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# Water restriction in cowpea plants [*Vigna unguiculata* (L.) Walp.]: Metabolic changes and tolerance induction[1]

## Restrição de água em plantas de feijão-caupi [*Vigna unguiculata* (L.) Walp.]: Alterações metabólicas e indução de tolerância

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*HIGHLIGHTS:*
*Acclimation mechanisms of cowpea include metabolite synthesis for reactive oxygen species elimination and drought tolerance.*
*Elicitors modulate the activity of antioxidant metabolism enzymes in cowpea plants.*
*Interaction between Bradyrhizobium and salicylic acid modulates water deficit effects on cowpea crop.*

**ABSTRACT:** Global climate change tends to intensify water unavailability, especially in semi-arid regions, directly impacting agricultural production. Cowpea is one of the crops with great socio-economic importance in the Brazilian semi-arid region, cultivated mainly under rainfed farming and considered moderately tolerant to water restriction. This species has physiological and biochemical mechanisms of adaptation to these stress factors, but there is still no clear vision of how these responses can not only allow survival, but also ensure yield advances in the field. Besides acclimation mechanisms, the exogenous application of abiotic (salicylic acid, silicon, proline, methionine, and potassium nitrate) and biotic (rhizobacteria) elicitors is promising in mitigating the effects of water restriction. The present literature review discusses the acclimation mechanisms of cowpea and some cultivation techniques, especially the application of elicitors, which can contribute to maintaining crop yield under different water scenarios. The application of elicitors is an alternative way to increase the sustainability of production in rainfed farming in semi-arid regions. However, the use of eliciting substances in cowpea still needs to be carefully explored, given the difficulties caused by genotypic and edaphoclimatic variability under field conditions.

**Key words:** rainfed farming, elicitors, salicylic acid, silicon, rhizobacteria

**RESUMO:** As mudanças climáticas globais tendem intensificar a indisponibilidade de água, principalmente na região semiarida brasileira, impactando diretamente a produção agrícola. O feijão-caupi é uma das culturas de grande importância socioeconômica no semiárido, cultivado principalmente em regime de sequeiro e considerado moderadamente tolerante à restrição hídrica. Essa espécie apresenta mecanismos fisiológicos e bioquímicos de adaptação a esses fatores de estresse, mas ainda não há uma visão clara de como essas respostas podem permitir não apenas a sobrevivência, mas também garantir avanços na produtividade no campo. Além dos mecanismos de aclimatação, a aplicação exógena de eliciadores abióticos (ácido salicílico, silício, prolina, metionina e nitrato de potássio) e bióticos (rizobactérias) é promissora na mitigação dos efeitos da restrição hídrica. A presente revisão de literatura pretende discutir os mecanismos de aclimatação do feijão-caupi e algumas técnicas de cultivo, principalmente a aplicação de eliciadores, que podem contribuir para a manutenção da produtividade da cultura em diferentes cenários hídricos. A aplicação de eliciadores é uma forma alternativa de aumentar a sustentabilidade da produção em sistemas de sequeiro no semiárido. No entanto, o uso de substâncias eliciadoras no feijão-caupi ainda apresenta um campo a ser explorado com cautela, dadas as dificuldades causadas pela variabilidade genotípica e edafoclimática em condições de cultivo no campo.

**Palavras-chave:** agricultura de sequeiro, eliciadores, ácido salicílico, silício, rizobactérias

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## Introduction

Semi-arid region has a high variation in the pattern and total annual rainfall, as well as high levels of solar radiation and air temperature. In this region, rainfed farming is a high-risk acitivity concerning the number and intensity of dry spells through the rainy season, especially in the years of severe drought (Marengo et al., 2017; Cavalcante et al., 2021). Besides, in this region, a portion of the water sources has high salt levels, which, associated with low technological level employed in agriculture, make it even more difficult to grow cowpea [*Vigna unguiculata* (L.) Walp.] in this region (Oliveira, 2015; Chagas et al., 2018; Tavares et al., 2021).

Thus, efforts are required to increase drought tolerance in genotypes adapted to semi-arid conditions and, currently, cultivated by farmers (Gomes et al., 2020; Tankari et al., 2021). There is also a reason for the improvement of cultivars with good performance as well as using techniques such as abiotic elicitors that minimize the effects caused by environmental stresses and strengthen this tolerance in cowpea (Boukar et al., 2019; Andrade et al., 2021; Narayana & Angamuthu, 2021).

