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Potassium silicate enhances drought tolerance of *Bellis perennis* by improving antioxidant activity and osmotic regulators

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Abstract: Ornamental plants can usually encounter various types of environmental stress, which reduce plant productivity. A proper application of fertilizers can improve plants' tolerance to drought stress. Nutrients such as potassium and silicon are known to have beneficial effects. This study aimed to evaluate the growth of *Bellis perennis* under drought stress (80, 70, and 60% FC) and with the application of potassium silicate (0, 2, and 4 mM). The results showed that potassium silicate (2 and 4 mM) increased K and Si accumulation in plants under drought stress. Plants treated with potassium silicate under drought stress exhibited a lower degree of electrolyte leakage and less MDA accumulation in the following order: 2 and 4 mM potassium silicate. An increase in relative water content and chlorophyll was observed with application of potassium silicate under drought stress. Regardless of potassium silicate, the plant enzymatic defense system was significantly improved compared to non-stressed plants. Potassium silicate enhanced the amount of osmotic regulators (carbohydrate and proline) and secondary metabolites (flavonoids and phenols) compared to control plants regardless of drought stress. The anthocyanin content in the flowers significantly decreased by 32.2% when the plants were treated with 4 mM potassium silicate at 60% FC, compared to 80% FC. In conclusion, potassium silicate mitigated the effects of drought stress, enhanced plant tolerance to drought stress, increased the activity of antioxidant enzymes, and improved the amounts of osmotic regulators and secondary metabolites.

1. Introduction

Plant growth is usually affected by numerous abiotic stressors (Calanca, 2017). Deficits in water supplies are a major environmental threat, currently affecting more than 41% of the world's land mass. Projections for 2050 show a further increase in the magnitude and impact of this environmental threat (Prăvălie, 2016). As global temperatures increase, the annual maximum temperature is estimated to increase by 5°C per year by the end of the 22nd century. This problem will lead to more frequent and extreme droughts in many parts of the world (Gao *et al*., 2020). Such environmental types of stress significantly cause a decline in crop yields falling below maximum potential (Raza *et al*., 2020). Environmental stress can suppress plant growth by interrupting various processes such as cell metabolism, nutrient uptake, and maintenance of turgor pressure (Kusvuran and Dasgan, 2017).

Regarding the proper use of fertilizers for improving plant tolerance to drought stress, the application of nutrients can be largely beneficial. Such applications have reportedly included potassium and silicon, with essential functions in plant metabolism (Bukhari *et al*., 2020; Ibrahim *et al*., 2020). Potassium is a vital fertilizer involved in numerous biochemical and physiological processes, including stress tolerance, plant growth, yield, and quality. Potassium (K) is necessary for many physiological processes, for example, maintaining turgor, translocation of photosynthetic substances to sinking organs, activation of enzymes, synthesis of proteins, transport of solutes in the phloem, and maintenance of cation-anion balance in the cytosol and vacuole. Furthermore, K reportedly facilitates osmoregulation, stomatal movements, and tropism, while it is mainly absorbed from the soil through the roots (Qi *et al*., 2019). However, drought stress causes a reduction in the absorption of elements. The reduced sensitivity of K-deficient plants to drought stress is related to several factors. These factors include the role of K in regulating stomata stomatal and water balance, as well as osmotic potential in vacuoles (Haworth *et al*., 2018). Applying potassium fertilizer mitigates the adverse effects of these stressors on plant growth (Qi *et al*., 2019).

Silicon (Si), the second most abundant element on Earth, can increase plant tolerance to biotic and abiotic stressors such as frost, heat, pests, drought, diseases, and nutrient imbalance (Wang *et al.*, 2021). Si deficiency reportedly decreased photosynthesis, also increased disease incidence, insect infestation, wilting, and postharvest decline. while all of these symptoms are signs of stress (Reynolds *et al*., 2009; Dallagnol *et al*., 2012; Weerahewa *et al*., 2015). Si usually contributes to healthy plant development and is essential for cell development and differentiation. The protective role of Si in drought conditions is mainly associated with an enhanced level of water retention, which promotes photosynthesis (Zhang *et al*., 2018). It accelerates the accumulation of osmolyte regulators (proline and carbohydrates) as well as antioxidant activities in plants exposed to stress in the environment (Moussa and Shama, 2019). Potassium silicate (K-silicate) is used as a source of highly soluble K and Si. K-silicate does not contain volatile organic compounds, and its application does not result in the release of hazardous or pollutant byproducts (Romero-Aranda *et al.*, 2006). In a relevant study, the application of K-silicate to the soil, for several plant species under irrigation with water-deficit conditions, resulted in the highest biomass of all species (Moussa and Shama, 2019). Si can act as a growth regulator and can potentially increase plant growth under drought stress. Spraying K-silicate and other nanomaterials can potentially reduce the adverse effects of drought stress on crops (Zahedi *et al*., 2020).

The common daisy (*Bellis perennis*) belongs to the Asteraceae family and is known as an archetype. *Bellis perennis* is an important ornamental and medicinal plant with a global distribution. It is one of the first flowering species and is a crucial member of spring bloomers (Siatka and Kašparová, 2010). Daisies are grown for their beauty, either for color or aesthetic reasons. They are naturally able to provide economic, environmental, and social benefits. However, water-deficit largely affects the ornamental value of this species.

