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Research Article

Interaction of reserves and osmoprotection in dwarf cashew clones under water stress[1]

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ABSTRACT

Adverse conditions such as low rainfall have led to a reduction in cashew productive areas in the Brazilian Northeast region. The use of rootstocks and scions with characteristic metabolites associated with drought tolerance influences the plant responses. This study aimed to evaluate the interaction between energetic reserves and osmoprotection in grafted dwarf cashew clones under water restriction. The experiment followed a randomized block design, in a 4 × 4 factorial scheme, consisting of four irrigation levels (25, 50, 75 and 100 % of the crop evapotranspiration - ETc) and four scion/rootstock combinations: CCP76/CCP76 (self-graft of CCP76), CCP76/BRS226 (CCP76 grafted onto BRS226), BRS226/BRS226 (self-graft of BRS226) and BRS226/CCP76 (BRS226 grafted onto CCP76), with three replications. Measurements included scion and rootstock stem diameter, relative water content, leaf moisture percentage, membrane damage, carbohydrates, total free amino acids, total soluble proteins, glycine betaine, proline and ionic content. The CCP76/BRS226 combination was efficient under water-restricted conditions (25 and 50 % of the ETc), as evidenced by a significant reduction in the oxidative damages to leaf membranes and a concomitant increase in osmoprotectants such as total free amino acids and proline. Proline emerges as a potential molecular marker for drought tolerance in early dwarf cashew trees. The self-grafted BRS226 and the BRS226/CCP76 combination under the irrigation with 25 % of the ETc were the most affected, exhibiting greater membrane damage, lower foliar potassium accumulation, moisture content and relative water content, and are therefore not recommended under water-restricted conditions.

KEYWORDS: *Anacardium occidentale* L., osmoprotectants, grafting.

RESUMO

Interação de reservas e osmoproteção em clones de cajueiro-anão sob restrição hídrica

Condições adversas como a baixa pluviosidade têm reduzido as áreas produtivas de cajueiro no Nordeste. O uso de porta-enxertos e copas com metabólitos associados à tolerância à seca influencia nas respostas das plantas. Avaliou-se a interação entre reservas energéticas e osmoproteção em clones de cajueiro-anão enxertados sob restrição hídrica. Utilizou-se delineamento em blocos casualizados, em esquema fatorial 4 × 4, com quatro níveis de irrigação (25, 50, 75 e 100 % da evapotranspiração da cultura - ETc) e quatro combinações de copa/porta-enxerto: CCP76/CCP76 (autoenxertia de CCP76), CCP76/BRS226 (CCP76 enxertado em BRS226), BRS226/BRS226 (autoenxertia de BRS226) e BRS226/CCP76 (BRS226 enxertado em CCP76), com três repetições. Foram avaliados o diâmetro do caule da copa e do porta-enxerto, conteúdo relativo de água, porcentagem de umidade foliar, danos à membrana, carboidratos, aminoácidos livres totais, proteínas solúveis totais, betaína de glicina, prolina e conteúdo iônico. A combinação CCP76/BRS226 mostrou-se eficiente em condições de restrição hídrica (25 e 50 % da ETc), com redução significativa nos danos oxidativos às membranas foliares e aumento concomitante de osmoprotetores, como aminoácidos livres totais e prolina. A prolina surge como um potencial marcador molecular de tolerância à seca em cajueiros-anões precoces. Já a autoenxertia de BRS226 e a combinação BRS226/CCP76 sob irrigação a 25 % da ETc foram as mais prejudicadas, apresentando maiores danos às membranas, menor acúmulo foliar de potássio, teor de umidade e conteúdo relativo de água, não sendo recomendadas sob condições de restrição hídrica.

PALAVRAS-CHAVE: *Anacardium occidentale* L., osmoprotetores, enxertia.

INTRODUCTION

Cashew (*Anacardium occidentale* L.) is a crop of significant socioeconomic importance in the Northeast region of Brazil. It is extensively cultivated due to its agro-industrial potential, which includes the production of cashew nuts, pseudofruits (peduncles), starch and wood (Souza Junior et al. 2022). However,

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a progressive reduction in cultivated areas has been observed, mainly attributed to abiotic factors such as water scarcity and inadequate management practices (Costa et al. 2024).

The Northeast region, which encompasses the largest portion of the Brazilian semi-arid zone, is marked by critical edaphoclimatic conditions characterized by high evapotranspiration rates, low rainfall, shallow soils, intermittent rivers and limited availability of groundwater resources (Lacerda et al. 2022). These conditions promote the frequent occurrence of abiotic stresses, including water deficit, salinity and extreme temperatures, which constrain the cultivation of various agricultural species (Lira et al. 2021).

In response to these challenges, plants have evolved biochemical and physiological mechanisms to mitigate the effects of water stress. Among them, osmotic adjustment stands out, as it enables the maintenance of cellular water content, protects biomolecular structures and reduces the accumulation of reactive oxygen species (Jales Filho et al. 2023). This process involves the synthesis and accumulation of osmoregulatory compounds such as soluble sugars, amino acids (proline), glycine betaine and other organic osmolytes, which act by reducing osmotic potential, thereby preserving cell turgor and water homeostasis under stress conditions (Padilla et al. 2021, Jales Filho et al. 2023).

In this scenario, grafting has emerged as a promising strategy to enhance plant adaptability and productivity by combining scion and rootstock genotypes with complementary traits. Studies have shown that the appropriate selection of rootstocks can improve tolerance to adverse conditions, including water stress, due to physiological and biochemical changes induced by the interaction between grafted tissues (Padilla et al. 2021, Yang et al. 2022, Galaz et al. 2024). However, the mechanisms underlying stress resistance in grafted plants are complex and still not well understood, particularly regarding the biochemical and physiological responses involved in the scion-rootstock interaction.

The resistance mechanisms in grafted plants are highly complex, and the biochemical and physiological changes associated with the interaction between scion and rootstock genotypes remain poorly characterized. Moreover, there is still a lack of knowledge concerning the physiology of dwarf cashew clones cultivated under different water regimes. From this perspective, this study aimed to evaluate the interaction between storage compounds and osmoprotection in grafted dwarf cashew clones under water restriction.

MATERIAL AND METHODS

The study was conducted at the Universidade Estadual da Paraíba, in Catolé do Rocha, Paraíba state, Brazil, from December 2017 to December 2018. The region has a hot and dry semi-arid climate (BSh', according to Köppen) (Alvares et al. 2013).

