

ORIGINAL ARTICLE

Physiological and morphological responses of two sweet potatoes (*Ipomoea batatas* (L.) Lam) to drought stress

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ABSTRACT

In this study, two sweet potato (*Ipomoea batatas* (L.) Lam) cultivars (white-fleshed and orange-fleshed) were grown in greenhouse conditions. The drought stress levels were imposed by maintaining the soil water content at 25%, 50%, 75% and 100% of field capacity to evaluate the effects of drought on growth parameters (shoot and root dry weight, leaf area (LA), specific leaf area (SLA), relative water content (RWC), total chlorophyll proline and soluble sugars content in plant organs (leaf and root). The results showed that as drought increased, the amount of the above growth parameters in plant organs of both cultivars decreased. However, in all drought treatments, white-fleshed sweet potato had significantly higher shoot and root dry weight, leaf area (LA), specific leaf area (SLA) and relative water content (RWC) than orange-fleshed. The most reduction on dry weight was mainly in level 4 of stress 25% FC in two cultivars. Drought stress led to reductions in the relative leaf water content (RWC) by 25% FC. The lowest content of total chlorophyll and total nitrogen content was observed in drought conditions while between control and drought treatments there were significant differences. As drought increased, the amount of proline content of white-fleshed sweet potato was higher than orange-fleshed sweet potato. Also, drought increases soluble sugars contents. Therefore, it seems that white-fleshed sweet potato is more tolerance than orange-fleshed sweet potato.

Keywords: Sweet potato (*Ipomoea batatas* (L.) Lam), Drought stress, Proline, Soluble sugars, Chlorophyll, Nitrogen content

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Abbreviations: LA, leaf area; RWC, relative water content; SLA, specific leaf area

INTRODUCTION

Adaptive mechanisms adopted by plants in response to abiotic environmental stresses (e.g. high soil salinity, drought, chilling, heat and excessive osmotic pressure) cause some changes in morphological and developmental patterns as well as physiological and biochemical processes [14, 32]. Plants overcome the water stress effects by accumulation of compatible osmolytes such as proline and soluble sugars in their roots and shoots [6, 29]. Proline has been proposed to act as a compatible solute that adjusts the osmotic potential in the cytoplasm. Thus, proline can be used as a metabolic marker in relation to drought stress which can protect proteins and cell membranes from inactivation or denaturation under drought stress [13,11]. Of note, under water stress the accumulation of total soluble sugars and proline in different plant parts would be increased [37].

Sweet potato (*Ipomoea batatas* (L.) Lam) is a plant that requires a period of moist conditions after planting until the root system becomes fully developed, however this plant can tolerate for brief periods of drought stress, recovering quickly when soil moisture is restored [2]. Understanding of the mechanisms taken by this plant for response to drought conditions is necessary to improve crop

productivity in where rainfall is limited or unreliable [35]. This species is one of the most important root crops in the world wide which is the most abundant crop globally after wheat, rice, maize, potato, barely and cassava [22]. Sweet potato is a gamopetalous dicot and belongs to the order polemoniales and family convolvulaceae [26]. The sweet potato has two varieties, "orange-fleshed" contain an orange skin with orange flesh which is rich in β -carotene and "white-fleshed" with a Red skin and white flesh. Despite the name sweet, it may be a good food for diabetics as it helps to stabilize blood sugar levels and to lower insulin resistance [12]. Leaf traits play a substantial role in carbon assimilation, water relations and energy balance. Leaf size and Specific leaf area (SLA) decline along with decreasing in moisture availability [19]. Reich *et al.* [1997] have declared that, SLA is negatively correlated with leaf life span and leaves with low SLA and long life span have lower assimilation rates (per unit mass) [36]. Notably, greater longevity promotes nutrient retention and enhancing long-term photosynthetic nitrogen-use efficiency [18].

Selection for good cultivar performance under drought conditions is considered to be of major importance. Some experiments have been conducted to identify sweet potato cultivars with superior drought tolerance [31]. Drought stress provide stomatal closure, reducing CO₂ uptake for photosynthesis and it affects plant growth and yield in sweet potato [30]. This signifies the importance of screening techniques for drought resistance genotypes and better water management practices. It is generally accepted that, drought stress affects sweet potato by retarding growth, reducing root yield, dry matter and affecting root quality [1].