In the current study, we focused on the response of daisies to drought stress, while monitoring their antioxidant enzymes, substances for osmotic regulation, and secondary metabolites. Although many studies have already considered the role of potassium silicate in reducing the adverse effects of drought stress in various plants, there is little information about the effects of potassium silicate on ornamental plants under drought-stress conditions. Therefore, the objective of the current study was to investigate the effects of potassium silicate on the characteristics of daisies under drought-stress conditions. The mechanisms of action by potassium silicate, their advantages for ornamental plants, and their ability to create drought tolerance provide a scientific basis for using potassium silicate to alleviate drought stress.

2. Materials and Methods

Plant culture, drought stress, and potassium silicate treatments

This study was carried out at the Ferdowsi University of Mashhad (autumn-spring 2021). Seeds of *Bellis perenesis* L. were purchased from Takii seed company. In September 2021, the seeds were grown in polyethylene bags containing a mixture of peat and perlite (3:1) for four weeks (trifoliate stage) under controlled conditions (21°C/17°C day/night and 45-55% humidity under 100 mmol photons m^{-2} s^{-1}. Four weeks later, the trifoliate seedlings were transplanted into pots. For each treatment, the experiment was laid out with three pots. The pots were placed in a greenhouse (air temperature of 21±2°C and relative humidity of 62±2%) during the growing periods. Irrigation started after one day, and the plants were well watered for a few months (90-85% FC). Drought treatment was initiated by omitting irrigation, and potassium silicate (K_2SiO_3) was used as the Si source. Potassium was administered to the plants in the form of liquid potassium silicate (K_2SiO_3) (10% K_2O, 25% SiO_2) at three concentrations (0, 2, 4 mM) (The concentrations of potassium silicate were selected according to a pretest). In March, the plants were treated with different solutions, i.e. (1) 1/2 Hoagland's solution without the addition of K_2SiO_3, (2) 1/2 Hoagland's solution with the addition of 2 mM K_2SiO_3, (3) 1/2 Hoagland's solution with the addition of 4 mM K_2SiO_3. Potassium silicate was applied as a treatment for one month in March, and irrigation treatments began with drought stress (80%, 70%, and 60% FC) in April. Three levels of water deficit (i.e. 80, 70, and 60% of field capacity, FC) were applied from April to June. The gravimetric method (Campbell and Mulla, 1990) was used for irrigation for two months. First, several pots were completely irrigated so that the water permeated all pores in the soil. Then, the pots were wrapped with plastic covers to prevent evaporation and transpiration. The pots were weighed until their weight remained constant for two consecutive measurements. Then, a soil sample was taken to the laboratory. The fresh weight was measured and the dry weight was calculated after 12 hours of storage in an oven at 105°C. The percentage of moisture content by weight, required for suitable crop production, is calculated based on the following equation:

$$FC = (A\text{-}B / B) \times 100$$

where FC, A, and B are the field capacity, the weight of moist soil after gravity drainage, and the weight of the sample dried at 105°C for 12 hours, respectively.

The weight difference between water-saturated and oven-dried soil was taken as the weight of water needed to bring the pots to field capacity, and then lower water contents in the soil (% field capacity) were calculated accordingly. During the period of treatments, the pots were regularly weighed, and additional water was supplied when necessary. For each test, there were three replicates containing five plants, making a total of 15 plants. At the end of the experiment, the fresh leaves were used for measuring electrolyte leakage, RWC, and chlorophyll content. For determining the nutrition concentration and proline content, dried leaves were frozen in liquid nitrogen and stored at -80°C until the time of measurements.

Determination of K and Si concentration

The K and Si concentrations were determined on the dry leaves samples. Oven-dried leaves (300 mg of the dried samples) were weighed and burned in a muffle furnace at 550°C for 8 hours. The K concentration was determined by flame photometry (PFP7, Jenway, UK). The Si concentration was determined by the colorimetric ammonium vanadate method (Jaiswal, 2003).

Measurement of electrolyte leakage and relative water content

Electrolyte loss was determined according to a method used by Gusta *et al.* (2003), and relative water content (RWC) was calculated via a method used by Pieczynski *et al*. (2013).

Measurement of antioxidant activity and malondialdehyde (MDA)

Antioxidant activity was determined using 1,1-diphenyl-2-picrylhydrazyl (DPPH). The extract (100 mg of fresh weight + ethanol) was blended with 960 µL of DPPH in methanol. The supernatant was centrifuged for 5 min and kept in the dark room. The DPPH was determined using a Shimadzu UV-1800 spectrophotometer at 515 nm (Kedare and Singh, 2011). Malondialdehyde (MDA) content was measured according to Velikova *et al.* (2000) methods. Leaf tissues (0.5 g of each) were homogenized in 8 ml of 0.1% (w/v) trichloroacetic acid and the homogenates were centrifuged for 10 min at 4 °C, after which the supernatants were used for malondialdehyde analysis. Equal volumes of extracts were mixed with 0.5% (w/v) of thiobarbituric acid made in 5% (w/v) trichloroacetic acid and heated at 100°C water bath for 20 min, after which their actions were stopped in the ice bath. After centrifuging,the absorbance of the supernatant was measured at 450, 532, and 600 nm.