A randomized block design was used in a 4 × 4 factorial arrangement, combining four irrigation levels (25, 50, 75 and 100 % of the crop evapotranspiration - ETc) and four scion/rootstock combinations: CCP76/CCP76 (self-graft), CCP76/BRS226 (CCP76 grafted onto BRS226), BRS226/BRS226 (self-graft) and BRS226/CCP76 (BRS226 grafted onto CCP76), with three replications.

Early dwarf cashew seeds from the CCP76 and BRS226 clones were provided by the Embrapa Agroindústria Tropical (Fortaleza, Ceará state, Brazil) and sown in polyethylene bags filled with black earth substrate. At 60 days after sowing (DAS), when the plants had approximately 10 leaves, lateral cleft grafting was performed using scions from adult plants of the same clones. Once grafting was successful, seedlings were selected at 120 DAS and transplanted into 6-L pots containing a mixture of sand and vermiculite (1:1). Irrigation was carried out with deionized water alternating with the Hoagland & Arnon's (1950) nutrient solution at ¼ ionic strength for a period of 120 days.

The experimental area was georeferenced using an RTK GPS CHC X900. Planting holes (0.40 × 0.40 × 0.40 m) were prepared with a spacing of 5 × 5 m. At 30 days prior to transplanting, base fertilization was applied according to the soil chemical analysis (Table 1) and recommendations of Crisostomo et al. (2003).

At 240 DAS, the seedlings were transplanted to the field and staked. During the establishment period (approximately 5 months), plants were irrigated with 100 % of the ETc. Monthly topdressing was applied as recommended by Crisostomo et al. (2003), along with foliar sprays of micronutrients containing Mg (1.8 %), B (0.2 %), Cu (0.2 %), Fe (1.5 %), Mn (1.5 %), Mo (0.06 %), Zn (1.5 %) and S (2.6 %).

Table 1. Soil chemical analysis of the experimental area (Catolé do Rocha, Paraíba state, Brazil).

pH	P	K	Na	Ca + Mg	Ca	Mg	Al	H + Al	C	OM	SB	CEC	V
H_2O	Mg dm^{-3}	—— cmol$_c$ dm^{-3} ——							—— g kg^{-1} ——		– cmol$_c$ dm^{-3} –		%
6.5	5.48	0.467	0.08	1.96	1.47	0.49	0.00	0.74	7.55	13.01	2.51	3.25	77.19

OM: organic matter; SB: sum of bases ; CEC: cation exchange capacity; V: base saturation.

Following the establishment period (5 months post-transplanting), the irrigation treatments were initiated and maintained for 30 days, with a 48-hour irrigation interval. Well water (1.1 dS m^{-1}) was used, and the irrigation depths (25, 50, 75 and 100 % of the ETc) were applied using three pressure-compensating emitters (2 L h^{-1} flow rate each, spaced 10 cm apart) per plant. The ETc was calculated daily using data from a weather station installed at the experimental site, based on the method described by Mantovani et al. (2006), according to the following equation: $ETc = [Kc * (Ev * Kp)]/0.9$, where ETc is the crop evapotranspiration (or gross irrigation depth), Kc the crop coefficient (0.5), Ev the water evaporation from the pan (mm day^{-1}), Kp the Class A pan coefficient (Allen et al. 1998) and 0.9 the method efficiency.

The plants were arranged in 12 single rows, each with 4 useful plants. The total experimental area consisted of 48 experimental units plus border plants.

At 30 days under each water regime, the stem diameter above the graft union and at 5 cm below the graft point, corresponding to the rootstock, were measured using a digital caliper. Simultaneously, 10 median leaves from the canopy projection of each plant were collected. Five of these were dried in a forced-air oven at 65 ºC, for determination of carbohydrate content, soluble proteins and free amino acids.

The leaf ion analysis followed specific protocols: sodium (Na^+) and potassium (K^+) were extracted and quantified according to Vogel (1981); the chloride (Cl^-) content was determined by aqueous extraction, as described by Malavolta et al. (1997); and the calcium (Ca^{2+}) content was measured using the method described by Tedesco et al. (1995). All analyses were performed in triplicate to ensure data reliability.

The relative water content (RWC) was determined according to Weatherley (1950): $RWC\ (\%) = [(FM - DM)/[(TM - DM)] * 100$, where FM is the fresh mass, TM the turgid mass and DM the dry mass. The moisture content (U) was calculated using the formula: $U\ (\%) = [(FM - DM)/FM] * 100$.

Membrane integrity was estimated based on electrolyte leakage, following Lutts et al. (1996), whereas membrane damage (MD) was calculated by the formula: $MD\ (\%) = (L_1/L_2) \times 100$, where L_1 is the initial and L_2 the final conductivity.

The total soluble protein content was determined using the method of Bradford (1976), adapted to extract 100 mg of fresh mass in 15-mL tubes with 5 mL of distilled water, using 300 µL of the extract for analysis. The total free amino acid content was measured following the protocol by Peoples et al. (1989), using 500 µL of extract per assay.

The proline content was determined using the method described by Bates et al. (1973), adjusted for 250 mg of dry sample in 15-mL tubes with 5 mL of distilled water. Glycine betaine was quantified according to Grieve & Grattan (1983), using 100 mg of the dry sample in 2-mL Eppendorf tubes.

The total soluble sugar concentration was measured by the phenol-sulfuric acid method (Dubois et al. 1956), adapted for 1.5 mg of fresh material in 15-mL tubes, using 5 mL of distilled water for extraction.

The data were subjected to analysis of variance (Anova) at $p \leq 0.01$ and $p < 0.05$, using the F-test. When significant, the clone combination treatments were compared using the Tukey test at $p \leq 0.05$, and irrigation treatments were analyzed using first and second-order regression models, with the Sisvar 5.6 software (Ferreira 2019). The Pearson's correlation and cluster analysis were conducted using the R software, with the R-Studio interface, applying a significance threshold of $p < 0.05$.

RESULTS AND DISCUSSION

The dwarf cashew plants grafted in different combinations were significantly affected by the water restriction treatments. The analysis of phenological traits indicated physiological variations and differing responses to drought depending on the scion/rootstock combination. A positive correlation was observed between the water status variables - moisture content and relative water content - and total soluble sugars (Figure 1). Conversely, a negative correlation was found between these water status variables and total free amino acids, what may be attributed to the osmotic adjustment mechanism triggered under water deficit conditions. In such scenarios, plants reduce their cellular water potential while maintaining water uptake, thereby inducing the synthesis and accumulation of compatible osmolytes such as soluble proteins and amino acids (Ozturk et al. 2021).