The aims of this study were to assess the effect of four drought stresses on some physiological and morphological traits of two sweet potato cultivars. Drought tolerance in sweet potato was related to quantitative aspects of the leaf osmolytes status such as proline and soluble sugars in the leaves and roots. Since plants behavior responses to drought are complex and different mechanisms are adopted by plants when they encounter drought, examination of physiological reactions of different sweet potato species to drought stress can help to recognize effective tolerant mechanisms to drought stress and selection of tolerant species.

MATERIAL AND METHODS

Current research was conducted in 2014 and in the greenhouse of the Department of Biology, Islamic Azad University, Shahrekord branch, Iran (31° 43' N, 51° 06' E) at the altitude of about 2400 m above sea level. A pot experiment according to factorial random design with four treatment and three replications was performed. The water stress levels were imposed by maintaining the soil water content at 25%, 50%, 75% and 100% of field capacity. The total number of experimental units was 50 pots with one plant per pot. Soil was sandy loam containing 1.65% organic matter with a pH of 7.3 and an EC of 2034 ds/m. Tip cutting of two sweet potato cultivars (orange and white fleshed) with each cultivar 30cm long were planted in of 1-L volume of pots. Control plants were maintained continuously in greenhouse where the temperature varied from 18 to 28 °C. During the day the greenhouse temperature varied from 22 to 28°C. To prevent evaporation, the whole pots were covered with aluminium foil. After 21 days of drought stress, symptoms of wilting were seen in some plants in late morning and the experiment was also terminated. The hypoxia experiment was also finished at the same time.

Growth and dry matter partitioning

First the shoots and roots were separated completely and then roots were washed three times with de-ionized water to remove adhering nutrients. The process of preparation followed by desiccation in a forced-air oven at 70°C for about 24 h to achieve a constant weight. In order to preserve their original quality, leaves were stored in a refrigerator at 4 °C for 2 h before drying experiments. One part was used for the analysis of fresh leaves and the remaining batches were dried. Relative water content (RWC) was measured using leaves after imposing drought conditions. Immediately after cutting, lamina leaves were sealed within plastic bags and quickly transferred to the laboratory. Fresh weights were determined within 1 h after excision. Turgid weights were obtained after soaking leaves in distilled water in test tubes for 4 to 6 h at room temperature (about 20°C) and under the low light conditions of the laboratory. After soaking, leaves were quickly and carefully blotted dry with tissue paper in preparation for determining turgid weight. Dry weights were obtained after oven drying the leaf samples for 24 h at 70°C. The RWC of each leaf was determined according to the method of Levitt (1980) by using the following formula: $RWC\% = (\text{Fresh weight} - \text{dry weight}) / (\text{turgid weight} - \text{dry weight}) \times 100$. Leaf area (LA) corresponding to the second pair of leave was estimated using leaf area meter. Specific leaf area (SLA) was determined as the ratio of leaf area to leaf dry weight of individual leaves (cm² g⁻¹).

Determination of total nitrogen and chlorophyll

Nitrogen content was determined in dried samples by using the Kjeldahl method. The analysis carried out after digestion in acid with potassium sulphate by the Kjeldahl procedure using selenium sulphate as catalyst. Total chlorophyll was determined by chlorophyll-meter (Minolta Reading SPAD-502).

Determination of Proline

Proline accumulation in fresh leaves and roots was determined based on the Bates method (1973) (7). Free proline was extracted from the leaves and roots of plants using aqueous sulfosalicylic acid 3%. The homogenate was centrifuged at 3000 g for 15 min. The filtrate (2 ml) was mixed with equal volumes of glacial acetic acid and ninhydrin reagent (1.25 g ninhydrine, 30 ml of glacial acetic acid, 20 ml 6NHPO₄) and incubated for 1 h at 90 °C. The reaction was stopped by placing the test tubes in cold water. The samples were rigorously mixed with 4 ml toluene. The light absorption of toluene phase was estimated at 520 nm using spectrophotometer. The proline concentration was determined using a standard curve. Free proline content was expressed as $\mu\text{mol g}^{-1}$ FW of plant parts.

