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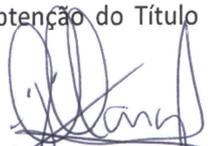
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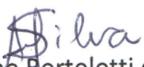
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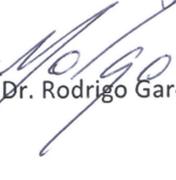
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Prof. Dr. Adriano Bortolotti da Silva
Coordenador do Programa em
Agricultura Sustentável

To my dear children, Ana Letícia and Gabriel.

My "Mom" and my "Dad", unforgettable.

I dedicate

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ABSTRACT

Maize is a crop known to be highly sensitive to water stress. When water becomes a limiting factor, the water potential and the water content of the plants are substantially reduced. Under these conditions, exogenous application of Si can substantially improve water use efficiency, photosynthetic rate and yield in maize plants. The objective of this work was to evaluate calcium silicate efficiency as a water stress reducer in two maize cultivars. Two experiments were conducted, the first using cv. BR-1010, (sensitive to water stress) and the second using cv. DKB-390 (tolerant to water stress). The experiments were organized in a completely randomized design, in four replicates, with two doses of calcium silicate: 0 % (absence) and 100 % (presence) of calcium silicate indicated in the calculation of soil liming, and two irrigation blades: 30 and 100 % water replacement, determined according to the soil water retention curve, in four replicates. In each experiment, the parameters evaluated were gas exchange, net photosynthetic rate, transpiration rate, stomatal conductance, putrescine content, leaf contentes of Ca, K, Zn and Fe quantification by neutron activation, dry matter production on leaves and stem, weight of 1000 seeds and crop yield. It was concluded that two maize cultivars studied, cv. BRS-1010 (water stress sensitive) and DKB-390 (water stress tolerant) showed higher dry matter production on leaves and stem, higher weight of 100 seeds and higher crop yield in the presence of calcium silicate. The content of putrescina increased in plants submitted to water restriction. The leaf contents of Ca, K, Zn and Fe varied according to the cultivars and water blade studied. Calcium silicate favored a greater efficiency in the use of water under conditions of low water availability, using 30 % irrigation blade. In cv. DKB 390, the application of calcium silicate favored an increase in the net photosynthetic rate, transpiration rate, stomatal conductance.

Keywords: Calcium Silicate. Water Use Efficiency. *Zea mays* L. Gas Exchanges. Polyamines.

RESUMO

O milho é uma planta conhecida por ser altamente sensível ao estresse hídrico. Quando a água se torna um fator limitante, o potencial hídrico e o teor de água das plantas são substancialmente reduzidos. Nestas condições, a aplicação exógena de Si pode melhorar substancialmente a eficiência no uso da água, a taxa fotossintética e o rendimento nas plantas de milho. O objetivo deste trabalho foi avaliar a eficiência da aplicação de silicato de cálcio como redutor do estresse hídrico em duas cultivares de milho. Foram conduzidos dois experimentos, o primeiro utilizando a cv. BR-1010, (sensível ao estresse hídrico) e o segundo utilizando a cv. DKB-390 (tolerante ao estresse hídrico). Os experimentos foram organizados no delineamento inteiramente casualizado em esquema fatorial 2 x 2, com duas doses de silicato de cálcio: 0 % (ausência) e 100 % (presença), indicadas de acordo com o cálculo de calagem do solo, e duas lâminas de irrigação: 30 % e 100 % de reposição de água, de acordo com o determinado pela curva de retenção de água no solo, em quatro repetições. Utilizou-se vasos com volume de 23 dm^{-3} com uma planta por vaso. Em cada experimento os parâmetros avaliados foram trocas gasosas, taxa fotossintética líquida, taxa de transpiração, condutância estomática, teor de putrescina, quantificação dos teores foliares de Ca, K, Zn e Fe foliares por ativação neutrônica, peso da matéria seca de folhas e caule, peso de 100 sementes e produção de grãos. Conclui-se que as duas cultivares de milho estudadas, cv. BRS-1010 (sensíve) e cv. DKB-390 (tolerante) apresentaram maior produção de matéria seca do caule e das folhas, maior peso de 100 sementes e maior produção de grãos quando se utilizou o silicato de cálcio, independente da lâmina de irrigação aplicada. O teor de putrescina aumentou nas plantas submetidas à restrição hídrica. Os teores foliares de Ca, K, Zn e Fe variaram em função das cultivares e das lâminas de água estudadas. O silicato de cálcio favoreceu uma maior eficiência no uso da água, sob condições de baixa disponibilidade hídrica na lâmina com 30 % de irrigação. Na cv. DKB 390, a aplicação de silicato de cálcio favoreceu o aumento da taxa de fotossíntese líquida, da taxa de transpiração e da condutância estomática.

Palavras-chave: Silicato de Cálcio. Uso Eficiente da Água. *Zea mays* L. Trocas Gasosas. Poliaminas.

SUMMARY

OBJECTIVE

Main objective

To analyze and evaluate the efficiency of the application of calcium silicate in the induction of tolerance to water stress in two maize cultivars.

Specifics objectives

- To evaluate the efficiency of soil fertilization with silicon in mitigating the effects of reduced water availability on maize cultivars.
- To evaluate the effect of calcium silicate and different irrigation blades on gas exchange, putrescine content, quantification of Ca, K, Zn and Fe by neutron activation and yield of two maize cultivars: tolerant and sensitive to water stress.

CHAPTER 1

1 INTRODUCTION

The agricultural scenario shows that crops are continuously subjected to different abiotic stress conditions. Approximately 33% of the world's soils are considered prone to reduced water availability, which is a serious threat to agricultural production (WANG et al., 2015). When environmental factors harm plant physiological conditions, they are called stress factors or only stress. Of all the stress factors involved in cereal cultivation, water availability corresponds to the most important group to be studied (ZHU, 2016).