Membrane damage was negatively correlated with leaf moisture and positively correlated with leaf area reduction (Figure 1), a pattern commonly observed under water deficit conditions. Water stress induces the excessive production of reactive oxygen species, which damage cell membranes and stimulate osmolyte synthesis (Razi & Muneer 2021). A positive correlation was found between total soluble protein and antioxidant activity, as well as with Ca^{2+} content. Conversely, the K^+ and Na^+ ions exhibited a negative correlation (Figure 1).

The positive correlation between total soluble protein and antioxidant activity (Figure 1), and with

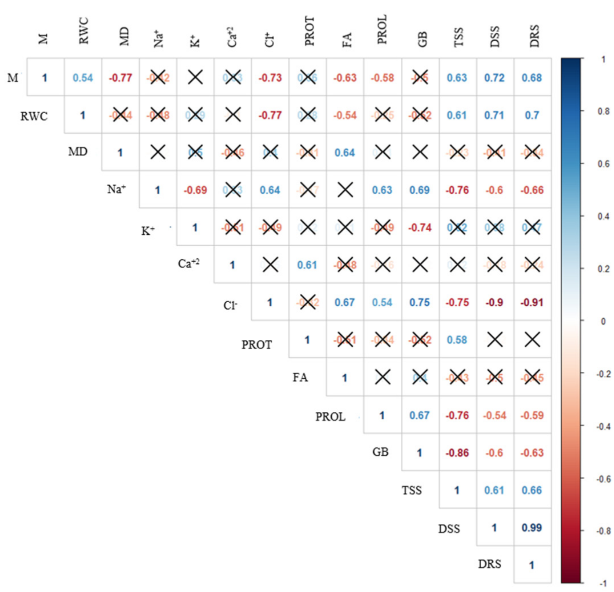


Figure 1. Correlation among the studied parameters at $p < 0.05$ of significance, assessed under different irrigation levels (25, 50, 75 and 100 % of the crop evapotranspiration - ETc) and scion/rootstock combinations for 30 days. M: leaf moisture percentage; RWC: relative water content; MD: membrane damage; Na^+: leaf sodium; K^+: leaf potassium; Ca^{2+}: leaf calcium; Cl^-: leaf chlorine; PROT: protein; FA: total free amino acids; PROL: proline; GB: glycine betaine; TSS: total soluble sugars; DSS: scion stem diameter; DRS: rootstock stem diameter.

Ca^{2+}, suggests that calcium-mediated signaling plays a direct role in enhancing protein and antioxidant synthesis under stress conditions. The influx of Ca^{2+} activates calcium-dependent protein kinases, which induce defense gene expression, resulting in the accumulation of soluble proteins and antioxidant metabolites. Furthermore, Ca^{2+} regulates ion transporters, promoting K^+ retention and Na^+ exclusion, what explains the observed negative correlation between these ions (Ikram et al. 2025).

Growth variables (scion and rootstock stem diameter), water status and antioxidant activity were negatively correlated with Na^+ and Cl^- ions (Figure 1). This behavior is related to osmotic adjustment, which involves the accumulation of compatible solutes (such as sugars) in vacuoles or cytosol to maintain the water balance, thus reducing saline ion concentrations in shoot tissues (Semida et al. 2020, Bañón et al. 2022). In contrast, positive correlations were found among Na^+, Cl^-, proline and glycine betaine, as well as between leaf area reduction and Cl^-.

The graft combinations CCP76/CCP76, CCP76/BRS226, BRS226/BRS226 and BRS226/CCP76 exhibited increases in scion and rootstock stem diameter in response to the higher soil water availability. This increase was proportional to the irrigation level, reaching 34, 7.54, 17.3 and 22.3 %, respectively, at 100 % of the ETc (Figure 2). This pattern is associated with the negative effects of water deficit on plant metabolism, particularly inhibiting cell elongation and expansion, which limit plant growth (Bonfim et al. 2024).

Among the combinations, the CCP76/CCP76 self-graft was the most sensitive to water deficit, showing the lowest scion (13.02 mm) and rootstock (16.93 mm) stem diameter values under 25 % of the ETc. A study by Lima et al. (2023), on the initial development of cashew progenies, similarly found that CCP76 seedlings grown under 70 % of available water exhibited reduced stem diameter.

In contrast, the BRS226/BRS226 self-graft (16.93 mm) and the CCP76/BRS226 combination (16.46 mm) had the largest scion stem diameter under the same deficit condition (Figure 2A). Furthermore, BRS226/BRS226 achieved the highest rootstock stem diameter (22.94 mm) under 25 % of the ETc (Figure 2B), whereas CCP76/BRS226 showed a better tolerance to water deficit, as it did not exhibit growth suppression of rootstock stem diameter, despite the reduced water availability.

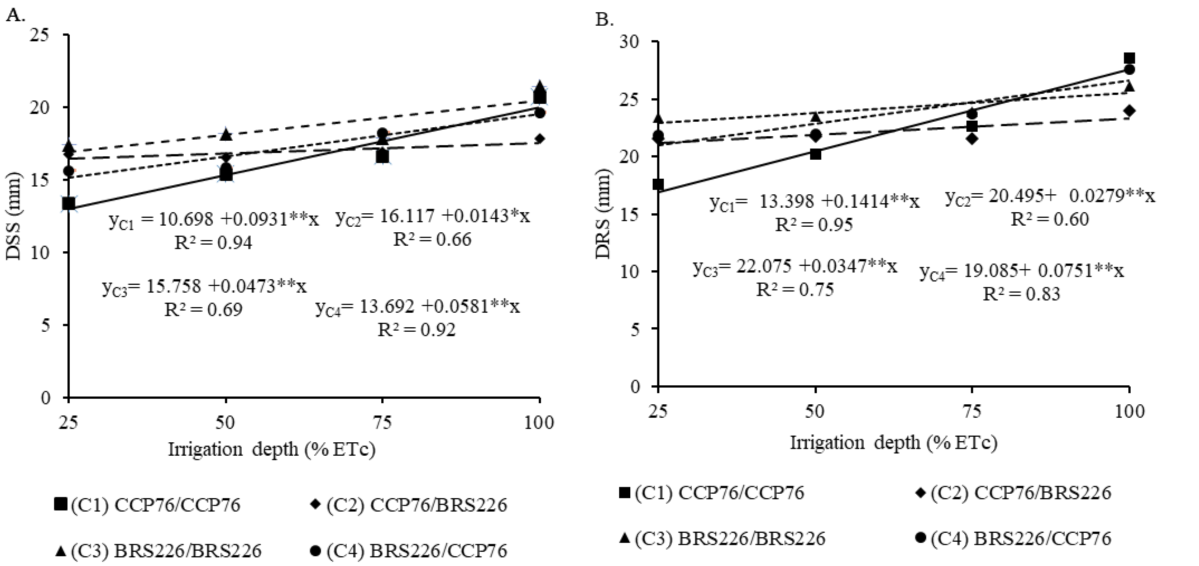


Figure 2. Scion (DSS; A) and rootstock (DRS; B) stem diameter in combinations of dwarf cashew tree clones (C1: CCP76/CCP76; C2: CCP76/BRS226; C3: BRS226/BRS226; C4: BRS226/CCP76) grown under different irrigation levels (25, 50, 75 and 100 % of the crop evapotranspiration - ETc) for 30 days. * and ** : significant at $p \leq 0.05$ and $p \leq 0.01$, respectively, by the F-test.