This literature review presents the results of research on cowpea production in semi-arid regions, particularly in the Brazilian semi-arid region, and highlights the concern with rainfed and irrigated crops due to global climate changes. The stress tolerance mechanisms and use of elicitors to mitigate the effects of water deficit on cowpea are also discussed, focusing on physiological and biochemical processes, especially those related to osmotic adjustment and antioxidant metabolism.

## Climate Change and Cowpea Cultivation in Semi-Arid Environments

Global climate change scenarios result in increasingly higher temperatures and deregulate rainfall patterns (Stocker et al., 2014), which intensifies the problems of water shortage and harms all sectors of the economy, mainly in semi-arid regions (Marengo et al., 2017; Del Buono, 2020). These scenarios have important implications for global food policy. The Food and Agriculture Organization (FAO) of the United Nations (UN) predicts a 34% increase in the human population by 2050, concentrated mainly in urban areas, which will restrict the production and distribution of food and result in hunger and malnutrition, especially among low-income groups (Philippidis et al., 2021). In this context, the combined effect of population growth and climate change will have a major impact on agricultural production, driven by increased demand for food production (Blattner, 2020).

Although climate change is a threat to socio-economic development, agricultural production activities are generally more vulnerable to environmental constraints than other production sectors. The problem becomes more complex for semi-arid regions, such as the Northeastern region of Brazil, which has a difficulty in keeping the farmer in the countryside because it is hampered by the delimitation of agricultural areas due to drought problems, the main constraints for agricultural development (Camara et al., 2018). In this region, it is necessary to use irrigation and nutrient application to achieve adequate yield levels, which raises the cost of crop production each year and encourages producers to seek new options for their production arrangements (Liu et al., 2020; Melo et al., 2020).

In semi-arid regions knowledge of the crops that are tolerant to soil salinity and drought conditions is of great importance for the success of small and large farms, and their harvests could improve as climatic risks are minimized. In the concept of Climate-Smart Agriculture (CSA), FAO indicates leguminous crops as one of the most promising to integrate into the set of innovations, tools, and agricultural policies that can help farmers to produce food under new climate change scenarios (Palombi & Sessa, 2013). Legume plants are still an important part of the subsistence cultivation system in the arid and semi-arid regions in the world since they are a rich source of nutrients and require simple cultivation techniques (Choudhary, 2013).

Among leguminous species, cowpea is a plant with good adaptability in tropical and subtropical regions in the world (Rathore et al., 2015; Narayana & Angamuthu, 2021). In semi-arid regions, cowpea plays a fundamental role because it has low demands for agricultural inputs, and it tolerates water deficit. As consequence, this species shows relatively better growth and development than other crops in the regions with semi-arid climate (Silva et al., 2016).

In this scenario, cowpea stands out as one of the main cultivation alternatives in the semi-arid region, mainly due to its moderate degree of tolerance to water deficit, wide temperature range (between 18 to 34 °C), and high nutritional value for human consumption (Silva et al., 2016). This species is grown on more than 10 million hectares worldwide, located mainly in the tropical and subtropical regions of America, Asia, and Africa, with global production of around 5.5 million tons (FAO, 2017). Thus, the main motivations to increase the yield of this crop are the profitability and efficiency of the cultivation system (Freitas et al., 2019; Azevedo et al., 2021).

The high nutritional value of cowpea is evidenced by the excellent source of energy (64-69% of carbohydrates), mineral nutrients (K, Ca, Mg, P, Zn, Fe, Na) (Famata et al., 2013), and high protein content (20-25%), with emphasis on the levels of globulins (51% of total proteins) and albumin (45% of total proteins) (Freitas et al., 2004). Its nutritional characteristics provide enormous potential to combat malnutrition in vulnerable populations in tropical and subtropical areas of the world because the quality of its protein is an essential natural supplement to the diet, especially of children, pregnant women, and breastfeeding women (Modu et al., 2010).

Unlike the common bean (*Phaseolus vulgaris* L.) production scenario, the cultivation of cowpea in Northeastern Brazil has increasing demand and reached 1.05 million hectares of cultivated area and production of 409.3 thousand tons in the 2018/2019 harvest, which represents 67% of the cultivated area and 55% of the production of total beans production in this region (CONAB, 2019). Adaptability to drought conditions, low production costs, short time to complete phenological cycle, and seed production under adverse edaphoclimatic conditions are characteristics that increase its farming and relevance to the local economy (Colman et al., 2014; Medeiros et al., 2017; Martins et al., 2018). Growing cowpea is extremely important because it provides employment and generates profits for small and medium farmers (Camara et al., 2018).