Determination of soluble sugars content

Soluble sugars was determined colorimetrically with anthrone methods (27). The reagent used in this study was anthrone reagent. Soluble sugars are defined as carbohydrate extracted from dry plant material by hot 96% ethanol. Anthrone in sulphuric acid gives a colour reaction with soluble sugars at high temperatures. The content of test tubes were mixed well and then the tubes were put in boiling water for 10 minutes to determine soluble sugars and immediately were cooled on ice. This colour has an absorption peak at 625 nm. Content of soluble sugars were determined by using glucose as standard and expressed as mg g^{-1} DW.

Statistical analysis

Analyses of variances were conducted for all characters measured. Significant treatments or combination of main effects were stated based on the Duncan Multiple Range Test at a 0.05 probability level. Excel 2007 software was used to draw the figures and histograms.

RESULTS

Effect of drought stress on dry weight components

Data recorded in Table 1 indicated clearly that total dry weights decreased drastically under water stress condition compared with unstressed condition. Dry weight of The Whole plant individuals was higher than in control (100% FC). Also the lowest values were observed under drought stress conditions ($p < 0.01$). The dry weight of shoots was reduced down to about 50% of the control (100% FC) by the highest levels of drought-stress (25%FC). Also, Root/Shoot Dry weight ratio increased in both cultivars as compared with control (100% FC).

Table 1. Root dry weight, shoot dry weight, Root/Shoot dry weight ratio of two cultivars of sweet potato (orange and white fleshed) under three treatment of drought. Data are means of three replicates. Means \pm standard deviations (SD) within each column followed by different letters are significantly different at 0.05 probability level.

| Treatment | Root DW (g) | | Shoot DW (g) | | Root/Shoot DW ratio | |
|-----------|------------------|------------------|-------------------|-------------------|---------------------|------------------|
| | Orange-Fleshed | White-Fleshed | Orange-Fleshed | White-Fleshed | Orange-Fleshed | White-Fleshed |
| 100% FC | 0.24 \pm 0.1a | 0.32 \pm 0.05a | 0.86 \pm 0.002a | 1.08 \pm 0.01a | 0.27 \pm 0.07b | 0.29 \pm 0.04b |
| 75% FC | 0.22 \pm 0.1a | 0.26 \pm 0.05b | 0.81 \pm 0.03ab | 0.94 \pm 0.01ab | 0.27 \pm 0.1b | 0.27 \pm 0.01b |
| 50% FC | 0.19 \pm 0.1ab | 0.23 \pm 0.03c | 0.56 \pm 0.08b | 0.63 \pm 0.02b | 0.33 \pm 0.1a | 0.26 \pm 0.01b |
| 25% FC | 0.17 \pm 0.15b | 0.20 \pm 0.02d | 0.42 \pm 0.07c | 0.50 \pm 0.02c | 0.34 \pm 0.03a | 0.32 \pm 0.05a |

Effect of drought stress on relative water content

Both orange and white-fleshed cultivars had lower relative water contents in the drier circumstance (25% of field capacity). Water stress caused significant decrease in the leaf relative water content of both cultivars (Table 2).

Table 2. Relative water content (RWC), leaf area (LA), specific leaf area (SLA) of two cultivars of sweet potato (orange and white fleshed) under three treatment of drought. Data are means of three replicates. Means \pm standard deviations (SD) within each column followed by different letters are significantly different at 0.05 probability level.