This suggests that this combination is drought-tolerant, likely due to the BRS226 rootstock, a trend also observed in the BRS226 self-graft, which maintained the rootstock stem diameter stability from 25 to 75 % of the ETc (Figure 2B). This may be attributed to its greater vigor and likely sustained photosynthetic capacity, which support the vegetative growth (Gisbert-Mullor et al. 2023). This phenomenon may result from certain grafting combinations accumulating more osmolytes, enhancing antioxidant enzyme activity and improving root architecture, all of which contribute to stress tolerance (Bahadur & Kumar 2024).

The BRS226/CCP76 combination was the only one to show an increase in leaf moisture with higher water availability, reaching a peak of 69.64 % at 74 % of the ETc (Figure 3A). It is noteworthy that this combination exhibited the lowest leaf moisture under 25 % of the ETc (Figure 3A), indicating that it was more severely affected by water deficit, possibly due to xylem cavitation impairing the water uptake from the soil (Maia Júnior et al. 2025).

The CCP76/BRS226 and BRS226/CCP76 combinations showed no significant changes ($p > 0.05$) for relative water content under water restriction, and also had the highest relative water content values under 25 % of the ETc, indicating a potential drought tolerance. This is because grafted genotypes may enhance drought tolerance by activating stress-responsive genes during drought, involving long-distance ABA signaling, transport and regulation of cellular metabolic pathways, thereby improving the leaf water status (Shehata et al. 2022).

Similar results were observed by Galaz et al. (2024), when evaluating grapevine genotypes grafted for drought tolerance. They found that specific rootstock/scion combinations, such as CS/1103P and CS/101-14, were less affected, suggesting that these rootstocks enhance drought resilience. In contrast, the CCP76 and BRS226 self-grafts showed significant reductions in relative water content, with values of 76.65 and 78.09 %, respectively, under 25 % of the ETc. These represented decreases of 13 and 17 %, respectively, when compared to 100 % of the ETc (Figure 3B).

The self-grafting resulted in a significant reduction of relative water content (Figure 3B), possibly associated with multiple physiological factors. This reduction can be primarily attributed to a decrease in leaf water potential, resulting from water loss in plant tissues (dehydration) induced by water deficit (Padilha et al. 2021). Additionally, environmental factors such as high temperatures and increased transpiration rates may have exacerbated this effect.

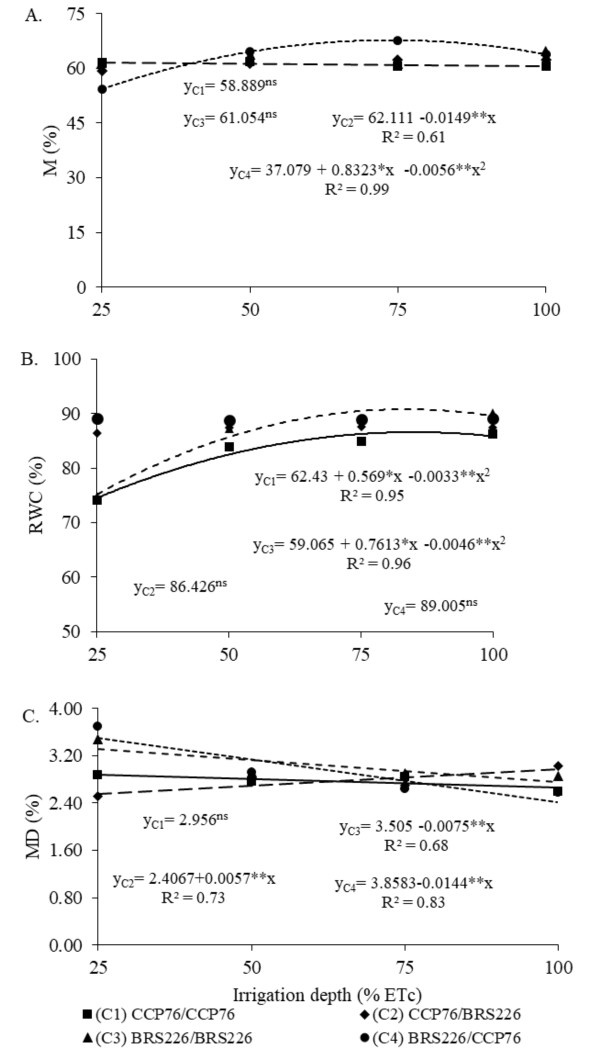


Figure 3. Leaf moisture (M; A), relative water content (RWC; B) and membrane damage (MD; C) in dwarf cashew tree clone combinations (C1: CCP76/CCP76; C2: CCP76/BRS226; C3: BRS226/BRS226; C4: BRS226/CCP76) grown under different irrigation levels (25, 50, 75 and 100 % of the crop evapotranspiration - ETc) for 30 days. *, ** and ^{ns}: significant at $p \leq 0.05$ and $p \leq 0.01$, and not significant, respectively, by the F-test.

Reduced soil water availability caused greater membrane damage in the BRS226/BRS226 and BRS226/CCP76 plants, with membrane damage values of 3.49 and 3.31 %, respectively, under irrigation corresponding to 25 % of the ETc. Generally, water deficit reduces the turgor pressure of guard cells, leading to stomatal closure and subsequent membrane damage (El-Mogy et al. 2022).

However, in the CCP76/BRS226 combination, a clone-specific response was observed, in which membrane damage decreased under water restriction - showing a 14.48 % reduction when comparing the values obtained at 100 and 25 % of the ETc (Figure 3C). This combination likely promoted adaptations in lipid composition, increased antioxidant activity and accumulation of osmolytes such as proline and glycine betaine, or regulation of genes involved in membrane stability and repair under drought conditions (Bahadur & Kumar 2024). Similarly, Sousa et al. (2023) observed variations in the behavior of scion/rootstock combinations of dwarf cashew during the seedling stage under salt stress (which causes water deficit), with membrane damage increases of 29.56 % for CCP 09/CCP 76, 26.46 % for CCP 76 self-graft and 19.66 % for CCP 76/CCP 09, when comparing NaCl concentrations of 100 to 0 mM L^{-1}. However, no changes were observed for the CCP09 self-graft.