Determination of antioxidant enzyme activities

Extraction was performed according to a method used by DaCosta and Huang (2007). Samples (0.5 g of fresh weight) were ground in liquid nitrogen and were homogenized in 4 mM phosphate buffer (pH 7.8), 60 M riboflavin, 195 mM methionine, 3 M EDTA, and 1.125 mM nitro blue tetrazolium chloride (NBT). Enzyme activities were expressed per fresh weight of the sample. One SOD activity unit was defined as the amount of enzyme required to cause 50% inhibition of nitro blue tetrazolium chloride (NBT) photoreduction (Sairam *et al.,* 2002). Catalase activity (CAT) was measured as described by Abedi and Pakniyat (2010). The reaction solution consisted of 50 mM K-phosphate buffer (pH 7.0), ten mM H_2O_2, and 50 mL enzyme extract. The decomposition of H_2O_2 was measured at 240 nm. The peroxidase activity (POD) was measured by the guaiacol method (Guan *et al*., 2015). The oxidation of guaiacol was monitored by observing changes in the absorbance values at 470 nm for 3 min. The reaction mixture contained 50 ml of 100 mM PBS (pH 6.0), 10 mM H_2O_2, 2.58 mM of guaiacol. The reaction was started by adding the enzyme extract to the reaction mixture solution.

Measurement of photosynthetic pigments

Chlorophyll contents (Chl a, b, and total Chl) were measured by squashing the leaves (200 mg) in 10 ml 80% acetone solution, and the chlorophyll content was determined at 645 and 663 nm, respectively using a Shimadzu UV-1800 spectrophotometer (Nagata and Yamashita, 1992).

Determination of osmotic regulators

Carbohydrates were determined using the Anthrone reagent method. Fresh leaves (500 mg) were placed in 70% methanol and reached the required volume with distilled water. The samples were used for estimations of carbohydrate content using the Anthrone reagent (McCready *et al.,* 1950). Proline content was calculated according to Bates *et al.* (1973). The leaf extract (0.1 mg leaf sample + 10 ml sulfosalicylic acid) was homogenized in glacial acetic acid and ninhydrin acid. Then, the solution was heated in a boiling water bath. After cooling, 5 mL of toluene was added, and then the top layer of the solution was removed and centrifuged at 3000 g for 5 minutes. The proline content was determined at 520 nm using a Shimadzu UV-1800 spectrophotometer.

Secondary metabolite measurements

Total phenolic content was measured using the Folin-Ciocalteu reagent method (Singleton and Rossi, 1965). In the Folin-Ciocalteu method, 250 µl of the alcoholic extract (100 mg + 10 ml ethanol) was diluted to a known volume with distilled water, 10% Folin reagent, and 7.5% sodium carbonate. The phenolic content was determined at 675 nm using a Shimadzu UV-1800 spectrophotometer. Assaying the total anthocyanin content followed, a method by Sukwattanasinit *et al.* (2007), where two buffer solutions were used (25 mM K-chloride pH 1.0 and 0.4 M Na-acetate pH 4.5). The values were noted at 510 nm using a Shimadzu UV-1800 spectrophotometer. Flavonoid content was assayed according to a method by Zou *et al*. (2004). The extract (500 mg + 5 ml ethanol) was homogenized in 4.5 mL distilled water and 0.3 mL 5% $NaNO_2$. Next, after mixing the solution properly, 1 mL of 10% $AlCl_3$-$6H_2O$, 2 mL of 1 M NaOH, and distilled water were added to the reaction mixture. The absorbance values were determined at 510 nm using a spectrophotometer (Shimadzu UV-160A).

Statistical analysis

The difference between treatments was determined using a factorial layout and a completely randomized experimental design with three replicates followed by the LSD testing (P<0.01). Data were subjected to two-way analysis (ANOVA) with repeated measures and were analyzed using the SAS statistical package (version 9.2, SAS Institute, Cary, NC, USA).

3. Results

The potassium and silicon concentrations were significantly (*P*<0.01) affected by fertilizer and drought stress. Potassium (K) concentration in the control plants decreased by 14.9% under drought stress at 60% FC compared to 80% FC. A decrease in leaf K content was observed by the effect of potassium silicate at a concentration of 2 and 4 ppm by 8.08 and 21.2%, respectively, under 70% FC. However, the amount of decrease was 8.7 and 18.2%, respectively, under 60% FC (Fig. 1 a). The Si concentration was significantly improved by all potassium silicate applications under the water deficit conditions. The Si concentration increased in response to 4 mM potassium silicate under 80 and 60% FC (by 926 and 998%, respectively) compared to control plants (Fig. 1 b).

The results showed that the interaction of potassium silicate and drought stress significantly (*P*<0.01) affected electrolyte leakage, RWC, antioxidant activity, and MDA accumulation. Potassium silicate signifi-

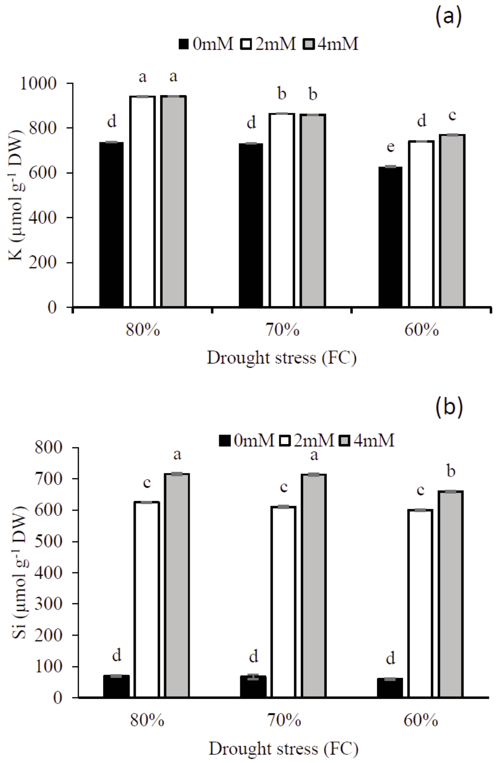

Fig. 1 - Effect of exogenous application of potassium silicate on K (a), and Si (b) of daisy under water-stress conditions. Bars with a different letter differ significantly (P<0.05) according to the LSD test.

cantly inhibited the decrease in electrolyte leakage, whereas a more significant level of decrease was observed in the control plants at 60% FC. As shown in figure 2a, electrolyte leakage was increased by 102, 150, and 220% at 60% FC in control plants, 2 and 4 mM compared to 80% FC, respectively. RWC was reduced by 8.6 and 11.7% under drought stress (60% FC) in response to 2 and 4 mM potassium silicate compared to 80% FC. Compared with the control, the application of 4 mM potassium silicate significantly increased the RWC of plants, whereas 2 mM potassium silicate had no significant effect on the RWC compared to the control plants (Fig. 2 b).

