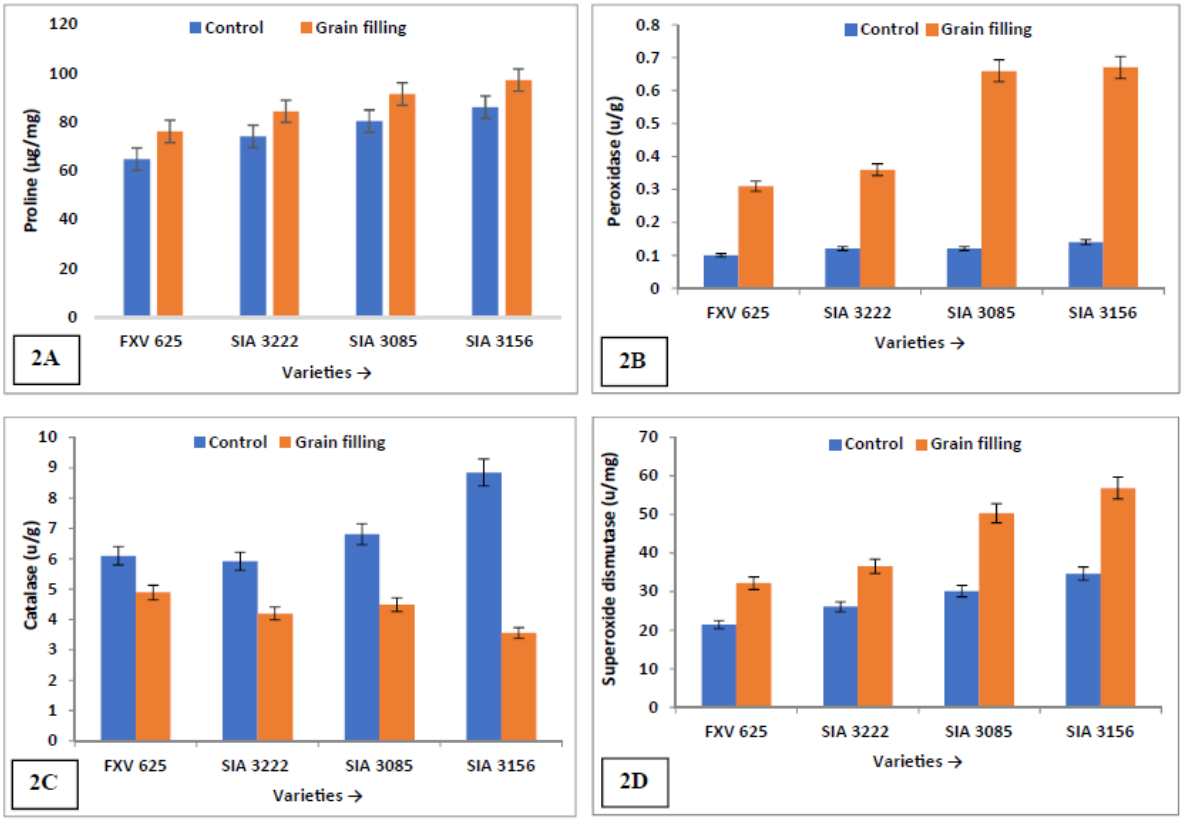

Figure 2A – 2D. Responses of biochemical traits under drought stress in foxtail millet at grain filling stage

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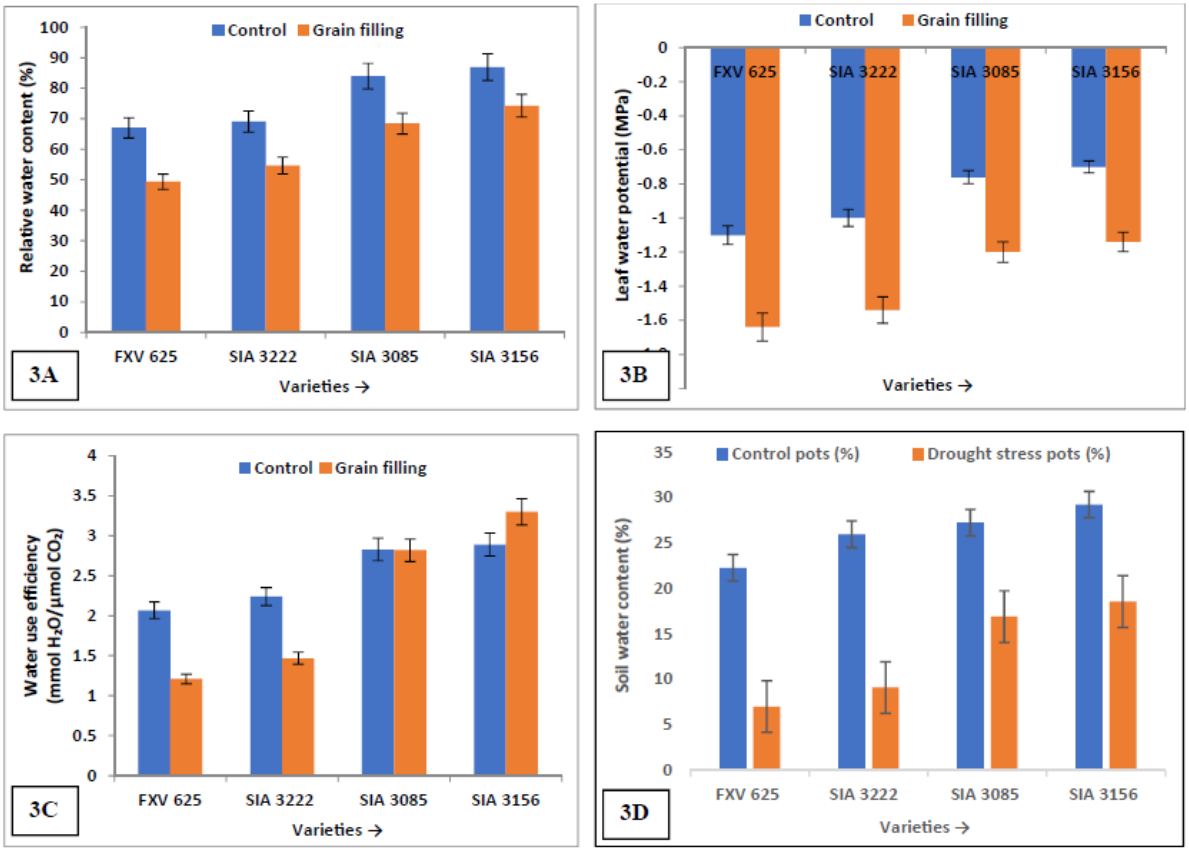