Despite the low water demand compared between the harvests 2010/2011 and 2018/2019, there was a reduction of around 33%, both in planted area and yield in the Northeast region of Brazil (CONAB, 2019). This decrease overlies the drought and severe drought scenarios in this region between the years 2012 and 2016, associated with irregular and poorly distributed rainfall during the rainy season (Marengo et al., 2017; Martins & Vasconcelos Júnior, 2017). In addition, the production of cowpea cultivars can also be affected by air temperature, and when the night temperature reaches around 35 °C, cowpea flowers abort due to the little pollen development, resulting in pod malformation (Hall, 1993). In this case, global warming may damage cowpea yield even more, especially in the tropical semi-arid region.

## Cowpea Development and Metabolic Changes Under Water Deficit

Despite the adaptability and tolerance to water deficit shown by cowpea (Dutra et al., 2015), this species has most of its physiological and biochemical processes affected by water restriction. The germination capacity of cowpea seeds is one of the most common methods to ascertain the species tolerance to water deficit since it corresponds to one of the most critical stages of its life cycle (Araújo et al., 2017). During the germination process, water restriction increases the time and decreases the efficiency of germination (Araújo et al., 2018). Impairment in the seed's reserves degradation inhibits metabolic and biochemical processes, which slows down and/or reduces germination, impacting the initial development of more sensitive cowpea genotypes under water restriction.

Disturbances caused by water deficit in the germination process have a direct effect on the initial growth of seedlings, in which the inhibition of cell expansion and division can reduce their height by up to 80%, as well as negatively affect the cowpea biomass (Araújo et al., 2017). At the beginning of the vegetative stage, decreasing cell water content destabilizes the membrane system because the damage to its structures impairs its functionality. In the thylakoid membrane, for example, dehydration causes a reduction in the concentrations of chlorophylls, photosynthetic pigments necessary in the light energy conversion into carbohydrates (Khadour et al., 2020).

In cowpea, the damage to membrane systems induces reactive oxygen species (ROS) production during the beginning of vegetative growth. Increasing ROS stimulates the synthesis of carotenoids, pigments that protect plants against oxidative damage when chlorophyll 'a' and 'b' production is compromised. However, in a substrate water potential lower than -0.8 MPa, ROS production generates serious consequences to shoot and root biomass accumulation of cowpea, in addition to limiting seedling height (Araújo et al., 2017; Dutra et al., 2017; Araújo et al., 2018; Tavares et al., 2021).