The antioxidant activity increased significantly in response to drought stress, but the application of 2 and 4 mM potassium silicate under severe drought stress resulted in even higher values of antioxidant activity. Nonetheless, no significant difference was observed between potassium silicate-treated plants and the control plants at 80% FC. The antioxidant activity reached maximum values, increasing by 33.7 and 36.5% when the daisies were treated with 2 and 4 mM potassium silicate at 60% FC compared to the control plants, respectively (Fig. 2 c). The role of potassium silicate at 2 and 4 ppm was effective in reducing MDA accumulation under drought stress. Plants treated with potassium silicate under drought stress showed lower MDA levels in the following order: 2 and 4 mM of potassium silicate than control

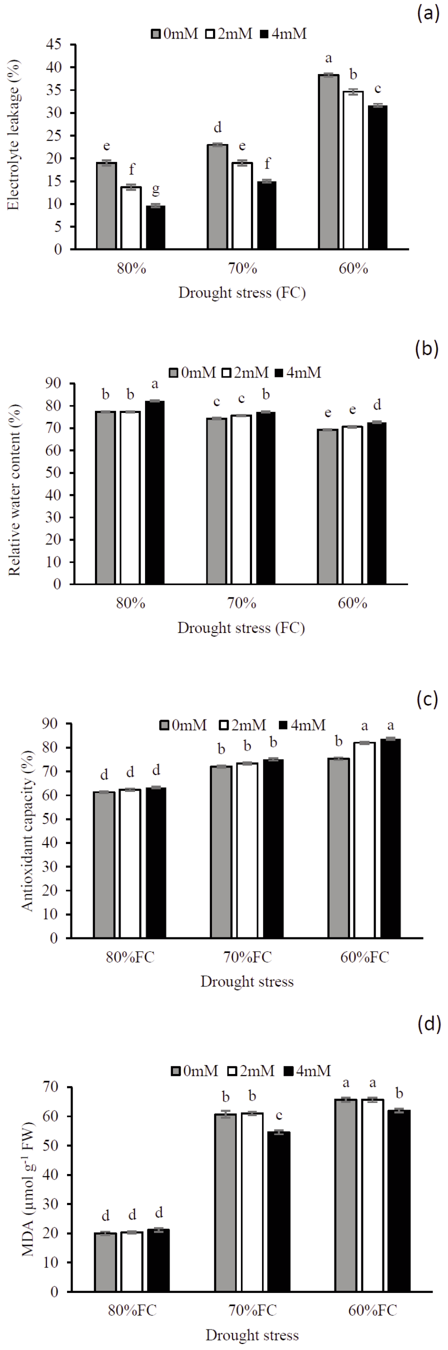

Fig. 2 - Effect of exogenous application of potassium silicate on electrolyte leakage (a), relative water content (b), antioxidant activity (c), and MDA (d) of daisy under water-stress conditions. Bars with a different letter differ significantly (P<0.05) according to the LSD test.

plants. Thus, decreasing effect on this trait resulted from using 4 mM potassium silicate at 70 and 60% FC. The MDA peaked when the daisies were treated with distilled water and 2 mM potassium silicate at 60% FC. However, no significant difference was observed between the control plants and either of the 2 and 4 mM potassium silicate treatments under the effect of 80% FC (Fig. 2 d).

Drought stress significantly (*P*<0.05) increased the activities of antioxidant enzymes, catalase, peroxidase, superoxide dismutase, and aspartate peroxidase by 7.76-31.54%, 313-323%, 127-181%, and 4.22-99.35%, respectively, under drought stress (Fig. 3). In general, potassium silicate increased all of the mentioned enzyme activities, but this increase was higher in reponse to the 4 mM treatment under drought stress. The application of potassium silicate at 2 and 4 mM significantly improved the activity of CAT by 29.4 and 35.2%, respectively, in daisies grown at 60% FC compared to the control plants (Fig. 3 a). All potassium silicate treatments significantly improved the activity of POD under drought stress conditions. The POD activity increased in response to the 70% FC compared to the control, but decreased more at 60% FC, compared to 70% FC. As shown in figure 3 b, the activity of POD increased by 42.7 and 50.3% in plants treated with 2 and 4 mM potassium silicate, respectively, compared to the control plants under 60% FC.

Under the conditions of drought stress, the application of potassium silicate significantly increased the activity of APX. In response to 60% FC, the plants showed the highest APX activity. Although no significant differences were observed between potassium silicate-treated and control plants at 60% FC, a sharp increase in APX activity was observed when 4 mM potassium silicate was used along with drought stress. The application of 4 mM potassium silicate increased the activities of APX by 14.5% at 80% FC and by 87.8% at 60% FC compared to the control plants (Figs. 3c). The application of potassium silicate increased the SOD activity under drought stress conditions. This pattern of increase was more prominent (37.5 and 30.2%) at both potassium silicate levels along with moderate drought stress, compared to 80% FC, whereas it was least prominent in severe conditions (60% FC). The activity of SOD in daisy leaves increased by 28.4 and 21.5% at 60% FC, using potassium silicate at 2 and 4 mM, respectively, compared to well-watered plants (Fig. 3 d).