Increased water availability did not affect ($p > 0.05$) the sodium (Na^+) concentration in the CCP76 self-grafts. In contrast, the BRS226 self-graft and the CCP76/BRS226 combination showed increased Na^+ levels, reaching maximum values under 100 % of the ETc, corresponding to 288.19 and 207.96 µmol of Na^+ g^{-1} of fresh matter (FM), respectively (Figure 4). The BRS226/CCP76 plants showed an increase in sodium concentration up to an estimated of 48 % of the ETc, with a maximum value of 230.16 µmol of Na^+ g^{-1} of FM. The BRS226/CCP76 combination accumulated the highest sodium content (253.68 µmol of Na^+ g^{-1} of FM) under 25 % of the ETc, while the BRS226 self-graft (138.92 µmol of Na^+ g^{-1} of FM) and the CCP76/BRS226 combination (169.52 µmol of Na^+ g^{-1} of FM) showed the lowest Na^+ content at the same irrigation level (Figure 4A).

The BRS226/BRS226 and BRS226/CCP76 combinations showed approximately 50 % of reduction in K^+ compartmentalization in response to increased water availability from 25 to 100 % of the ETc. However, these were the combinations with the highest K^+ accumulation when water was reduced to 25 % of the ETc (293.57 and 264.08 µmol of K^+ g^{-1} of FM, respectively) (Figure 4B). Increased Na^+ content interferes with K^+ uptake and reduces its levels in various plant organs, a response previously observed in ungrafted young cashew plants (Arruda et al. 2023). Furthermore, the difference among the grafting/rootstock combinations, especially BRS226/CCP76, which accumulated less Na^+ and more K^+ in the leaves, indicates a greater drought tolerance, as a form of acclimation to stress (Sousa et al. 2023).

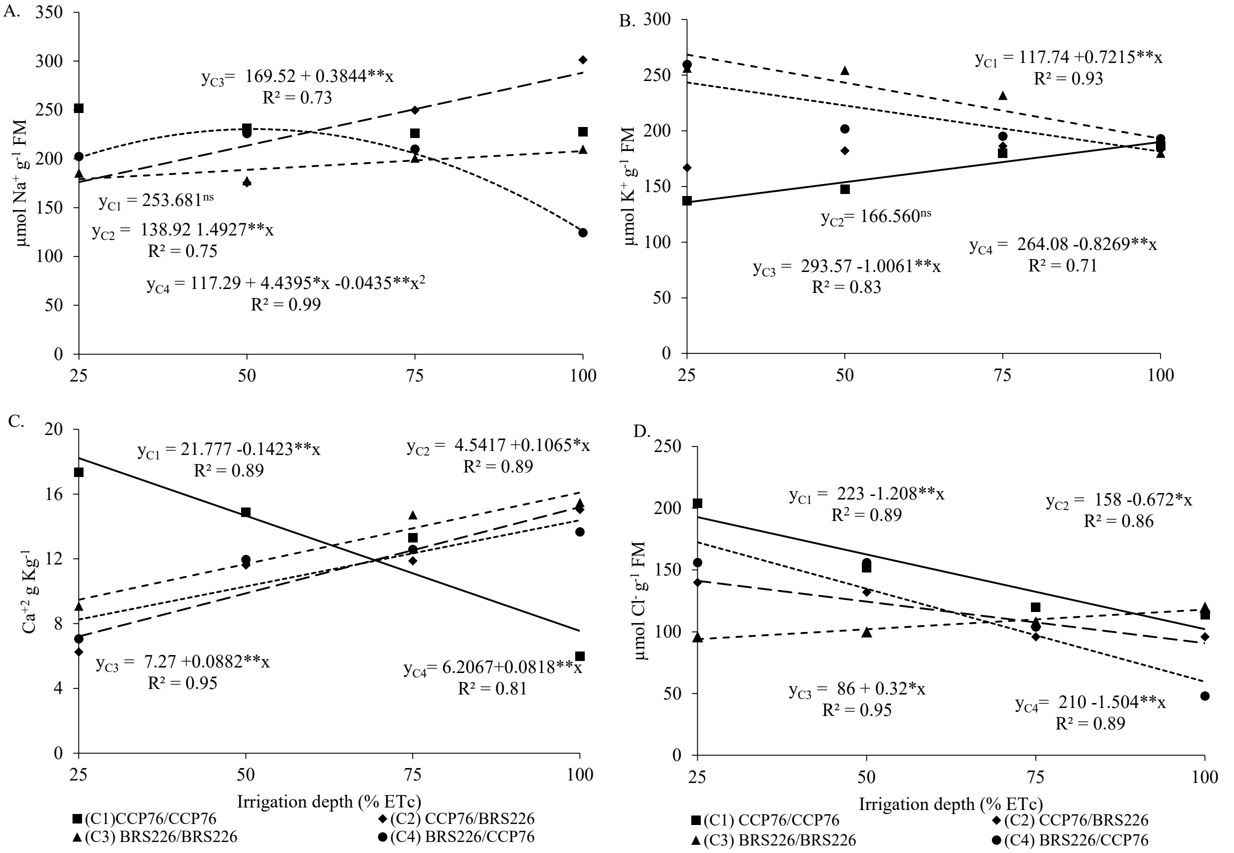


Figure 4. Sodium (Na^+; A), potassium (K^+; B), calcium (Ca^{2+}; C) and chloride (Cl^-; D) contents in leaves of grafting/rootstock clone combinations (C1: CCP76/CCP76; C2: CCP76/BRS226; C3: BRS226/BRS226; C4: BRS226/CCP76) of dwarf cashew trees cultivated under different irrigation depths (25, 50, 75 and 100 % of the crop evapotranspiration - ETc) for 30 days. *, ** and ^{ns}: significant at $p \leq 0.05$ and $p \leq 0.01$, and not significant, respectively, by the F-test. FM: fresh mass.

Conversely, the CCP76 self-graft presented lower K^+ accumulation when cultivated under 25 % of the ETc (117.74 μmol of K^+ g^{-1} of FM) (Figure 4B).