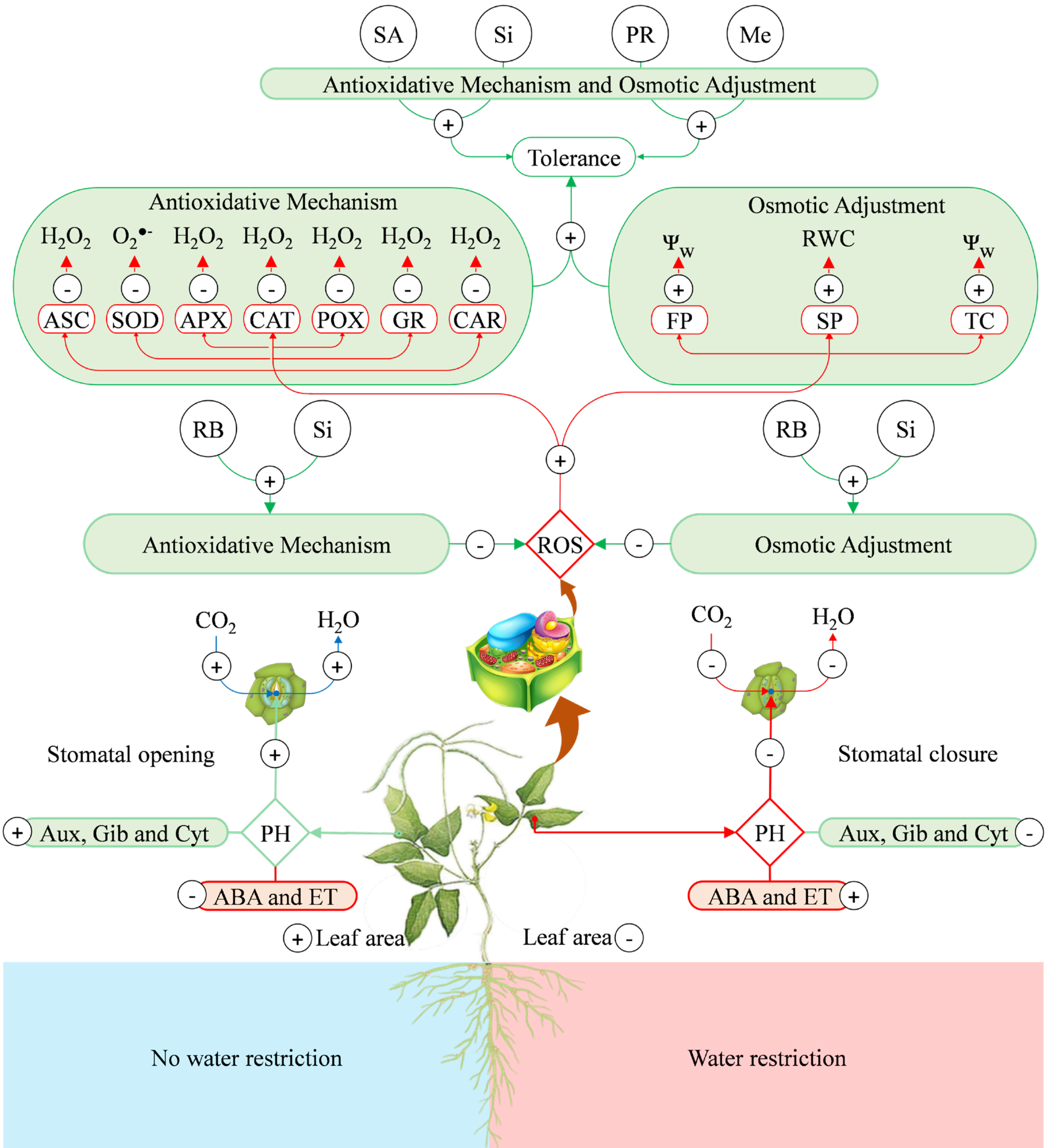
In cowpea, the water potential of tissue is reduced under water deficit conditions, which decreases cell turgor (Goufo et al., 2017; Merwad et al., 2018; Silva et al., 2019). During water stress, the decline of leaf water potential alters the permeability and sustainability of the membranes and interferes with the regular plants' functions mainly due to osmotic and redox system imbalance, which causes losses in the developing organs during the growth stage (Silva et al., 2019). As a result of the oxidative stress, an increment in lipid peroxidation is observed in cowpea under water restriction, mainly due to the overproduction of hydrogen peroxide ($H_2O_2$). Cowpea genotypes more susceptible to stress have higher levels of malonaldehyde (MDA) than more tolerant ones (Carvalho et al., 2019) (Figure 1).

For mitigating the impacts of free radicals, cowpea plants have developed an efficient antioxidant metabolism with superoxide dismutase (SOD, EC 1.15.1.1), an enzyme that metabolizes the superoxide ion ($O_2^{\bullet-}$) into $H_2O_2$, ascorbate peroxidase (APX, EC 1.11.1.11) and catalase (CAT), which act in hydrogen peroxide ($H_2O_2$) removal. In addition, guaiacol peroxidase (POX, EC 1.11.1.7) and glutathione reductase (GR, EC 1.6.4.2) control ROS levels, at suitable concentrations for cellular function, and promote important changes in the water deficit tolerance mechanism (Dutra et al., 2017; Carvalho et al., 2019; Silva et al., 2019; Andrade et al., 2021) (Figure 1).

There is strong evidence of osmoprotective action associated with antioxidant metabolism, mediated by compatible solutes that contribute to cellular homeostasis and support development in the plant. In an attempt to minimize cellular water imbalance, cowpea seedlings produce compatible osmolytes, for example, proline, which promotes osmotic adjustment and prevents tissue dehydration (Araújo et al., 2017). The root proline synthesis, at the beginning of vegetative growth is an important cowpea tolerance strategy, because this organ is the first in contact with the substrate and responsible for absorbing the soil solution. Proline concentration is generally higher in shoot and root of tolerant genotypes when compared to those susceptible to stress (Dutra et al., 2017) (Figure 1).