The data revealed that the chlorophyll (chl) a, b, and total chlorophyll contents were significantly (*P*<0.05) affected by fertilizer and drought stress. Regarding chl a, b, and total chl in the leaves under drought stress, these parameters decreased in response to the drought stress severity . This downward trend was 34.68 and 55.4% higher in the case of Chl a, but was 2 and 6.25% lower in the case of Chl b when severity of drought increased. The application

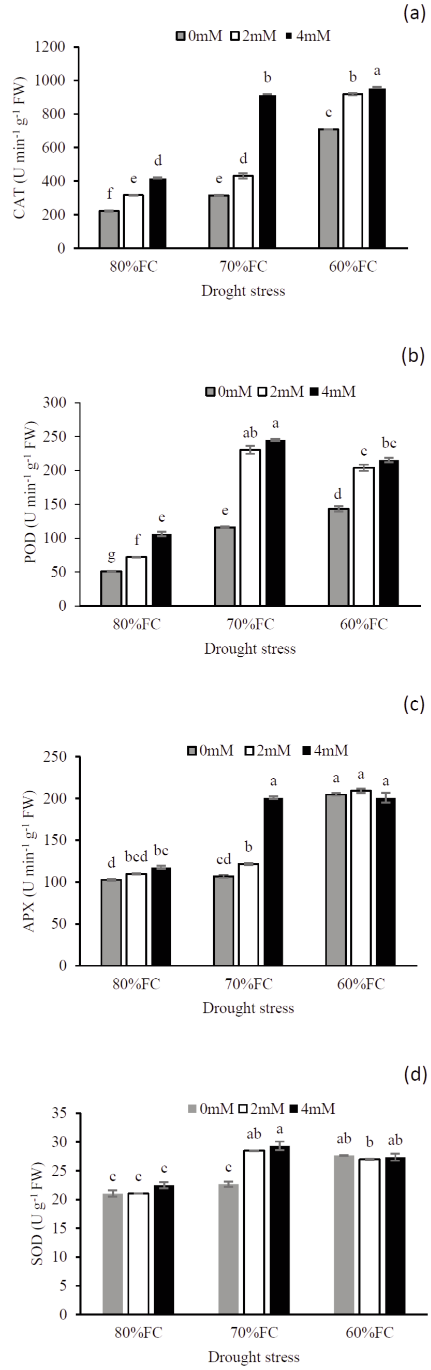

Fig. 3 - Effect of exogenous application of potassium silicate on CAT (a), POD (b), APX (c), and SOD (d) of daisy under water-stress conditions. Bars with a different letter differ significantly (P<0.05) according to the LSD test.

of potassium silicate at a concentration of 2 mM increased the chl a and chl b by 68 and 67%, respectively, at 70% FC. Furthermore, the mentioned values were increased by 41.4 and 97%, respectively, at 60% FC compared to the control. The highest content of chl a and b were observed when plants were treated with 4 mM potassium silicate at 80 and 70% FC (Figs. 4 a, b). During drought stress, total chl gradually decreased in response to greater intensity of drought stress. The total chl value decreased by 127% under 60% FC compared to 80% FC and by 98% compared to 70% FC. This value was also affected by potassium silicate under drought stress. Total Chl content was significantly improved by all potassium silicate applications under the drought stress conditions. Total chl content increased by 7.4 and 72% in response to 4 mM potassium silicate at 80 and 70% FC, respectively (Fig. 4 c).

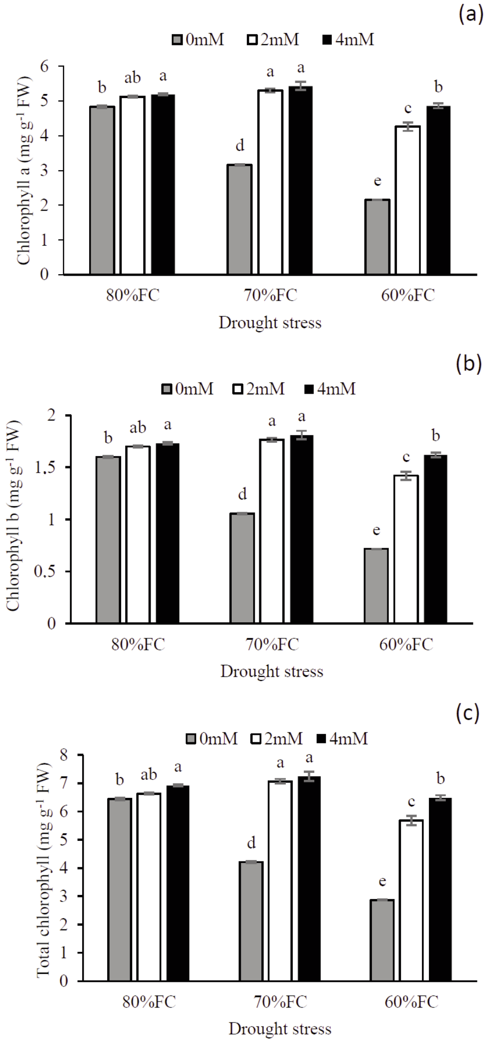

Fig. 4 - Effect of exogenous application of potassium silicate on chlorohyll a (a), chlorohyll b (b), and total chlorohyll (c) of daisy under water-stress conditions. Bars with a different letter differ significantly (P<0.05) according to the LSD test.