Araújo Junior et al. (2024) reported that, under moderate salinity levels, CCP76 cashew seedlings exhibited lower Na^+ levels in roots and leaves, what was associated with a greater control of stomatal conductance, indicating that the CCP76 presents a tighter regulation of Na^+ transport - findings that corroborate the present study. On the other hand, the effective regulation of Na^+ and Cl^- absorption and transport in grafted plants is generally attributed to the rootstock genotypes (Guo et al. 2023).

Calcium (Ca^{2+}) accumulation was observed under varying water regimes (25 to 100 % of the ETc) in the CCP76/BRS226, BRS226/BRS226 and BRS226/CCP76 combinations, with increases of 53, 41 and 43 %, respectively. In contrast, the CCP76 self-graft exhibited a 58 % decrease in the Ca^{2+} accumulation with increased irrigation from 25 to 100 % of the ETc (Figure 4C). Furthermore, CCP76 had the highest Ca^{2+} accumulation (18.22 μmol of Ca^{2+} g^{-1} of FM) at 25 % of the ETc (Figure 4C).

Restricted water conditions limit nutrient uptake due to reduced water and nutrient absorption (Yang et al. 2022). Each rootstock is unique and displays variability in nutrient absorption capacity and regulation of nutrient balance in tissues (Krishankumar et al. 2025); therefore, combinations with higher nutrient content are advantageous under such conditions (e.g., CCP76/CCP76). Calcium plays a vital role in cell wall formation and cell-to-cell relationships, and it also acts as a regulator in cation-anion balance and as a cofactor for some enzymes (Sousa et al. 2023).

The CCP76/BRS226 and BRS226/CCP76 combinations and the CCP76 self-graft showed a reduction in chloride (Cl^-) content with increasing water availability up to 100 % of the ETc, corresponding to reductions of 36, 65 and

47 %, respectively. The BRS226 self-graft, on the other hand, showed a 20 % increase in Cl^- ion accumulation from 25 to 100 % of the ETc. Among all combinations, CCP76/CCP76 grafted plants accumulated the highest Cl^- content (192.8 μmol of Cl^- g^{-1} of FM) under 25 % of the ETc (Figure 4D).

Ion exchange patterns revealed clear clone-specific traits regarding Na^+ and Cl^- alternation by K^+ and Ca^{2+}, suggesting this response may be a drought tolerance mechanism via maintenance of adequate potassium and calcium nutrition in plant tissues, thereby preventing their efflux (Silva et al. 2019). Proper selectivity in plant tissues requires a K^+/Na^+ ratio sufficient to meet K^+ demands for metabolic processes, ion transport regulation and osmotic adjustment (Silva et al. 2019). This was observed in the BRS226/CCP76 graft combination, a phenomenon that can be monitored through amino acid stability in osmotic regulators under stress conditions (Krishankumar et al. 2025).

The BRS226/CCP76 and CCP76/BRS226 combinations resulted in increased total soluble protein content in response to increased water availability. At 25 and 100 % of the ETc, the total soluble protein content increased by approximately 15 and 26 %, respectively. However, the BRS226 self-graft had the highest total soluble protein content at 61 % of the ETc, reaching 55.35 μg g^{-1} (Figure 5A). This is likely because the total soluble protein concentration is often affected when plants are subjected to water deficiency, as water stress causes several changes in cellular metabolism, including proteolysis, reduced protein synthesis, disruption of amino acid metabolism and increased protease activity (Jales Filho et al. 2023).

However, the CCP76 self-graft exhibited a reduction in total soluble protein content as irrigation levels increased, with the highest concentration observed at 25 % of the ETc. This response may be beneficial, as total soluble protein - such as late embryogenesis abundant proteins and osmotins - are common osmoprotectants that stabilize cell membrane proteins and enhance osmoregulatory capacity under water deficit conditions (Yang et al. 2022). Furthermore, the self-grafting promoted Ca^{2+} influx into leaf tissues as water availability decreased, contributing to osmotic stability and likely playing a role in cell signaling. This mechanism may help to maintain total soluble protein pools even under drought stress, as suggested by the positive correlation between Ca^{2+} and total soluble protein content (Figure 1) (Bhattacharya 2021).

The CCP76/BRS226 and BRS226/CCP76 combinations showed reductions in the total free amino acid content by approximately 12 and 26 %, respectively, as water availability increased. The CCP76 and BRS226 self-grafts did not differ statistically in response to irrigation levels. However, CCP76/BRS226 and BRS226/CCP76 accumulated higher levels of total free amino acid than the self-grafts at 25 % of the ETc (Figure 5B). These combinations may have upregulated stress-responsive genes, contributing to enhanced osmoregulation (via increased total free amino acid) and reduced oxidative damage, thereby conferring drought tolerance (Maia Júnior et al. 2025).

The proline content varied in response to the irrigation levels, except in the BRS226 self-graft. Between 25 and 100 % of the ETc, proline levels decreased by 12 % in the CCP76 self-graft, 16 % in CCP76/BRS226 and 30 % in BRS226/CCP76. Notably, the CCP76/BRS226 combination exhibited the highest proline accumulation across all irrigation levels, with the peak value of 61.98 ηg g^{-1} recorded at 25 % of the ETc. The lowest proline content was observed in the BRS226 self-graft (33.56 ηg g^{-1}) under 25 % of the ETc (Figure 5C).

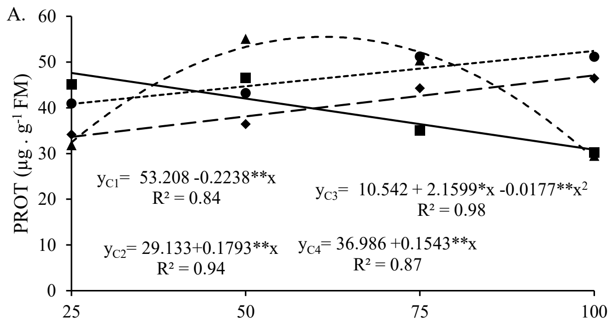
The increase in proline content may be linked to its protective role as a free radical scavenger. Proline also functions as a low-molecular-weight antioxidant that protects plants from abiotic stress (Padilla et al. 2021). Moreover, grafting seems to play a decisive role in enhancing proline content. Padilla et al. (2021) reported increased proline accumulation under water stress in grafted *versus* non-grafted pepper plants. Additional studies suggest that proline accumulation in plants grafted onto drought-resistant rootstocks contributes to membrane and protein stabilization under water deficit conditions (Jiménez et al. 2013, Schneider et al. 2019, Ozturk et al. 2021, Yang et al. 2022).