It is important to highlight that the non-enzymatic components, such as flavonoids and proline, have antioxidant activities in cowpea under water deficit, becoming an integral part of the adaptive response, rather than just indicators of stress (Goufo et al., 2017; Silva et al., 2019; Andrade et al., 2021). Proline accumulation is compatible with osmoprotective strategies, that is, it is regulated between source and sink organs in the plant similarly, regardless of the genotype (Zegaoui et al., 2017). In cowpea under water restriction, proline synthesis induction can increase the osmolyte concentration by more than 100% (Silva et al., 2019; Andrade et al., 2021), which confirms its importance in maintaining the cell water status of this species.

At the end of the cowpea vegetative stage, water restriction decreases stomatal opening and makes carbon assimilation difficult in photosynthetic metabolism (Melo et al., 2018b), which impairs growth, dry mass production, leaf area expansion (Melo et al., 2018a; Andrade et al., 2021), pod weight, and yield (Dutra et al., 2015). The regulation of stomatal conductance is controversial, since the assimilation of $CO_2$ under water stress contributes to the inefficiency of water use by the plant, while the water regulation by stomatal closure decreases water loss




SA - Salicylic acid; Si - Silicon; PR - Proline; Me - Methionine; PH - Plant hormones; $H_2O_2$ - Hydrogen peroxide; $O_2^{\bullet -}$ - Superoxide anion; $\Psi_w$ - Water potential; RWC - Relative water content; ASC - Ascorbate; SOD - Superoxide dismutase; APX - Ascorbate peroxidase; CAT - Catalase; POX - Phenol peroxidase; GR - Glutathione reductase; CAR - Carotenoids; FP - Free proline; SP - Soluble proteins; TC - Total carbohydrates; RB - Rhizobacteria; ROS - Reactive oxygen species; Aux - auxins; Gib - Gibberellin; Cyt - Cytokinin; ABA - Abscisic acid; ET - Ethylene; (+) - Increase and (-) - Reduction

**Figure 1.** Water deficit in cowpea plants: metabolic changes and tolerance induction

through transpiration. However, stomatal closure restricts $CO_2$ input and induces a decline in cowpea net photosynthetic rate (Figure 1). Such effects reduce the efficiency of instantaneous carboxylation, due to the unavailability of ATP and NADPH, in addition to the substrate for Ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) (Melo et al., 2018b; Osei-Bonsu et al., 2021).

More severe drought conditions gradually impose non-stomatal limitations in the photosynthetic pathway because of deficiencies in the chloroplast components, such as membrane integrity, lipid composition, photosynthetic pigments, photosystem efficiency, and activity of enzymes such as RuBisCO (Gomes et al., 2020). However, during the cowpea vegetative stage, there is evidence that reductions in photosynthetic capacity, observed in some genotypes, are mainly attributed to stomatal closure, being considered one of the first responses of the species and an efficient adaptive mechanism for transpiration control. The decrease in stomatal opening also limits the supply of $CO_2$ to RuBisCO, which causes metabolic regulation through the reduction of net photosynthesis (Melo et al., 2018b; Carvalho et al., 2019; Gomes et al., 2020). Osei-Bonsu et al. (2021) add that cowpea appears to have mechanisms that allow the light reactions to maintain high activity and low propensity for ROS generation, through a combination of highly active alternative energy sinks, including photorespiration and other, yet undefined, electron sinks.

For most cowpea genotypes, a reduction in grain yield, after water deficit, can be caused by water status reduction that decreases stomatal conductance and compromises photosynthetic processes, as well as energy expenditure to synthesize secondary metabolites, which compromises leaf area and production (Dutra et al., 2015). It should be noted that leaf area is more sensitive to water deficit than the rate of photosynthesis because its reduction is related to a change in the elasticity of the cell wall and a possible decrease in its turgor pressure.

Understanding the biochemical and physiological mechanisms, as well as the evident joint action between different mechanisms of water deficit tolerance, supported by the genetic basis of cowpea tolerance, demonstrates the existence of intergenotypic variability concerning the response to drought. These differential responses provide relevant information on the physiological and metabolic mechanisms bearing stress tolerance in different cowpea cultivars.