The development of sustainable alternatives that help mitigate the negative impacts of water stress is indispensable for the development of agricultural crops. Understanding the physiological parameters and their role in plant response to water stress, evaluating a set of metabolites, may help in the development of new cultivars with greater tolerance to stress conditions. In the maize crop, abiotic factors such as climate (soil water availability, air temperature, relative humidity and solar irradiation) are the most related to yield reduction. The factor that most frequently and intensely affects the maize crop yield is water availability (DANTAS JUNIOR et al., 2016).

Drought stress causes decline in turgor and water potential in plants, which negatively influences various physiological processes, inducing plant responses or adaptations, leading to alterations between phytohormones and their metabolites, especially amino acids, polyamines and enzymes. (LISAR et al., 2012). Primary metabolites such as sugars, amino acids and Krebs cycle intermediates are direct markers of photosynthetic dysfunction under water stress, as well as osmotic adjustment effectors. Secondary metabolites (derived from the major metabolites produced by plants due to various physiological changes) are more specific to genera and species and respond to particular stress conditions such as antioxidants, inactivating enzymes of reactive oxygen species, coenzymes and also as regulatory molecules (ARBONA et al., 2013).

In general, plant physiological responses to stress can be divided into three categories: homeostasis maintenance, which includes ion homeostasis and osmotic homeostasis or osmotic adjustment; detoxification of harmful compounds, for example reactive oxygen species or damaged proteins that originated during stress; and growth recovery, alleviating growth inhibition and effects on cell division and expansion, imposed during stress (FELISBERTO, 2015). These strategies involve a high metabolic cost, with increased respiration to provide energy to the processes of physiological maintenance and cell damage repair.

It has already been convincingly demonstrated that Si fertilizers improve the growth of several crops and increase their tolerance to biotic and abiotic stresses (MA and YAMAJI, 2008; AMIN, M. et al., 2018). Silicon (Si) is an element that can be absorbed, translocated and accumulated in large quantities in plants without toxic symptoms (MA et al., 2001); in addition, Si is non-corrosive and does not cause pollution (WANG et al., 2016). Silicon (Si) sources for agricultural use range from chemical products to natural minerals and by-products of steel and iron industries. Slag-based silicate fertilizers refer to calcium silicate fertilizers that are processed using slags, by-products or industrial waste materials from the processing of iron and steel-making industries, free of toxic components, being considered high quality fertilizers (LIANG et al., 2015). The slag used as a silicon source and soil corrective has additional benefits, such as controlling environmental pollution by effectively utilizing industrial waste (PRADO; FERNADES, 2000).

The beneficial effects of Si are mostly attributed to its deposition in different organs. Si is deposited beneath the cuticle to form a cuticle-Si double layer in the leaf, which prevents water loss by evapotranspiration, protecting the plants that face water deficit. Amin et al (2016) evaluated the growth of two maize hybrids under water deficit situations affected by Si application, and concluded that Si-induced improvement in growth and yield under water stress was mediated through enhanced gas exchange. The application of Si in maize plants minimizes the transpiration of plant leaf and water flow rate in the xylem vessel and improves water use capability (GAO et al., 2006).

Considering the complexity of water stress, only an approach that considers soil-plant-environment interactions can generate relevant knowledge that guarantees sustainability in agriculture.

Therefore, the objective of this research was to evaluate the effect of fertilization with silicon on biochemical, physiological and biometric parameters of maize cultivars under water stress.

2 THEORETICAL BACKGROUND

2.1 The maize crop

Maize (*Zea mays* L.) is a grass belonging to the Poaceae family. It is a herbaceous, monoecious plant belonging to the C_4 group, and the third most important cereal in the

world after rice and wheat (FAROOQ et al., 2015). The maize producing regions of the world range from Latitude 58 ° N to Latitude 40 ° S, which includes the entire national territory. The Brazilian production of maize in the 2016/2017 harvest was 83.8 million tons and average yield of 5.5 thousand kilos per hectare, with an estimate for the 2017/2018 harvest of a production of 87.3 million tons (CONAB, 2018).

The maize production chain is one of the most important in the Brazilian agribusiness, considering that only primary production corresponds to approximately 37% of national grain production. Maize is grown in practically the entire Brazilian territory, 90% of which is concentrated in the South, Southeast and Central-West regions (CONAB, 2018). Brazil stands out as one of the main world producers, surpassed only by the United States and China; it is the main cereal produced in the country, constituting an indispensable raw material capable of boosting the most diverse sectors of agriculture, playing a relevant socioeconomic role.

In the last seven decades, the Brazilian maize production increased 4.61 times, accompanied by an expansion of only 3.86 times the cultivated areas (GALVÃO et al., 2014), which is a reflection of the constant adoption of new technologies in the production chain of this crop. However, it is necessary that production continues to grow to ensure food security, since there is no prospect for stabilizing the world's population in this century, reaching between 9.6 and 12.3 billion people by 2100 (GERLAND et al., 2014).

Due to its C_4 metabolism, maize has high photosynthetic efficiency, which allows the crop to reach yield levels higher than 10 Mg ha^{-1} (BERGAMASCHI et al., 2004). Due to the absence of photorespiration, the light compensation point of C_4 plants is close to zero, which favors the photosynthetic process (TAIZ; ZEIGER, 2017). The climatic variables that most affect maize growth are temperature, solar radiation and rainfall, which will define its productive potential. The water requirement of maize varies according to the time and place of sowing, as well as to the leaf area and the genotypes used, ranging between 500 and 800 mm of water slide during its cycle, able to exceed 900 mm in places where crop evapotranspiration is very high (ABDRABOO et al., 2016).