In response to increased water availability, the BRS226 self-graft exhibited no significant changes in glycine betaine content (Figure 5D). However, the CCP76 self-graft showed an increase of approximately 5 % in glycine betaine levels from 25 to 100 % of the ETc. In contrast, glycine betaine concentrations decreased in the BRS226/CCP76 combination as water availability increased, with a reduction of 7 % from 25 to 100 % of the ETc (Figure 5D).

The CCP76/BRS226 combination reached a maximum glycine betaine content of 4 ηg g^{-1} at 60 % of the ETc. Grafted plants with CCP76 exhibited higher glycine betaine concentrations at lower irrigation levels, averaging 3.92 and 3.57 ηg g^{-1} for CCP76 and CCP76/BRS226, respectively, under 25 and 50 % of the ETc (Figure 5D).

The CCP76/BRS226 combination may have maintained cellular hydration by increasing the concentration of compatible osmolytes such as proline (Figure 5C), glycine betaine (Figure 5D) and total free amino acid (Figure 5B) under reduced irrigation. This osmoregulatory function may serve to protect plant tissues under water deficit conditions. It is further supported by the negative correlation between total free amino acid, glycine betaine and proline with water status indicators (Figure 1), reinforcing that lower water availability results in a higher accumulation of these compounds.

The BRS226 rootstock led to increased total soluble sugar content in response to enhanced water availability. The BRS226/CCP76 combination showed the highest total soluble sugar concentrations across all irrigation regimes, with a maximum of 359.8 ηg g^{-1} at 100 % of the ETc. The lowest total soluble sugar content was recorded in the CCP76 self-graft (136.66 ηg g^{-1}) under 25 % of the ETc. However, CCP76-grafted plants exhibited no significant changes in total soluble sugar content in response to irrigation (Figure 5E).



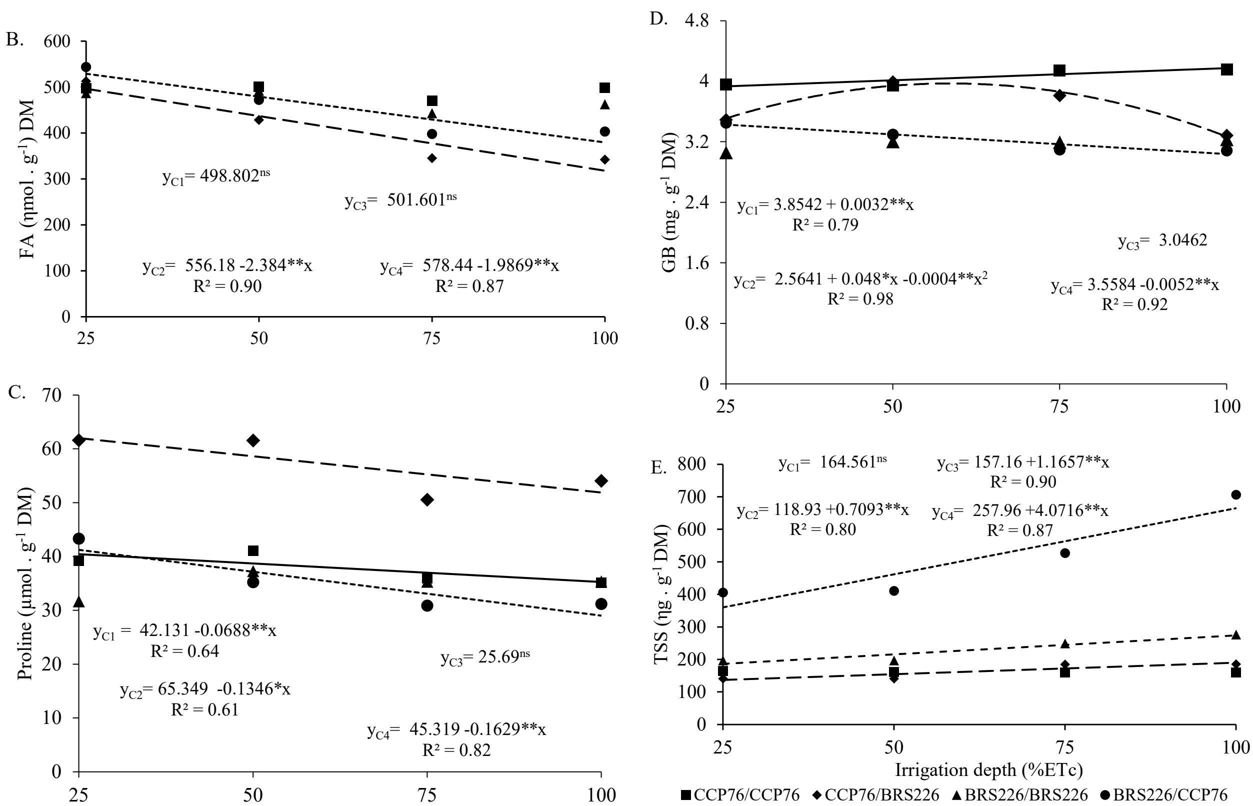


Figure 5. Total soluble proteins (PROT; A), total free amino acids (FA; B), proline (C), glycine betaine (GB; D) and total soluble sugars (TSS; E) in leaves of scion/rootstock combinations (C1: CCP76/CCP76; C2: CCP76/BRS226; C3: BRS226/BRS226; C4: BRS226/CCP76) of dwarf cashew trees cultivated under different irrigation levels (25, 50, 75 and 100 % of the crop evapotranspiration - ETc) for 30 days. *, ** and ns: significant at $p \leq 0.05$ and $p \leq 0.01$, and not significant, respectively, by the F-test. FM: fresh mass; DM: dry mass.

When analyzing the total soluble sugar content, it is notable that the CCP76/BRS226 combination did not exhibit a significant reduction in accumulation at 25 and 50 % of the ETc, when compared to 100 % of the ETc. Carbohydrate accumulation may be related to osmotic adjustment, a common mechanism employed by plants under water scarcity (Jales Filho et al. 2023). On the other hand, the BRS226/CCP76 combination and BRS226 self-graft showed marked decreases in total soluble sugar under these same conditions (Figure 5E), likely due to reductions in water status. This is corroborated by the positive correlation between total soluble sugar and water status variables observed in the present study (Figure 1).

Hierarchical clustering analysis revealed the formation of four distinct clusters, grouping treatments with similar physiological and biochemical characteristics in response to the various irrigation regimes (Figure 6). The first cluster notably included the CCP76 and BRS226 self-grafts under 75 % of the ETc, which showed higher graft union and rootstock diameters.