The application of potassium silicate significantly (P<0.05) increased the amount of carbohydrate and proline content in the leaves under drought stress. At 80% FC, potassium silicate-treated plants had no significant difference from the control plants in terms of carbohydrate content. By applying drought stress, an increase in carbohydrates was observed in the leaves when the plants were treated with potassium silicate. In response to 2 and 4 mM potassium silicate, the carbohydrate content increased by 31.3% and 26.6% at 70% FC, and by 60.8% and 53.2% at 60% FC, respectively, compared to the 80% FC (Fig. 5a). Regarding proline changes in the leaves, there was an increase of 4.7- and 1.6-fold by the effect of 60% FC and 70% FC, respectively, compared to the 80% FC. The application of 2 and 4 mM potassium silicate increased this parameter further by 75 and 42% at 70% FC, respectively, but by 385 and 312% at 60% FC, compared to the control plants. The highest proline

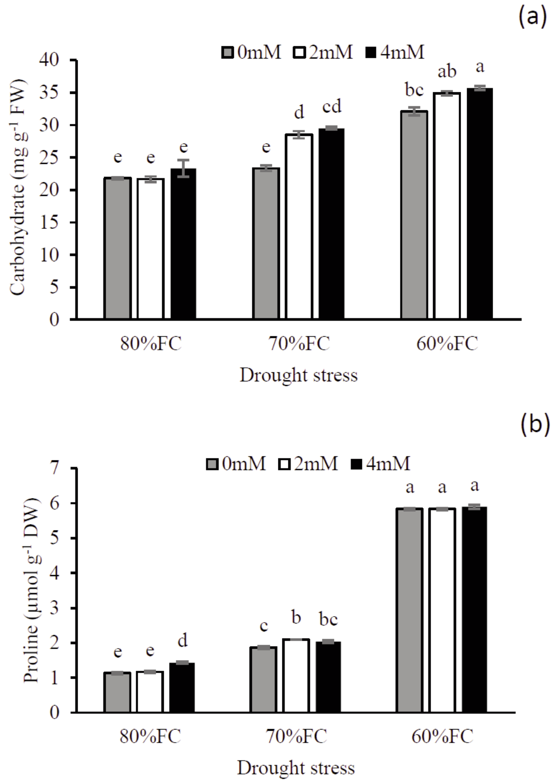

Fig. 5 - Effect of exogenous application of potassium silicate on carbohydrate (a), and proline (b) of daisy under water-stress conditions. Bars with a different letter differ significantly (P<0.05) according to the LSD test.

content was observed in drought-stressed plants (60% FC) treated with potassium silicate. However, no significant difference was observed between 2 and 4 mM potassium silicate under severe drought stress (Fig. 5b).

In general, potassium silicate (2 and 4 mM) at 80% FC significantly (*P<0.01*) increased the flavonoid content by 36 and 45.5% compared to the control plants. In the control plants. Increasing the severity of drought stress at 70 and 60% FC decreased this trait by 50.2 and 97.2%, respectively. The application of 2 and 4 mM potassium silicate increased the flavonoid content by 10.3 and 41.9%, respectively, at moderate water deficit (70% FC), but by 51.7 and 62.3%at severe water deficit (60% FC), respectively, compared to the 80% FC (Fig. 6 a). Figure 5b shows that the phenolic content increased in response to the intensity of drought stress, and the highest value was found at 60% FC. Total phenolic content increased significantly by 31.1 and 43.8% when potassium silicate-treated plants (4 mM) were under the effect of 80 and 70% FC, respectively, compared to the control plants. Potassium silicate (2 mM) increased the phenolic content by 27 and 46%, respectively. At 4 mM, it caused an increase of 39 and 57%, respectively, under the effect of 70 and 60% FC, compared to 80% FC. The highest anthocyanin content occurred when the potassium silicate-treated plants were grown at 80% FC. As for anthocyanin changes in the flowers, there was a decrease in response to the intensity of drought, but potassium silicate increased the value further. The anthocyanin content decreased in response to 4 mM potassium silicate at 60% FC, compared to 80% FC (11.2%). Both concentrations of potassium silicate significantly increased the anthocyanin content in the flowers by 228% at most, under the effect of 80% FC, compared to the control plants (Fig. 6 c).