2.1.1 Effects of water stress on the maize crop

Maize is a plant known to be sensitive to water stress (WELCKER et al., 2007), which is the factor that most frequently affects crop yield (DANTAS JUNIOR et al., 2016). Evapotranspiration and crop coefficient (Kc) are of great value to determine the

water demand, since these variables establish the moment and the quantity of water that must be applied in the crop (ALLEN et al., 1998). The Kc numerically expresses the relation between potential evapotranspiration and reference evapotranspiration; this coefficient is determined for each crop development period (SOUZA et al., 2012). Different environmental conditions, especially those in the crop, soil and irrigation management practices can affect Kc values and result in variations for the same crop (DJMAN; IRMAK, 2013).

Maize expresses high sensitivity to drought; thus, the occurrence of periods with reduced water supply to plants at critical crop development periods, between flowering and physiological maturation, can lead to a direct reduction in final yield. The water restriction has the potential to reduce the number of grains per spike, which can lead to a gradual reduction in final yield. Under conditions of low water availability in the soil or high evaporative demand, maize plants have less accumulation of dry matter and reduced transpiration (WU et al., 2011). Water deficiency prior to anther emission in maize plants may result in a 50% reduction in grain yield and, if it occurs at full bloom, it causes a decrease of 20% to 50% in a period of 2 to 8 days, respectively (CARVALHO et al., 2013).

The effect of lack of water, associated with grain production, is particularly important in three stages of plant development: a) floral initiation and inflorescence development, when the potential number of grains is determined; b) period of fertilization, when the production potential is fixed; at this stage, the presence of water is also important in order to avoid dehydration of the pollen grain and ensure the development and penetration of the pollen tube; c) grain filling, when there is an increase in dry matter deposition, which is closely related to photosynthesis. In case of a stress situation, this will result in a lower production of carbohydrates, which would imply a lower dry matter volume in the grains (MORAES, 2009).

Numerous changes occur in plant metabolism kept under abiotic stress, drought affects many processes involved in plant growth and development. When plants are subjected to stress conditions, such as water deficit for an extended period, there is a decrease in the distribution of photoassimilates, leading to the reduction in morphological activities and losses in crop productivity (MALDANER et al., 2014). The rates of stomatal conductance and internal CO_2 concentration may be affected by abiotic factors, such as water deficit (TAIZ and ZEIGER, 2017). A stressful environment for crops, such as water deficit, induces different metabolic events that result in the production of reactive

oxygen species. The maize response to water stress is a crucial and complex process, including osmotic adjustment, antioxidant capacity, photosynthetic rate reduction and abscissic acid accumulation (CRAMER et al., 2011). These processes are controlled by many proteins, which are differentially expressed in various stress-tolerant species, in various biochemical functions and pathways, and in various development stages. During abiotic stress conditions, plants induce the synthesis of osmolytes, such as soluble sugars and amino acids, which contribute to turgor maintenance by osmotic adjustment. Among the amino acids, proline (Pro) is the main agent in this response (besides hexoses), contributing to about 50% of the osmotic adjustment at the tips of maize roots (NISHIZAWA et al., 2008).

In this context, the great variability of maize production in Brazil has as its main cause the climatic variation that can condition water deficit, due to the regime of unstable rains in the different regions of the country (SOUZA et al., 2015). Yield losses in maize crops in the largest producing areas in Brazil are related to the water availability from each region. Souza et al. (2016) analyzed several maize hybrids under water deficit in the state of Minas Gerais, concluding that the highest tolerance to water deficiency was observed in the hybrids DKB 390, tolerant to water stress. The authors state that tolerance is related to the adaptation of the hybrids, exposed to water limitation, at different development stages, also reporting that tolerant maize genotypes present a higher root system, especially of fine roots, and higher aerenchyma proportions.

2.2 Silicon

Si is not considered an essential element for plant growth and development. However, many studies have suggested its beneficial effects on plant growth and production in stress environment (GONG et al., 2005; ASHRAF et al., 2010). Most of the Si present in the soil is in insoluble forms and has no use for plants. In order to make Si available to the plant, the soil is subjected to chemical and physical weathering. The weathering process of minerals with silicates depends on environmental factors, such as temperature and pH, as well as the physicochemical characteristics of the minerals (GÉRARD et al., 2002).

The concentration of Si in plants depends mainly on the concentration of silicic acid in the soil solution (DING et al., 2008; HENRIET et al., 2008) and not on the total concentration of Si present in the soil. The concentration of silicic acid in the soil solution

below pH 9 ranges from 0.1 to 0.6 mM (KNIGHT and KINRADE, 2001). Tropical and subtropical soils generally have low levels of Si due to leaching and weathering processes. In addition, intensive cultivation removes Si from the soil, since it is estimated that 210 to 224 million tons of Si are taken from the world's arable land annually (MEENA et al., 2014).

Basically, Si is absorbed by plants as monosilicic acid $[Si(OH)_4]$ or its anion, which can cross the plasma membrane of the root at physiological pH (RAVEN, 2001). Its absorption in rice occurs through specific inflow channels (called Lsi1) and efflux transporters (called Lsi2), which will mediate Si in the xylem and thus facilitate the transport that will move Si to the plant shoot, where it is deposited as amorphous SiO_2. Soluble $Si(OH)_4$ can passively penetrate cell membranes. After absorption in the root, $Si(OH)_4$ is rapidly translocated to the leaves in the transpiration flow (MA; YAMAJI, 2015).