## Farming Strategies to Induce Cowpea Tolerance to Water Deficit

Conventional cowpea breeding has been widely carried out by different national and international research programs to strengthen this crop, including increasing abiotic stress tolerance. However, this process is time-consuming, laborious, and expensive. Agricultural practices, which minimize the effects of stress on plants, have received more attention and, the most promising ones involve exogenous use of biotic or abiotic compounds applied exogenously (Chakraborty et al., 2019).

The use of elicitors, due to their low molecular weight, stimulates a range of biochemical reactions that modify the secondary metabolism of plants (Chakraborty et al., 2019). In cowpea, for example, the eliciting action of salicylic acid, silicon, and rhizobacterial inoculation contributes to the adaptive mechanism of plants under water restriction conditions (Silva et al., 2019; Andrade et al., 2021).

Exogenous elicitors are important to intensify the mechanisms of stress tolerance in plants and include growth regulators or their derivative products such as salicylic acid, silicon, jasmonic acid, nitric oxide, sugars, amino acids, and phytohormones (Ahmad et al., 2019a, b). These exogenous elicitors have been advantageous and could be a new strategy for inducing adaptative responses in plants, whether they are constitutive or induced in nature. Thus, studies with these substances are necessary because they contribute to the improvement of production chains in modern agriculture and, at the same time, they collaborate to reduce harmful compounds to the environment and human health.

As an abiotic elicitor, the inoculation of diazotrophic bacteria *Bradyrhizobium* can be used to improve cowpea cultivation because it has the potential to increase the grain yield of this species, and it may provide an amount of nitrogen equivalent to fertilization with 70 kg $ha^{-1}$ of urea in the Brazilian savanna (Batista et al., 2017). Additionally, inoculation with *Bradyrhizobium* promotes improvements in water homeostasis and redox metabolism of cowpea, in addition to ensuring the maintenance of crop growth and increments of up to 100% in biomass of this species under deficit irrigation (Andrade et al., 2021).

Diazotrophic bacteria establish beneficial relationships with bean plants. In this symbiosis, the bacteria use part of the host plant's photoassimilates as an energy source and, in return, fix atmospheric nitrogen ($N_2$) to the plant. Besides fixing nitrogen, rhizobium promotes crop development under drought conditions (Barbosa et al., 2018; Verma et al., 2020). However, the efficient symbiotic compatibility between *Bradyrhizobium* and cowpea under stress conditions depends on the genotype. Overall, rhizobacterial inoculation is an important tool that ensures the maintenance of antioxidant metabolism because it preserves low levels of ROS and enhances the activity of enzymes such as SOD, CAT, and APX, improving photosynthesis and the development of cowpea (Andrade et al., 2021) (Figure 1).

Biotic agents (rhizobacteria) associated with inorganic compounds (salicylic acid) improve the efficiency of nitrogen assimilation of cowpea, regardless of the phenological stage, as there is an improvement in the biochemical reactions of plants due to the considerable production of proteins and enzymes. In these cases, nitrogen fertilization can induce positive effects on enzymes and proteins responsible for the synthesis and maintenance of plasma membranes, which allows a better arrangement of their structures during the storage period and seed germination (Possenti & Villela, 2010). The process of soaking cowpea seeds into a potassium nitrate solution ($10^{-5}$ M) for eight hours promotes an increase in germination percentage, emergence speed index, seedling height, activities of SOD, CAT and APX, and proline, even under water deficit (Araújo et al., 2017).

The joint action of biotic and abiotic elicitors under stress conditions, such as the inoculation of *Bradyrhizobium* plus the foliar application of salicylic acid (SA), is also an efficient strategy to maintain leaf water status and plant growth, mediated by increasing the concentration of osmoregulators and antioxidant enzymes activity (Andrade et al., 2021). This interaction is positive and suggests a good joint action of these two factors mitigating the effects of water deficit and increasing cowpea drought tolerance. While SA increases the synthesis of osmoprotectants and the activity of antioxidant enzymes, rhizobium acts by increasing the levels of nutrients and compatible osmolytes, represented by increments in growth indicators and proline (Andrade et al., 2021).

The use of SA alone induces metabolic responses in cowpea, despite the effects of water restriction (Figure 1). Classified as a phenolic compound, SA is derived from two metabolic pathways: the isochorismate and phenylalanine pathways, both from the chorismate (Lefevere et al., 2020). Widely distributed in plants, SA is related to numerous regulatory functions of metabolism and promotes the activation of defense mechanisms against water deficit.