| Treatment | RWC (%) | | LA (cm ²) | | SLA (cm ² g ⁻¹) | |
|-----------|------------------|-----------------|-----------------------|-----------------|--|------------------|
| | Orange-Fleshed | White-Fleshed | Orange-Fleshed | White-Fleshed | Orange-Fleshed | White-Fleshed |
| 100% FC | 88.04 \pm 0.1a | 89.2 \pm 0.5a | 43.3 \pm 0.5a | 44.3 \pm 0.2a | 653.4 \pm 0.5a | 659.4 \pm 0.5a |
| 75% FC | 86.6 \pm 0.4a | 87.6 \pm 0.5a | 39.9 \pm 0.1a | 40.4 \pm 0.2a | 558.2 \pm 0.2b | 640 \pm 0.1a |
| 50% FC | 68.8 \pm 0.5b | 74.4 \pm 1.2b | 27.6 \pm 0.1b | 37 \pm 0.1ab | 464 \pm 0.2c | 483.8 \pm 0.2b |
| 25% FC | 52.4 \pm 0.1c | 66.2 \pm 2c | 22.6 \pm 0.2bc | 21.3 \pm 0.1b | 385 \pm 0.3d | 444 \pm 0.2b |

Effect of drought stress on leaf area (LA) and specific leaf area (SLA)

Table 2 presents the data related to effects of drought stress treatments on leaf area (LA) and specific leaf area (SLA) of orange and white fleshed sweet potato plants. Leaf area and specific leaf area (SLA) were decreased under drought stress (25% FC). Drought treatment also reduced substrate water content in pots.

Effect of drought stress on total chlorophyll and nitrogen content

Total chlorophyll content was lower in plants under drought stress than control (fig. 1). Leaf nitrogen content expressed percentage showed significant differences between drought stress treatments and control (4.2% to 3.2% in orange-fleshed and 5.8% to 4.8% of white-fleshed). Among the treatments, irrigation treatment (25% FC) was significant for total nitrogen content (Fig. 2).

Effect of drought stress on Proline

In our study, accumulation of proline as an osmolyte occurred in orange-fleshed and white-fleshed sweet potato. The amount of proline in roots and leaves increased in plants under drought effect (fig. 3 and 4). There was a significant variation in proline content ($p < 0.01$). The results indicated that intensity of stress levels significantly increased the proline accumulation in studied cultivars of sweet potato (fig. 3 and 4). It is worth noting that increase of proline content in white-fleshed sweet potato was higher than orange-fleshed sweet potato and proline content of leaves was higher than roots in both cultivars of sweet potato.

Effect of drought stress on total soluble sugars

Total soluble sugars content in leaves and roots significantly increased under drought stress ($p < 0.01$). However soluble sugars levels in treatment of 25% FC in orange-fleshed sweet potato cultivar was more than control mainly as compared with 100% FC (fig. 5 and 6). The data revealed that the highest content of soluble sugars was found in treatment 50% FC under drought stress in white-fleshed sweet potato and also the most reduction detected in treatment of 100% FC (non-stress).

DISCUSSION

The data released from both cultivars (Table 1) showed that drought stress significantly decreased the dry weight of different parts of the plants (shoot and root) as compared to those of the untreated control plants. The highest dry weights of genotypes belong to white-fleshed sweet potato (0.32 g of root and 1.08 g of shoot, respectively). We could not determine remarkable effect in treatment of 75% FC for orange-fleshed compared to 100% FC (Dry weight Root and Shoot basis). According to the result, under drought stress condition, dry weight has been reduced. A similar result on dry weight under water stress has been reported by Ali (1993) Imposed stress during different growth stages might decrease translocation of assimilates to the grains resulting lower fresh and dry weight of shoots. Under water stress treatment of 100% FC (non-stress) produced the largest detected dry weight plant [1]. This observation indicates that this dry weight would be associated with the cell division and new material synthesis [3]. Results obtained in this experiment demonstrated that drought stress significantly decreased the leaf water potential and relative water content of sweet potato which had pronounced effects on photosynthetic rate. These changes in dry matter production and partitioning may be due to decrease in whole plant photosynthesis and alterations in the priority among sinks for assimilate supplied by source leaves of sweet potato plants.