Plants differ widely in their ability to absorb Si from the external environment; thus, they differ widely in the benefits they receive from Si. The concentration of silicon varies significantly within and between plant species and the variation of Si concentration within species is lower than between species (BROADLEY et al., 2011). In the plant leaves, the concentration of Si ranges from 0.1 to 10% dry matter (MA et al., 2001; RICHMOND; SUSSMAN, 2003). The absorption rate of Si is higher in the families *Poaceae* and *Cyperaceae*, that is, monocotyledons absorb more Si than dicotyledons. The hypothesis proposed for this process is that monocotyledons contain much smaller concentrations of secondary metabolites that are involved in the metabolic responses of the plants to the different stress conditions. Therefore, monocotyledons depend on other mechanisms, such as Si-based defenses, to protect themselves against stress (OSAKABE et al., 2014).

The ability of the roots to absorb Si is considered the reason for differences in the accumulation of Si in different plants (MA; YAMAJI, 2006). The deposition of Si in the plant tissue increases the strength and stiffness of the cell walls, being concentrated in the epidermal tissue as a thin layer of silicon cellulose membrane associated with pectin and calcium ions. Therefore, the double-cuticular layer can mechanically protect and strengthen the structures of the plants. $Si(OH)_4$ is polymerized by increasing silicon concentration in the plant sap. The chemical nature of the polymerized silicon has been identified as silica gel or biogenic opal. Amorphous SiO_2 is hydrated with several numbers of water molecules. It is a type of condensable polymerization with gradual

dehydration of Si(OH)$_4$ and then polysilicic acid (SNYDER et al., 2007). Due to this polymerization, several studies have reported that Si-treated plants maintain greater stomatal conductance and transpiration rate, leaf water content and hydraulic conductivity of roots and of the whole plant (LIU et al., 2015; YIN et al., 2013).

Although the regulation of the expression level of Si transporters has already been elucidated in several species (MA et al., 2011), the mechanism that regulates these genes in many other agronomically important species and cultivars still needs to be elucidated.

2.2.1 Effect of silicon on plant tolerance to water stress

Water stress or deficit is the result of the interaction between factors in the rhizosphere, plant and atmosphere in relation to the amount of moisture available to the plants. Drought-induced suppression in photosynthesis and growth induces significant alterations in important biochemical plant processes, negatively influencing crop yield. Furthermore, the decrease in photosynthesis due to drought stress is associated with disrupted activities of enzymes, loss of membrane integrity and stomatal closure (ARBONA et al., 2013). Under water stress conditions, not only does Si act as a physical or mechanical barrier to minimize transpiration losses, but it also participates in many metabolic and physiological processes that subsequently improve drought tolerance (HATTORI et al., 2005).

The use of Si fertilization is beneficial to protect plants from various types of stress, activating natural defense reactions and producing phenolic compounds that act as antioxidants (QIN; TIAN, 2009). The water potential in plants under water deficit is affected by Si, which stimulates the formation of a double silica layer under the leaf epidermis, minimizing water loss (GONG et al., 2003; LUYCKX et al., 2017). Si is precipitated as $SiO_2.nH_2O$ in the cell wall and in the cellular lumen of plant tissues, which could help maintain water balance in the plant and protect tissues from the harmful effects of water stress (GONG et al., 2005). Due to its deposition on the cuticle, Si modifies cell wall properties and minimizes stomatal conductance in relation to the turgor loss of guard cells, reducing transpiration and increasing internal water storage under water stress conditions (LUYCKX et al., 2017). Silicon application as a fertilizer to plants such as maize depicted decreased leaf transpiration under water stress and improved leaf water content (GAO et al., 2006).

Silicon deposits on the cell walls of xylem vessels prevent vessel compression under conditions of high transpiration caused by drought or heat stress. The silicon-cellulose membrane in the epidermal tissue protects the plants from excessive water loss through transpiration due to reduced stomatal pore diameter and, consequently, reduced leaf transpiration. The application of Si can improve the hydraulic conductance of the roots, modifying their growth and increasing the root/shoot ratio, besides increasing the activity of aquaporins and the osmotic motive force. The higher hydraulic conductance of the root results in increased water uptake and transport, which helps maintain a higher photosynthetic rate and improve plant resistance to water deficiency (LUYCKX et al., 2017, CHEN et al., 2018), increasing the absorption of mineral nutrients by plants and altering the attributes of gas exchange in plants (RIZWAN et al., 2015).

In situations of abiotic stress (by salinity, drought, temperature and heavy metals, etc.), one of the immediate responses of plants is the generation of Reactive Oxygen Species (ROS), as singlet oxygen ($^1O_2$), superoxide (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radicals ($\bullet OH$), which cause severe damage to the cell structure, organelles and functions. In order to alleviate and repair this damage, the plants developed a complex antioxidant system to maintain homeostasis through non-enzymatic (carotenoids, tocopherols, ascorbate and glutathione) and enzymatic (superoxide dismutase - SOD, catalase - CAT and ascorbate peroxidase - APX, glutathione reductase - GR, among others) antioxidants.

The exogenous application of Si can induce stress tolerance, regulating ROS generation, reducing electrolyte leakage and the content of malondialdehyde (MDA), immobilizing and reducing the absorption of toxic ions under stressful conditions. However, the interaction of the antioxidant enzyme system of Si in the plant remains poorly understood. Therefore, deeper analyses at the transcriptomic level are necessary to understand the mechanisms responsible for the Si-mediated regulation of stress responses (KIM et al., 2017). Under abiotic stress conditions, the application of Si shows a variable response to the elimination of ROS, activating the plant defense system. By doing so, the activity of antioxidant arsenals (CAT, SOD, PPO, POD, APX, GPX and GSSH) may also fluctuate depending on the intensity of the stress and the type of plant.