Soaking cowpea seeds with $10^{-5}$ M SA increases the germination percentage and the antioxidant activity of SOD, CAT, and APX in seedlings under negative water potential in the substrate (Dutra et al., 2017; Araújo et al., 2018; Uddin et al., 2021). In cowpea under water restriction, 1 mM of SA prevents damage to membranes and increases proline content (Araújo et al., 2018). Besides this, 1 mM of SA regulates the initial growth and increases the levels of chlorophyll 'a', 'b', and carotenoids under water deficit (Araújo et al., 2018). After foliar application of 300 ppm of SA on cowpea irrigated with 70% of available water, this species reached an yield of approximately 2,732 and

2,640 kg ha$^{-1}$ in the first and second crop cycles, respectively (Nassef, 2017). For Nassef (2017), SA induces the expression of 11 new proteins in cowpea under water deficit, which are related to improved growth and production of this species.

As an elicitor of agricultural interest, 100 and 200 mg L$^{-1}$ of silicon minimize the deleterious effects of water deficit on different cowpea cultivars by increasing leaf water potential, proline concentration, and ascorbate peroxidase activity, which guarantees the growth of the species (Silva et al., 2019). Additionally, Si improves the anatomical characteristics of cowpea leaf under water restriction, which ensures better translocation of photoassimilates and nutrients to be used in different metabolic processes. Such effects contribute to vigorous growth and promote structural changes in xylem diameter, mesophyll, and epidermis thickness, and in cross-sectional area occupied by the collenchyma, resulting in a satisfactory yield under moderate or severe water stress (Merwad et al., 2018).

Si deposition occurs in various parts of the plants, especially on the epidermis of shoots. This element effectively contributes to increase the absorption of other nutrients, alters the gas exchange mechanism, increases antioxidant defense system, promotes changes of osmolytes and phytohormones, besides acting directly in reducing transpiration with its deposition into leaf apoplast, even in leguminous plants (Zhang et al., 2017).

Exogenous doses of 6.0 mM of proline and 4.0 mM of methionine applied to cowpea plants under water deficit also change the osmotic metabolism and activity of antioxidant enzymes, which contributes to the absorption of N, P, and K, improving the growth and production (Merwad et al., 2018). Under moderate water deficit, both proline, and methionine enhance the activities of SOD, CAT, and peroxidase (POD) enzymes, which eliminate ROS from cellular metabolism and ensure the maintenance of water status and membrane integrity by reducing leakage of electrolytes that guarantee the regulation of photosynthetic processes (Sharma et al., 2012; Merwad et al., 2018; Oliveira, 2020).

Proline and methionine regulate cellular water status and promote the efficient use of water by plants due to cell membrane stability improvement. This action has a positive impact on the integrity of photosynthetic pigments, increasing the concentration of compatible osmolytes and improving the growth and yield of cowpea (Merwad et al., 2018; Oliveira, 2020). The application of 20 mM proline in two cowpea development stages (six leaves and flowering) also increases seed production under water restriction (Ardabili et al., 2013).

Due to its relative rusticity and efficient defense mechanisms to overcome the adverse effects of water restriction, cowpea has developed several changes in its metabolism that involve cellular signaling pathways, which ensure survival at the expense of production. To surpass the effects of water restriction, in addition to cowpea's endogenous apparatus, it has been demonstrated that the exogenous application of biotic and/or abiotic elicitors agents can increase secondary metabolism and induce a wide range of defense mechanisms in plants to improve drought tolerance. Under such circumstances, it is relevant to develop procedures that increase the yield of the crop at a low cost so that it can, at the same time, be profitable to the farmer and accessible to the entire population.

## Conclusions

1. Drought conditions impact cowpea physiology and yield under tropical semi-arid conditions. Technology that can mitigate these effects was developed to improve the capacity for internal defense by the exogenous application of eliciting substances. This technology can increase cowpea yield even when subjected to moderate water deficit, ensuring the sustainability and profitability of crops.

2. Several biotic (diazotrophic bacteria) and abiotic (silicon, salicylic acid, jasmonate, selenium, ascorbate, potassium nitrate) elicitors act simultaneously in different adaptive ways, especially inducing antioxidant defense (enzymatic and non-enzymatic), osmoprotection and secondary metabolism, and increase the capacity of cowpea plants to face water restriction.

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