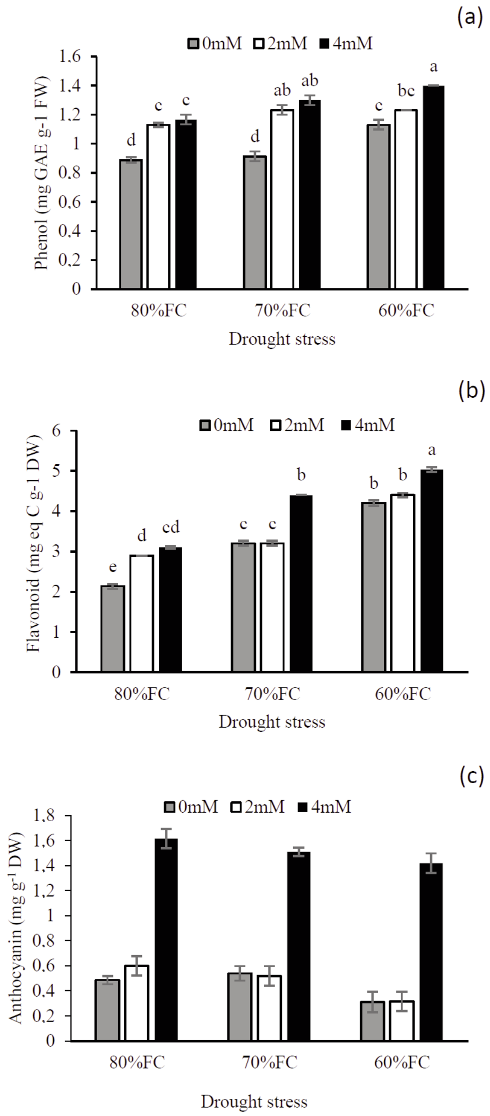

Fig. 6 - Effect of exogenous application of potassium silicate on phenol (a), flavonoid (b), and anthocyanin (c) of daisy under water-stress conditions. Bars with a different letter differ significantly (P<0.05) according to the LSD test.

4. Discussion and Conclusions

The application of potassium silicate improved nutrient uptake under drought stress. Si is not an essential nutrient but protects plants from a variety of biotic and abiotic stresses (Ranjan *et al.,* 2021). The highest concentration of K and Si in the plant occurred in response to 4 mM potassium silicate at 80% FC. These results emanate from the ability of plants to enhance root growth after potassium and silicon application, thereby increasing nutrient uptake (Sustr *et al*., 2019). The increase in K uptake is usually concomitant with a decrease in plasma membrane permeability and an increase in Si-induced H-ATP activity in plasma membranes (Zhu and Gong, 2014). K deficiency decreases the uptake and transfer of some nutrients by inhibiting enzymatic activities such as synthases, transferases, and kinases (Liu *et al*., 2013). Si leads to more significant root activity, consequently, a greater amount of nutrient uptake. Sarto *et al*. (2014) attributed the beneficial effects of Si to its concentration in the leaves and stems of wheat. Si is also known to influence the development of apoplastic barriers in roots by controlling apoplastic pathways, followed by its translocation through the root apoplast to the shoot (Vaculík *et al*., 2012). One explanation for the increased tolerance in plants growing under water-deficit conditions could be a decrease in transpiration through the stomata and cuticle due to Si application. Silicon not only affects nutrient availability and uptake but also nutrient translocation from the roots to the shoots (Greger *et al*., 2018). In this study, drought significantly decreased the concentration (%) of K and Si. Also, drought stress can have a significant impact on plant nutrient ratios. Several studies have shown that drought can reduce nutrient uptake from the soil (Ge *et al*., 2012; Bista *et al*., 2018).

Under water-deficit conditions, potassium silicate reduces electrolyte leakage. Potassium silicate plays an important role in plant resistance to environmental stress. Within the plant, silicate is an immobile element that becomes a polymer gel and reduces the loss of ions from biomembranes after being deposited in the cell. The results of this study are consistent with a previous study by Othmani *et al.* (2021) who found that the more significant stability of the cell membrane in the presence of silicon was due to the hardening and strength of the cell wall. The water content of leaves under drought stress (70 and 60% FC) decreased compared to the 80% FC. Drought stress reportedly caused a decrease in leaf water content in most plants (Santos *et al*., 2021). In our study, the administration of potassium silicate led to an increase in the relative water content of leaves. A lower rate of water loss in silicate-potassium-fed plants can also be attributed to the lower transpiration of the plants. The accumulation of silicate in the lower epidermal cells reduces water loss through the cuticle. Si is deposited in plant tissues in the apoplast of the cell wall to form silica, thereby maintaining tissue integrity (Guerriero *et al*., 2016). In addition, potassium is primarily an important osmotic regulator in plants. Between 30 and 50% of the osmotic potential of leaf tissue is regulated by K (Turcios *et al*., 2021).

In the current study, potassium silicate reduced plant injury by decreasing MDA and increasing antioxidant activity. Malondialdehyde is the peroxidation product of unsaturated fatty acids in phospholipids. Therefore, the production of malondialdehyde under stress conditions can be used as a marker of lipid peroxidation (Ayala *et al*., 2014). As a result of drought, the peroxidation of glycopeptides occurred in chloroplast thylakoid, followed by the formation of diacylglycerol, triacylglycerol, and free fatty acids, leading to an increase in malondialdehyde in plant tissues (Sofo *et al*., 2004). Fatty acids and lipids are reportedly sensitive to oxygen species and are rapidly oxidized. The results are in line with previous studies indicating a positive effect of potassium silicate on malondialdehyde levels in damask rose (*Rosa damascena* Miller) under drought stress (Farahani *et al*., 2020). The ability of plants to scavenge free radicals was impaired by both drought and the addition of potassium silicate compared to the control plants. DPPH inhibition levels were below 70% and 60% FC at 4 mM potassium silicate compared to the control. Under drought stress, DPPH levels increased, and potassium silicate further enhanced the DPPH levels (Zahedi *et al*., 2020).