The increases the content of MDA has been considered an indicator of oxidative damage. MDA is considered as a suitable marker for membrane lipid peroxidation. A decrease in membrane stability reflects the extent of lipid peroxidation caused by ROS (ANJUM, et al., 2011). Plants supplemented with Si show resistance to abiotic stress,

reducing MDA activity and ROS production, increasing CAT and APX activities, since both are involved in the conversion of H_2O_2 to H_2O (OSAKABE et al., 2014).

A change in plant-silicon nutrition has influence on the forms of phytoliths. The plants synthesize structures rich in silicon nanometric (molecular), microscopic (ultrastructural) and macroscopic (mass) dimensions. Ninety percent of the absorbed silicon is transformed into various types of phytoliths or silicon-cellulose structures, represented by amorphous silica. Partially biogenic silica is generated as single cells or intercellular structures at the nanometric level. The chemical composition of oat phytoliths (solid SiO_2 particles) showed to be amorphous silica (82-86%) and varied amounts of sodium, potassium, calcium and iron. Phytoliths are highly diversified and a plant can synthesize several forms (BARKER and PILBEAM, 2007).

The information revealing concentrations of Si in various portions harvested from different crops, especially grains, is limited. Some known data show a mean Si concentration of 2.6 g kg^{-1} in maize grains and 23 g kg^{-1} in rice panicles, including grains and husk (TUBANA et al., 2016).

The most efficient nutrient absorption may be another effect of Si on plant growth. Si is suggested to maintain the nutritional balance of plants under water deficit. BOKOR et al. (2017) studied the Si content in maize seeds and report that there is also a significant correlation between the deposition of Si and other nutrients such as Mg, P, S, N, P, Ca, Cl, Zn and Fe. The addition of silicon can increase Ca and K levels in drought-stressed maize leaves. A possible mechanism for increased nutrient uptake may be associated with the activation of silicon-mediated H^+-ATPase in the plasma membrane (KAYA et al., 2006). Apparently, Si increases transcellular K^+ uptake through the increased activity of K^+ channels and transporters across the plasma membrane due to the improved electrochemical gradient created by the high H + -ATPase activity (LIANG et al., 2006).

According to MEHRABANJOUBANI et al. (2015), the application of Si increases the uptake of transcellularly transported elements such as K^+, P, Zn^{2+} and Fe. In contrast, Ca2+ uptake through the apoplastic and transcellular pathways is decreased by the application of Si, possibly through the reduction in apoplastic uptake. The interaction between $Si(OH)_4$ and heavy metals, aluminum and manganese in the soil, is one of the factors that helps clarify the mechanism by which the toxicity of heavy metals of plants is reduced when Si is applied (MATICHENKOV; BOCHARNIKOVA, 2001).

However, the added silicon does not always decrease plant transpiration when soil water availability is low. HATTORI et al. (2005) suggested that the improvement in

silicon-mediated drought tolerance in sorghum may be associated with increased water absorption capacity, rather than decreased transpiration. In another study, SONOBE et al. (2011) confirmed that silicon mediates the active accumulation of soluble sugars and amino acids in sorghum roots, thus reducing the osmotic potential of the root, which induces the increase in water absorption.

Based on data derived from functional genomics, COSKUN et al. (2019) reported that claims that Si affects a wide range of molecular, genetic, biochemical, and physiological processes does not hold up. According to the authors, the prevention mechanisms of stress inherent to Si are basically due to indirect, not direct, effects, suggesting a unifying model, called the apoplastic obstruction hypothesis, by which it is possible to explain how Si can exercise its multiplicity beneficial effects. An important reinterpretation of the role of Si is therefore necessary, which is essential for guiding future studies and informing agricultural practice.

2.3 Physiological responses of plants to abiotic stress

The final yield of a plant is determined by several parameters, among which growth is the main contributor. Particularly relevant is the ability of a plant to maintain growth and continue its development under unfavorable conditions, which limit the obtention of its maximum potential production. Given the inability to move, plants that are exposed to different types of stress have evolved with physiological and biochemical adaptations to adjust and adapt to a variety of environmental stress. Plant adaptation to various abiotic stress factors is a complex process involving numerous changes, including increased expression of many stress-related genes responsible for the accumulation of compatible solutes, expression of antioxidant enzymes, and suppression of energy-consuming pathways (GILL; TUTEJA, 2010). Many plant molecules play an important role in integrating stress signals and controlling downstream stress responses by modulating gene expression and regulating the range of transporters/pumps and biochemical reactions. They include calcium, abscisic acid (ABA), jasmonates (JA), salicylic acid (SA), γ-aminobutyric acid (GABA), amino acids such as proline (Pro) and PAs (TUTEJA; SOPORY, 2008).

To understand how water deficit affects crop development, it is important to identify specific characteristics that determine the performance of crops under drought conditions and that are susceptible to changes by genetic transformation. A specific

physiological response to water deficit is actually combinations of molecular events that are activated or deactivated by the perception of stress. This defense occurs through an alteration in the gene expression model (NEPOMUCENO et al., 2001). ABA regulates the expression of many stress-responsive genes, including late embryogenesis abundant (LEA) proteins, leading to increased tolerance to water stress in plants (AROCA et al., 2008).