Drought treatment reduced substrate water content in pots. RWC of leaves under control conditions were 88% in orange-fleshed and 89% in white-fleshed genotypes, respectively (Table 2). However, the drought stress caused a decrease in RWC to 52.4% on orange-fleshed and 66.2% in white-fleshed genotypes. Higher relative water content in the plants grown at 100% FC of soil field capacity compared to those grown at lower soil water levels indicated that plants with higher relative water content had higher photosynthetic rates [39]. Moreover, leaf nitrogen content has been recognized as a determination of net

photosynthetic capacity. It should be noted that a positive correlation is usually observed between CO₂ assimilation rate and leaf nitrogen content [34]. The lowest nitrogen content being observed under drought and control conditions signifies that a larger surface area can be constructed with the same plant nitrogen investment, and then plants have a more extensive foliar display for interception and light capture [33].

In this context, we also analyzed the effects of drought stress on growth parameters and dry matter partitioning. Furthermore, in the drought treatments significant decreases determined in LA and dry weight accumulation in root and shoot when they were compared with control. Leaf area (LA) and specific leaf area (SLA) were decreased under drought stress (25% FC) (Table 2). In the both cultivars, the smallest leaves (22.6 Cm² in the orange-fleshed and 21.3 Cm² in the white-fleshed, respectively) were those of the treated plants. The largest leaves (43.3 Cm² in the orange-fleshed and 44.3 Cm² in the white-fleshed, respectively) were found in plants that had been treated with 100% FC. Specific leaf area data was higher in 100% FC of both of cultivars. There were 21% and 23% decreases in leaf area in two cultivars of sweet potato, respectively, in drought-stressed plants as compared to controls (Table 2). Although during the re-watering period the plants were able to resume growth in terms of leaf area (LA) which is one of the important determinants for dry matter production, the changes in LA of the both cultivars due to drought was always parallel to changes in dry weight. This predicts that in addition to LA, leaf photosynthetic ability and its response to drought may differently restrict the production ability of both cultivars [24]. Leaf size of sweet potato has been reported to have a negative correlation with apparent photosynthesis [8]. Water stress dramatically decreases leaf chlorophyll concentrations. This circumstance also can destroy the chlorophyll and prevent making it [4]. In the current research, Proline content of both cultivars elevated linearly with increase of water deficiency. In 25% of soil field capacity, root proline content varies from 3.4 fold in orange-fleshed cultivar to 4.7 fold in white-fleshed sweet potato, respectively. Besides, Shoots proline content ranges between 5.3 fold in orange-fleshed to 4.7 fold in white-fleshed sweet potato as compared to the control plants. Increase of proline content in white-fleshed cultivar was higher than in orange-fleshed and in shoots was higher than those of roots. The increases in the concentration of proline and soluble carbohydrates in sweet potato leaves and roots were found to be significant during water stress. For a long time, proline was considered as an inert compatible osmolyte that protects subcellular structures and macromolecules under osmotic stress [16, 25, 28]. The accumulation of proline in the leaves of all plants was greater than roots after 21 days of drought stress. A positive correlation was evidenced between drought tolerance and concentration of proline in plant tissues. The accumulation of high amounts of proline may be due to a higher rate of proline synthesis and a lower magnitude of proline oxidation in drought tolerant genotypes. Recent studies also suggested that the protective role of proline consists in protecting the protein turnover machinery against stress damage and up-regulating stress protective proteins [5]. Total soluble sugars content in leaves and roots significantly increased under drought stress. These observations suggest that the production of these osmotic adjustments is a common response of plants under drought conditions. Numerous studies have shown that the soluble sugars content in higher plants increases under different environmental stresses [15, 23].

Proline as a non-protein amino acid forms in most tissues subjected to water stress and accompanying with sugar, it readily metabolized upon recovery from drought [40]. Generally, the compatible solutes protect folded protein structures against denaturation, stabilize cell membranes by interacting with phospholipids, function as a hydroxyl radical scavenger, or serve as an energy and nitrogen source. In some plant species (for example, potato) proline plays a crucial role in osmotic adjustment [10]. Proline performs as a solute that protects macromolecules against denaturation via reducing acidity in the cell and additionally, It acts as a sink for energy to regulate redox potentials and as a hydroxyl radical scavenger (38;21). It has been shown that, the concentration of soluble sugars increased under drought stress in leaves and roots of sweet potato. The accumulation of sugars in response to drought stress is also quite well documented [20]. A complex essential role of soluble sugars in plant metabolism is well known as products of hydrolytic processes, substrates in biosynthesis processes, energy production but also in a sugar sensing and signaling systems. Recently it has been claimed that, sugar flux can be considered as a signal for metabolic regulation under water stress condition [34]. It is completely proved that the free proline content and soluble sugars can be used as drought tolerance indicators for selecting drought resistant genotypes [39]. The enhancement of sugar concentration may be as a result of the starch degradation [17;9].