Figure 3A – 3D. Fate of water related parameters under drought stress in foxtail millet at grain filling stage

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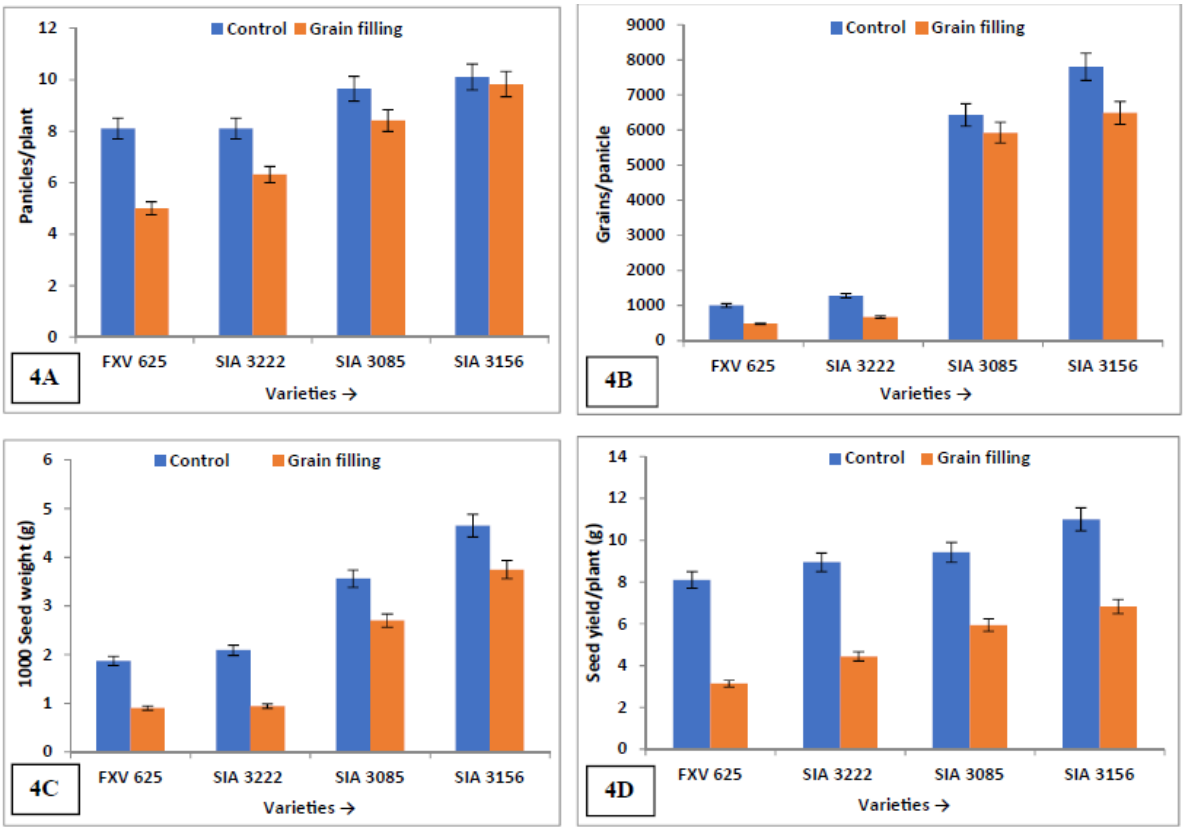

Figure 4A – 4D. Yield traits under drought stress in foxtail millet at grain filling stage