Water stress is characterized by subtle changes in the biochemical structure of cells, which appear to be the result of the accumulation of compatible solutes and specific proteins and can be rapidly induced by stress (SHAO et al., 2005). When the plant is subjected to adverse conditions, a series of internal protection mechanisms are activated, and osmotic adjustment is one of the most effective physiological mechanisms for maintaining cellular turgescence (MARIJUAN; BOSCH, 2013). Under conditions of low soil water potential, several metabolites are accumulated and act as osmolytes, not only in the maintenance of cellular turgor, but also in ROS detoxification and stabilization of proteins and cell structures. Water deficit induces similar response patterns or adaptation in plants, such as osmoregulation, accumulation of proline and polyamines, changes in the properties of cell membranes, inhibition of photosynthesis, increased respiration, activation of antioxidant systems and transcription factors, regulation of stomatal responses, reduction in dry matter production, foliar senescence and abscision, changes in root system size, depth and architecture, among others (ZINGARETTI, 2013; OSAKABE et al., 2014).

The mechanism most sensitive to abiotic stress is photosynthesis and when plants are subjected to adverse environmental conditions, such as drought, salinity, heat or cold, carbon assimilation and primary metabolism are largely affected. Primary metabolites such as sugars, sugar alcohols and amino acids have their concentration in plant tissues affected by stress, normally as a result of a weakening in the CO_2 assimilation process, but also as a result of a complex regulatory network (VALERIO et al., 2011; KRASENSKY; JONAK, 2012).

The accumulation of Pro in cells plays an important adaptive role in plant tolerance to stress, mainly due to its osmoprotective properties. During drought and high salinity conditions, its accumulation results in an increase in cell osmolarity, which leads to water inflow or reduction in efflux, which results in the maintenance of the necessary turgor for cell expansion. Free proline can accumulate to high levels in drought-stressed plants. For example, tissue proline levels in excess of 100 mM have been reported in the

root growth zone of maize seedlings exposed to low water potential (BHASKARA et al., 2015). Even under conditions of osmotic stress, the integrity of the membranes must be maintained in order to avoid protein denaturation. Pro interacts with enzymes and other proteins, preserving cell structures and their activities. Its accumulation would also have the function of protecting the cells from denaturation processes under water and saline stress, or even participating in the constitution of a stock of N and C that could be used after the stress period (SILVA, 2012).

However, there is an indication that the accumulation of Pro in adverse environmental conditions is more related to metabolic disorders than to osmotic adjustment, being a biochemical indicator of stress. In some plant species, Pro accumulation results from changes in amino acid metabolism associated with increased protein catabolism and plant senescence (OSAKABE et al., 2014). In addition to its known activity as a compatible solute, Pro also plays an important role in ROS elimination and DNA stabilization (GROPPA; BENAVIDES, 2008). ROS inactivate enzymes and harm important cellular components, as well as causing degradation of membrane phospholipids (BARTOLI, 2013; ABOGADALLAH, 2012), degradation of polysaccharides, denaturation of enzymes and DNA breakdown, besides bleaching of chlorophyll pigments (MILLER, 2010). The increase in the activity of defense enzymes that fight toxic compounds is an essential plant defense mechanism (MULLINEAUX; BAKER, 2010).

The physiology, development and cellular metabolism of plants are driven by nutrient homeostasis. The synthesis of organic macromolecules requires nutrient elements, which complete several functions in the key proteins. In addition, they also act as enzyme cofactors or as signaling molecules. Daily fluctuations in environmental conditions have dramatic effects on plant physiology and metabolism. These environmental fluctuations affect the demands of essential nutrients needed for chloroplast photosynthesis. In addition, nutrient transport pathways in the xylem are also altered by rhythmic changes in transpiration rates. Therefore, continuous mobilization of nutrients is necessary between organelles and tissues, particularly in nutrient-deficient environments (FAROOQ et al., 2018).

Studies on the adaptation and acclimatization to water stress that result in morphophysiological alterations are crucial to increase the tolerance ability to water stress. When metabolome is considered, which includes a huge variety of classes of endogenous and exogenous compounds, with differences in size, polarity, and compound

concentration, the balance between defense metabolites, signaling and damage can be used to assess plant tolerance to a given stress situation (KERCHEV et al., 2012).

2.3.1 Polyamines

The reactions of plants to stress occur through complex metabolic responses. Therefore, understanding physiological parameters and their role in plant response to water stress, evaluating a set of metabolites, especially hormones, polyamines, amino acids and enzymes, can help in the development of new cultivars more tolerant to stress conditions. Several plant-accumulated osmolytes under stress conditions are nitrogen compounds, such as polyamines (PAs), which are low molecular weight aliphatic nitrogenous bases containing two or more amino groups, and have potent biological activity (XU et al., 2014; VUOSKU et al., 2018).

For normal growth and development of prokaryotes and eukaryotes, PAs interact with many macromolecules, both electrostatically and covalently. They occur in free form, conjugated, associated with small molecules, such as phenolic acids or bound forms, associated with several macromolecules (MUSTAFAVI et al., 2018).

PAs play an important role in plant organogenesis, embryogenesis, flower initiation, floral and fruit development (GILL; TUTEJA, 2010). They can modulate functions of RNA, DNA, nucleotides and proteins and protect macromolecules under stress. They are also the modulators of gene expression regulated by stress. They have neutralizing and antioxidant properties, acting as anti-senescence and antistress agents. They also stabilize membranes and cell walls, binding to DNA, RNA, and negatively charged protein molecules (ZHAO and YANG, 2008). As a consequence of these varied forms of interaction, PAs trigger a variety of cellular effects. Among the PAs found in plants, the most abundant are putrescine (Put), spermidine (Spd) and spermine (Spm), which are involved in the regulation of various physiological processes, including responses to biotic and abiotic stress (LEITE et al., 2012).