CONCLUSION

The sweet potato cultivars differed significantly in their physiological and functional properties ($p < 0.05$). White-fleshed sweet potato was identified as genotype with good performance, high drought tolerance, high dry matter and high levels of nitrogen. Our findings revealed that although sweet potato is adapted to various climatic conditions, the crop is sensitive to water deficit stress. Drought stress impacts negatively the growth of sweet potatoes. It also leads to decrease in soil water content affected water relations and growth in sweet potato. Based on this study, the accumulation of compatible solutes in plant stems can be considered as a mechanism for drought tolerance in sweet potato. Increasing knowledge of the genes for the synthesis of compatible solutes, and identification of the stimuli that regulate solute biosynthesis provide an essential contribution to our understanding of their specific roles in the physiology of sweet potatoes.

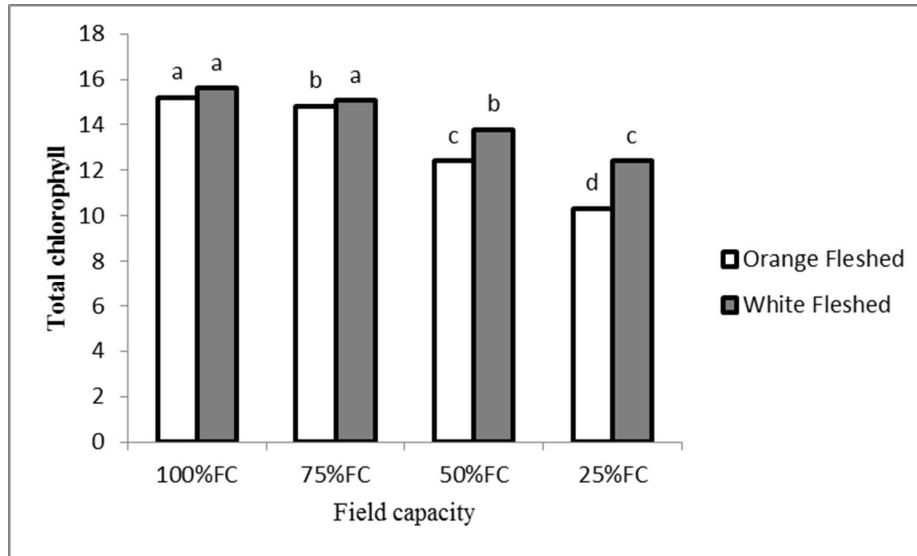


Fig. 1 Effects of different water stress on total chlorophyll content in Leaves of two sweet potato cultivars. Means with letters are significantly different at $p < 0.05$ by Duncan multiple range test. Obtained from three replicates.