In contrast, the second cluster included the BRS226/CCP76 combination under 50, 75 and 100 % of the ETc, as well as the BRS226 self-graft under 50 and 100 % of the ETc. These treatments exhibited higher levels of K^+, soluble proteins and sugars, along with lower accumulations of toxic ions (Na^+ and Cl^-) (Figure 6). This suggests an efficient osmoregulatory response, wherein osmotic adjustment through the accumulation of compatible solutes may have contributed to maintain ionic homeostasis and cellular water potential, even under varying levels of water availability.

The third cluster comprised the most sensitive combinations, particularly the BRS226 self-graft and the BRS226/CCP76 combination under 25 % of the ETc. These exhibited greater membrane damage, reduced foliar K^+ accumulation and lower moisture content and relative water content (Figure 6). These results reflect the severity of the stress imposed

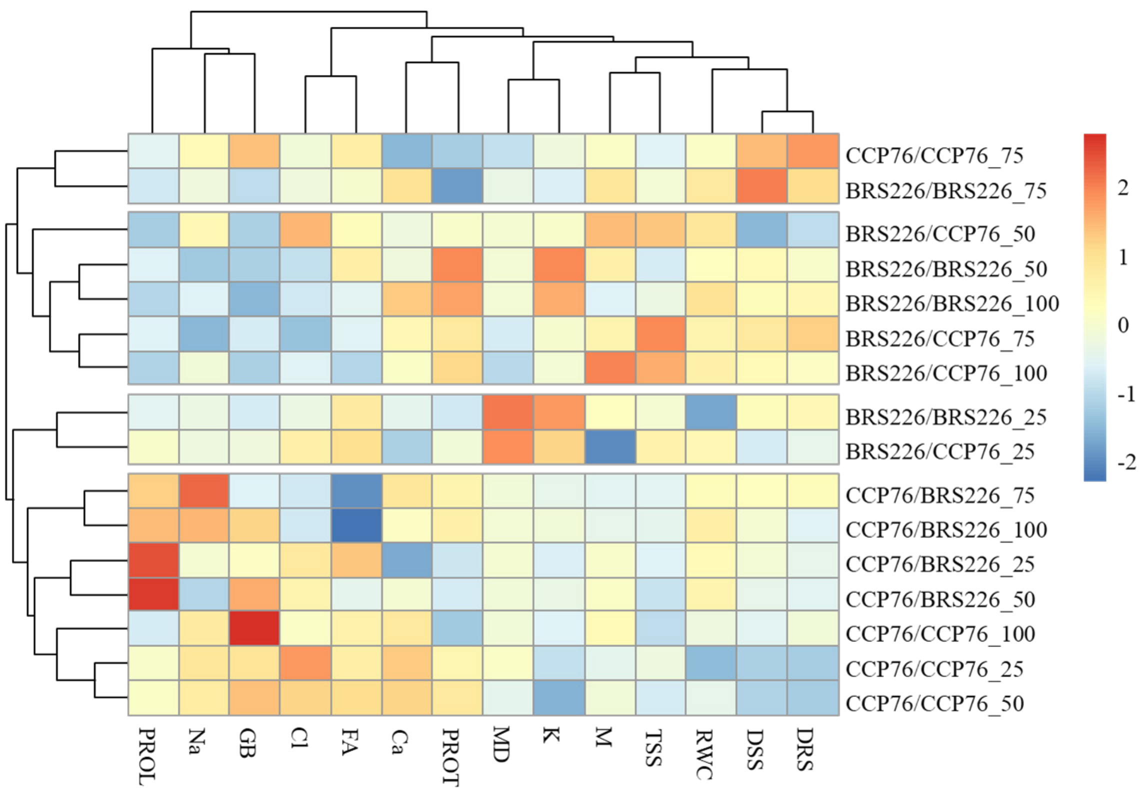


Figure 6. Hierarchical clustering and heatmap based on irrigation regimes and scion/rootstock combinations, considering the variables analyzed in dwarf cashew plants. Red and blue colors indicate higher and lower variable importance, respectively. DRS: rootstock diameter; DSS: scion diameter; RWC: relative water content; TSS: total soluble sugars; M: leaf moisture content; K: foliar potassium; MD: membrane damage; PROT: protein; Ca: foliar calcium; FA: total free amino acids; Cl: foliar chloride; GB: glycine betaine; Na: foliar sodium; PROL: proline.

by extreme water restriction, which compromised cellular integrity and ionic balance.

Finally, the fourth cluster grouped other scion/rootstock combinations, notably the CCP76/BRS226 combination under 25 and 50 % of the ETc (Figure 6), which demonstrated higher synthesis of proline, amino acids and glycine betaine - essential osmolytes for cellular protection under drought conditions. These compounds contributed to minimizing the foliar Na^+ accumulation, supporting a tolerance strategy based on osmotic adjustment and ionic detoxification.

The clusters highlighted that drought response is influenced by both the scion/rootstock combination and the level of water restriction. Water stress reduces plant growth in various species, and this response varies according to the degree of restriction, genotype and adoption of adaptive strategies, including common physiological and molecular mechanisms in plants (Martínez-Ferri et al. 2019, Aparicio-Durán et al. 2021).

Self-grafts and specific combinations (e.g., BRS226/CCP76) performed better under mild deficit conditions, while others (e.g., CCP76/BRS226) activated alternative metabolic pathways (e.g., proline accumulation) under severe stress. Ionic selectivity (K^+ *vs*. Na^+) and maintenance of foliar water status were key determinants of drought tolerance, in agreement with studies emphasizing the role of osmolytes and redox balance in drought resistance (Semida et al. 2020, Bañón et al. 2022). Therefore, selecting scion/rootstock combinations adapted to varying water availability scenarios can optimize the productivity of early dwarf cashew trees in semi-arid regions.

In summary, the results of the present study reinforce the hypothesis that resistant plants, even under water deficit conditions, are capable of maintaining adequate water supply, preserving their photosynthetic metabolism and, consequently, the production of photoassimilates - as observed in the CCP76/BRS226 combination irrigated with 25 and 50 % of the ETc.

CONCLUSIONS

1. The CCP76/BRS226 combination was efficient under water-restricted conditions (25 and 50 % of the crop evapotranspiration - ETc), as evidenced by a significant reduction in oxidative damage to leaf membranes and a concomitant increase in osmoprotectants such as total free amino acids and proline;
2. Proline emerges as a potential molecular marker for drought tolerance in early dwarf cashew trees;
3. The BRS226 self-graft and the BRS226/CCP76 combination under 25 % of the ETc were the most affected, exhibiting greater membrane damage, lower foliar potassium accumulation, moisture content and relative water content, and are thus not recommended for cultivation under water-restricted conditions.

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