In this study, the administration of potassium silicate under drought stress conditions (i.e. the application of irrigation water to maintain 70 and 60% FC) increased all antioxidant enzyme activities. An increase in antioxidant activity in the leaves occurred in response to both potassium silicate concentrations and drought stress. The high activity of antioxidant enzymes such as CAT, POD, APX, and SOD in plants is an adaptive mechanism that protects cells from oxidative damage by reducing the concentration of hydrogen peroxide generated by cellular metabolism (Jan *et al*., 2022). Improving potassium concentration leads to an increase in photosynthetic products, the control of ionic balance, osmotic regulation, and an increase in enzymatic activity. By stimulating the activity of POD and APX through the detoxification of hydrogen peroxide, Si prevents oxidative stress and inhibits the production of hydroxyl radicals (Kim *et al*., 2017). In agreement with the current results, Ahmad *et al*. (2019) reported that using silica on mung beans (*Vigna radiata* L.) increased catalase and superoxide dismutase activities under drought stress. Superoxide dismutase is an enzyme that converts superoxide free radicals into hydrogen peroxide and oxygen while playing an important role in protecting cells from the negative effects of free radicals. SOD is the first line of defense of cells against free radicals under stress conditions (Ighodaro *et al*., 2018). The effects of Si nutrition on SOD activity and free radical elimination have been reported in the available literature (Geng *et al*., 2018). Gong *et al*. (2005) reported that using potassium silicate increased the activity of antioxidant enzymes in wheat (*Triticum aestivum* L.) under drought stress. The removal of reactive oxygen species decreases cell membrane permeability and increases the activity of catalase, peroxidase, and superoxide dismutase, which indirectly decrease cell membrane lipid peroxidation and reduce the amount of malondialdehyde (Sharma *et al*., 2012).

The application of potassium silicate along with drought stress increased the amounts of photosynthetic pigments. A decrease in chlorophyll content occurred due to drought stress and was accompanied by an increase in the production of oxygen radicals in the cells. The radicals usually cause peroxidation, and consequently, the degradation of photosynthetic pigments. The effect of potassium silicate on the stability of plant pigments usually results from the accumulation of silicate in the epidermal cells, which has an indirect protective effect on the photosynthetic establishments, thereby reducing the stress-induced damage to photosynthetic pigments. Similar to the current results, a moderating effect of potassium silicate was reportedly observed on the chlorophyll content of *Rosmarinus officinalis* L. plants (Waly *et al*., 2019).

The results showed that the concentration of osmotic regulators (i.e. proline and total carbohydrates) increased significantly when potassium silicate was applied under water-deficit conditions. Silicon and potassium increase the production of carbohydrates and proline by increasing the osmotic potential, possibly through the accumulation of free radicals produced by the plant. They are thought to play an adaptive role in mediating osmotic adjustment and protecting subcellular structures in stressed plants (Hajiboland *et al*., 2017). These effects suggest that potassium and silicon may enhance leaf osmotic potential by converting starch to soluble sugars, especially under severe drought stress (Zahoor *et al*., 2017). It appears that potassium silicate stimulates carbohydrate production and, thus, alters the metabolism of plant-absorbed K and its conversion to proteins (Hafez *et al*., 2021). Si can directly or indirectly induce the biosynthesis of proline. Garg and Sing (2018) showed that the application of Si increased the activity of pyrroline-5-carboxylate synthetase (P_5CS) and glutamate dehydrogenase (GDH). In addition, the increase in proline because of potassium silicate treatment may highlight the importance of potassium and silicon in protecting cell membranes and maintaining relative water content under inadequate irrigation conditions. In this context, using silica on borage (*Borago officinalis* L.) plants reportedly increased the amount of proline in the leaves (Gagoonani *et al*., 2011). In agreement with these results, Ibrahim et al. (2020) reported that potassium silicate increased the proline content of maize plants under drought stress.

By reducing vegetative growth and altering the anatomical structure of the plant through the induction of secondary stress, e.g. oxidative stress, the effect of drought stress usually cause changes in the pathways of synthesis that make secondary compounds and metabolites (Ahanger *et al*., 2017). Polyphenols can improve plant tolerance to drought stress and play an important role as a carbon sink at times of stress. These effects may explain significant improvements in total phenolics in daisies because of their exposure to drought stress (Fig. 6 a). The increase in total soluble phenols in response to the application of K_2SiO_3 under drought stress could be a supporting effect of Si, thereby increasing plant tolerance, especially under water-deficit conditions. Fouda *et al*. (2021) found that potassium silicate increased the total flavonoid content in field beans. Feeding plants with Si and K-containing compounds has reportedly resulted in changes in the expression pattern of many genes. In particular, feeding plants with potassium- and silicon-containing compounds has led to changes in genes that encode enzymes involved in the phenylpropanoid pathway (Wang *et al.,* 2017). Indeed, the increase in phenylalanine ammonia-lyase activity is a common feature in plants treated with silicon, thereby enabling an increase in the synthesis of phenolic compounds. Potassium silicate increases polyphenols in many plants by activating enzymes that are relevant to the phenol production pathway, such as the phenylalanine ammonia-lyase (Vega *et al*., 2019).

The ability of plants to tolerate drought could be mainly explained by an increase in flavonoid content since flavonoids are compounds with strong antioxidant activity. Perin *et al*. (2019) suggested that the relationships between ABA metabolism, phenylpropanoid, flavonoid, and anthocyanin pathways can reduce drought stress. Probably, this could be one of the main reasons for the better tolerance of plants to drought stress. Drought largely affects the average performance of plant traits by reducing their properties, leading to a decrease in the associated anthocyanin content. Under drought stress, the anthocyanin content decreased, but potassium silicate increased the anthocyanin content of flowers (Fig. 6 c). These results are consistent with a previous study by Cirillo *et al*. (2021) in which anthocyanin content was reduced by the effects of stress. Jafari *et al*. (2015) reported that silicon treatment under osmotic stress significantly increased the amount of non-enzymatic antioxidants (e.g. anthocyanins, flavonoids, and total phenolic compounds) and nutrients (Si, K^+, and Ca^{+2}) in cucumber plants.

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