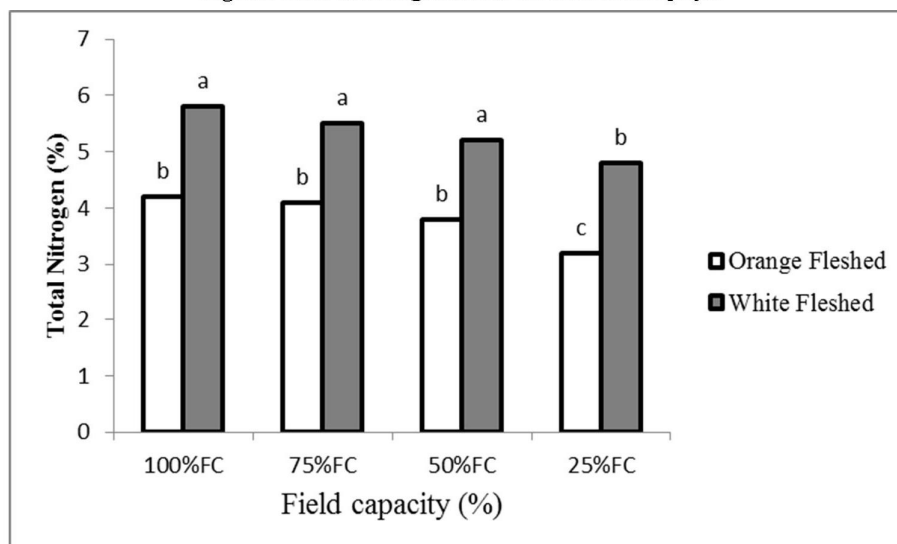


Fig. 2 Effects of different water stress on total Nitrogen content (%) in Leaves of two sweet potato cultivars. Means with letters are significantly different at $p < 0.05$ by Duncan multiple range test. Obtained from three replicates.

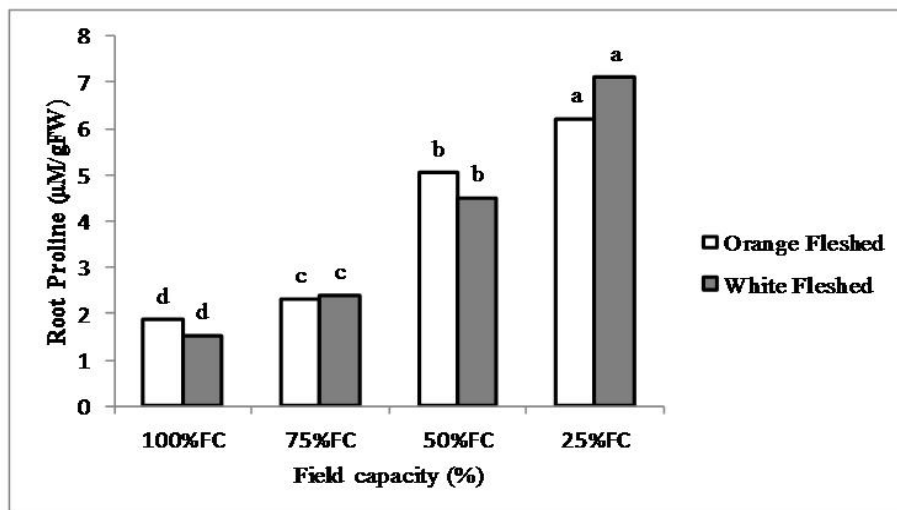


Fig. 3 Effects of different water stress on total proline content ($\mu\text{M g}^{-1}$ FW) in roots of two sweet potato cultivars. Means with letters are significantly different at $p < 0.05$ by Duncan multiple range test. Obtained from three replicates.

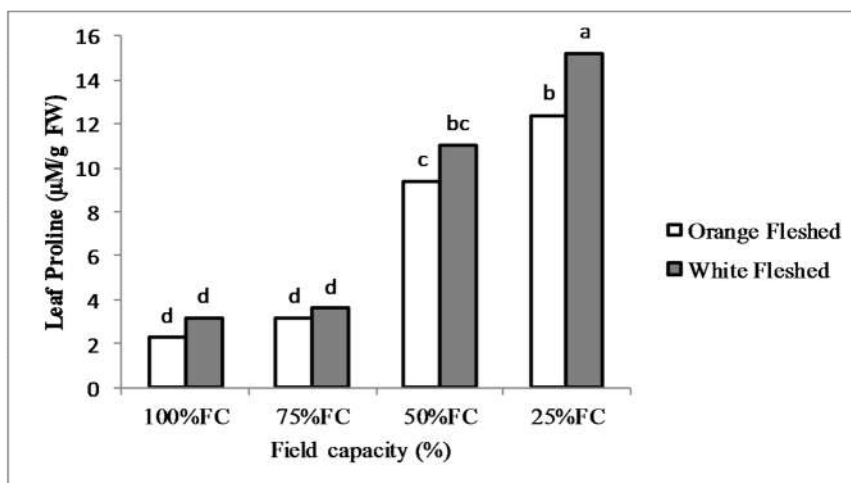


Fig. 4 Effects of different water stress on total proline content ($\mu\text{M g}^{-1}$ FW) in Leaves of two sweet potato cultivars. Means with letters are significantly different at $p < 0.05$ by Duncan multiple range test. Obtained from three replicates.