PAs are present in numerous stages of plant growth and differentiation, such as germination, cell division, leaf, flower and root differentiation, flower and fruit development, organ senescence, and others. In several types of environmental stress, mainly water, many authors have already observed the accumulation of PAs, mainly in relation to Put. However, it is not yet clear in what circumstances these compounds contribute to the adaptation of plants to stress (MUSTAFAVI et al., 2018). The role of

PAs in improving drought resistance has been examined from various perspectives, such as improving antioxidant capacity (SHI et al., 2010); regulating stress signaling (KASUKABE et al., 2004); inducing stomatal closure (LIU et al., 2000) and improving leaf water balance (ALCÁZAR et al., 2010).

Cumulative evidence indicates that PA levels undergo extensive changes in response to a number of abiotic stresses. Physiological, molecular and genetic approaches have been used to functionally identify and characterize genes that could be involved in stress tolerance to metabolites such as PAs in various plant species. However, the specific way in which PAs increase stress tolerance in plants is still not well understood. There are gaps in the information on the translocation of free PAs and their interaction with hormones, and also on their role in gene expression, as much about the exact cellular and subcellular localization of PAs and their biosynthetic enzymes in plants is not known, especially under stress conditions. The causal relationship between PA accumulation and stress tolerance has not been determined, despite numerous observations of changes in PA levels in response to abiotic stresses (SINGH, 2018).

In alfalfa, Put treatment improved seed germination and increased all growth rates (hypocotyl length, fresh and dry root and shoot matter) under water stress caused by different concentrations of polyethylene glycol (PEG 4000), *in vitro* (ZEID; SHEDEED, 2006). In *Arabidopsis*, ABA has been shown to modulate the metabolism of PAs at the transcriptional level by positively regulating the expression of the genes ADC2, spermidine synthase (SPDS1) and spermine synthase (SPMS) under water stress. The overexpression of the ADC2 gene, which controls Put levels, increases drought tolerance through induction of stomatal closure (ALCÁZAR et al., 2006).

The role of PAs as compatible solutes can be questioned based on their lower concentration, compared to a classical osmolyte, such as proline. PAs should not be considered simply as protective molecules, but as compounds that are involved in a complex signaling system and play a key role in the regulation of stress tolerance (XU et al., 2014; MUSTAFAVI et al., 2018).

The function of PAs can range between different plants and even between parts of the same plant, either under osmotic or water stress (SEN et al., 2018). Therefore, the plant response to exogenous PAs under osmotic and water stress will depend on the plant species. The exogenous application of these PAs seems to improve the germination of seeds developed under saline or water stress (MONTEIRO et al., 2014). They can also regulate the size of the K^+ transport channels and pore size in the plasma membrane of

guard cells, strongly regulating stomatal opening and closure, controlling water loss in the plants (LIU et al., 2000).

Many studies have shown that Put foliar application at an appropriate level can trigger physiological processes and induce the biosynthesis of osmotic-adjusting substances such as free amino acids, soluble sugars, and proline. This can compensate for the negative impacts of water stress on plant biomass and increase the quality and quantity of certain bioactive substances (MOHAMMADI et al., 2018). The increase in Put and Pro levels may be associated in plants, being related to drought resistance (TAIZ; ZEIGER, 2010). The exogenous application of Put induced stress tolerance and Pro accumulation in *Trifolium repens* L. during drought (LI et al., 2014).

2.4 Neutron Activation Analysis (NAA) for nutrients

Nuclear energy in agriculture has been used in Brazil through the use of stable isotopes and artificial radioisotopes since the 1970s. The objective has been to know the physical, chemical and biological processes, in order to be related to plant development and the obtention of yield gains in crops. Results of research in this area to date have shown promise for the possibility of evaluating soil fertility and metabolic routes involved in plant mineral nutrition (MALAVOLTA, 2006).

The determination of chemical elements by Neutron Activation Analysis (NAA) provides reliable, traceable and accurate results, being recognized as a primary technique, since it is traceable. Due to its characteristics, it is used successfully in the determination of chemical elements in several matrices around the world. In this context, this technique is being applied in the analysis of several chemical elements responsible for the development of an integrated system of mineral plant nutrition. Neutron activation is a powerful tool to evaluate the uptake and translocation of plant nutrients from various fertilizer sources (OLIVEIRA et al., 2011, 2012, 2013).

The basic principle of NAA consists in subjecting a sample to a neutron flux, in order to produce radioactive isotopes of the nuclei present in the original sample and, subsequently, to measure gamma emissions, determining several chemical elements (DE SOETE et al., 1972). Multi-elemental analysis by instrumental neutron activation, the k_0 method, can be used to determine the concentration of elements in soils, plants and fertilizers (OLIVEIRA et al., 2013). The method allows the determination of a wide

spectrum of chemical elements, being able to evaluate the elements that are at low levels in a very precise way, at a concentration range of mg kg^{-1}.

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CHAPTER 2

**ORIGINAL ARTICLE 1: Tolerance to hydric stress on cultivars of silicon-
fertilized corn crops: absorption and water-use efficiency**

ABSTRACT: Silicon (Si) plays specific functions in agriculture. Si is a beneficial element, as it accumulates at high amounts in plant tissue. Si accumulation in cell walls reduces water loss by transpiration and may be an adaptation factor to water stress. This study evaluated the efficiency of different corn crops using calcium silicate as a reducer

of hydric stress. The experiment was organized in a factorial scheme, completely randomized, with two doses of calcium silicate (0 and 100 % according to soil liming) with two irrigation depths: (30 and 100 % of necessary water reposition in the soil) and two corn cultivars: (cv. BRS-1010) considered sensitive to hydric stress and (cv. DKB-390) tolerant to hydric stress. The study comprised four repetitions. We studied dry matter production on leaves and stem, weight of 1000 seeds and crop yield. We measured efficiency of gas exchange and water use to compare the different treatments. The results for stem and leaves dry matter were better in both cultivars when using calcium silicate, regardless of irrigation depth. Both corn cultivars cv. BRS-1010, sensitive to hydric stress, and cv. DKB-390, tolerant to hydric stress, had greater yield in the presence of calcium silicate, when at the smallest irrigation dose was applied. The treatment with calcium silicate was the most efficient in water use, using 30 % of irrigation depth. cv. DKB 390 was the most productive, with greater tolerance to water stress.