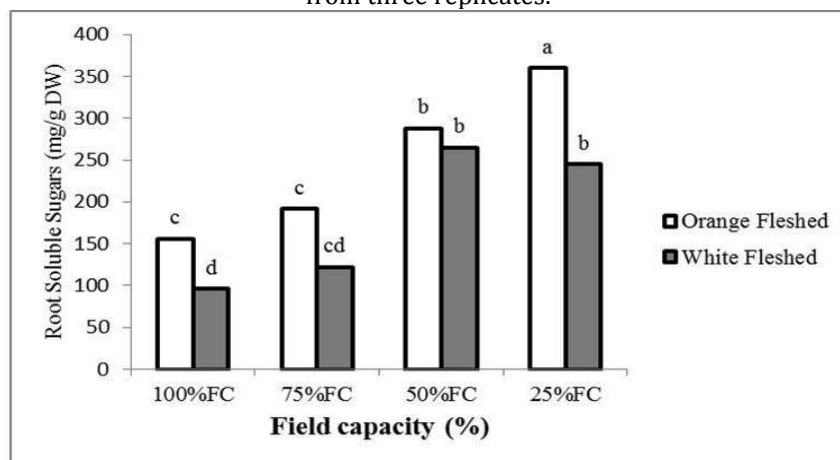


Fig. 5 Effects of different water stress on Soluble Sugars content (mg g^{-1} DW) in Roots of two sweet potato cultivars. Means with letters are significantly different at $p < 0.05$ by Duncan multiple range test. Obtained from three replicates.

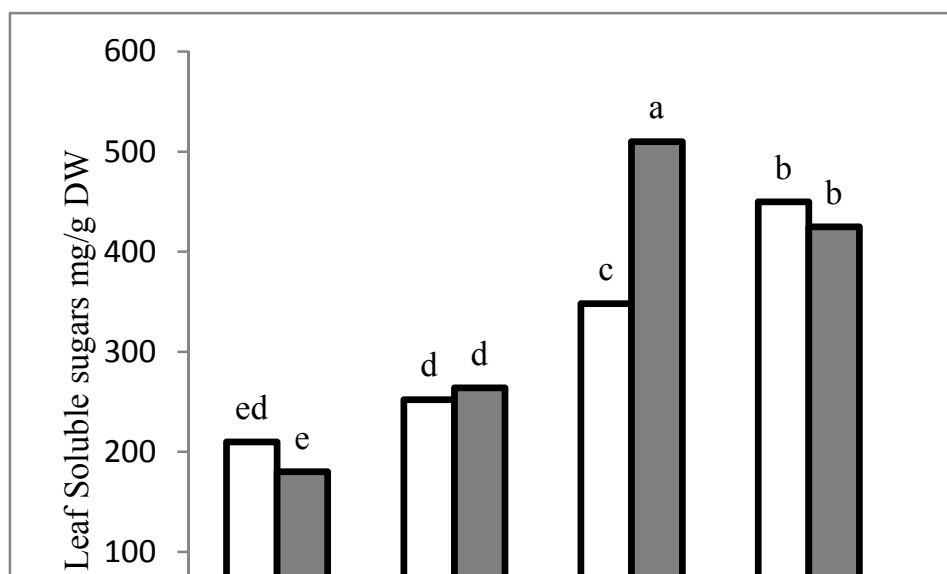


Fig. 6 Effects of different water stress on Soluble Sugars content (mg g^{-1} DW) in leaves of two sweet potato cultivars. Means with letters are significantly different at $p < 0.05$ by Duncan multiple range test. Obtained from three replicates.

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