INTRODUCTION

Recently, climatic phenomena have become extreme and long lasting, partially due to anthropic activities (YEPES; BUCKERIDGE, 2011). These changes affect plant cultivars because of temperature rises and shifts in rainfall regimes, directly affecting growth and yield of plants (NELSON et al., 2018). Water supply is an important factor in plant growth and water deprivation is one of the main causes of plant stress. According to Luna et al. (2012), hydric deficit occurs when the amount of water lost by the plant is greater than the amount of water absorbed. Plant tolerance to hydric stress depends on its intensity (GARAU et al., 2009).

Corn production in the main producing regions in Brazil is associated to water availability, especially during the critical period of the crop, from planting to the beginning of grain filling (BERGAMASCHI et al., 2004). The use of silicon (Si) in agriculture can reduce the abiotic stress caused by drought, enhancing water use (MA; YAMAJ, 2006). Si can reduce water stress and reduce transpiration in plants (EPSTEIN, 1994). In addition, the beneficial effect of Si is associated to ensuring the photosynthetic rate and plant stomatal conductance (HATTORI et al., 2005), due to transpiration reduction through the cuticle (MA; YAMAJ, 2006). In wheat, same corn family, Gong et

al. (2005) reported no difference between water content in irrigated plant leaves and plant leaves cultivated under water deficit that was supplied with Si. Si accumulation in cell wall reduces water loss by transpiration and may be an adaptation to water stress. However, plants that did not receive Si showed symptoms of water deficit.

Corn (*Zea mays* L.), belongs to the Gramineae family (Poacea) and the genus Zea, is a C_4 plant, characterized by high productive potential. Corn cultivation is expressive in Brazil and is cultivated in all regions. Corn productivity is low in the northeastern region due to production systems that use little or no technology and because of insufficient and irregular rainfall (MELO et al., 2013).

Corn cultivation is of great economic importance for the Brazilian agriculture and its productivity is linked to the use of potential cultivars, as well as edaphoclimatic conditions and crop management (SANTOS et al., 2002). Genetic improvement to increase plant tolerance to biotic and abiotic stress aims to develop anatomical and physiological mechanisms that help plants thrive in those conditions. Cultivar cv. DKB-390 stands out for its tolerance to hydric deficit, high productivity/yield, and excellent stalk and root quality (PARENTONI et al., 2016). On the other hand, cv. BRS-1010 is sensitive to hydric deficit, with early cycle, and highly efficient on phosphorus use.

In plants, beneficial effects of silicon are attributed to the high Si accumulation in the tissues (FENG, 2004). The mechanical protective effect in plants is attributed to its deposition as amorphous silicon ($SiO_2 \, H_2O$) onto the cell wall.

Si accumulation in transpiration organs forms a double layer of Si cuticle (silica), which reduces water requirement of plants by reducing transpiration (KORNDÖFER, 1999; MARQUES et al., 2014). Evaluation of different irrigation depths in a corn crop showed that the application of 100% of calcium silicate increased water potential in the xylem. In addition, calcium silicate benefited stomatal conductance, net photosynthesis rate and water use efficiency.

The effect of Si application on corn crops needs further studies, since research results are discordant (FREITAS et al., 2016). The low use of Si in agriculture is also attributed to the lack of knowledge about the advantages of its use, both by technicians and producers (MA; YAMAJ, 2006).

In this sense, the development of technical procedures that improve resistance to water stress in arid and semi-arid regions can be a sustainable alternative to mitigate the negative impacts of global climate changes.

This research evaluated the efficiency of different corn crops using calcium silicate as a reducer of hydric stress.

MATERIALS AND METHODS

The study was conducted under greenhouse conditions. Two contrasting corn cultivars were used two corn genotypes, distinct in terms of drought tolerance, more specifically cv. DKB-390 (tolerant) and cv. BRS-1010 (sensitive). The seeds were obtained from Embrapa Milho and Sorgo, located in the municipality of Sete Lagoas, Minas Gerais State, Brazil.

The soil was classified as Oxisol (EMBRAPA, 2013) and samples were collected at a depth of 0-20 cm. The samples were placed to dry, crushed through a 5-mm sieve and mixed to describe the chemical and physical compositions. Chemical and physical compositions of the soil used in this study, according to Raij (2001), were: pH in water (1:2.5) = 5.2; level of organic matter (OM) = 1.42 (dag kg^{-1}); P and K by Mehlich I extraction = 3.69 and 30.41 (mg dm^{-3}); Mg, Ca and Al extractable by 1 M KCl solution = 7.59, 1.12 and 0.20 (cmol dm^{-3}); Si= 3.29 (mg dm^{-3}); Zn= 1.05 (mg dm^{-3}); Cu= 1.38 (mg dm^{-3}); S = 13.24 (mg dm^{-3}); B = 0.07 (mg dm^{-3}); Fe = 53.62 (mg dm^{-3}); T = cation exchange capacity at pH 7.0 (3.62 %); t = cation exchange capacity effective (5.02 %); m = aluminum saturation index (12.50 %); V = Base saturation index (27.85 %). Soil granulometry was the soil physical composition used in this study, determined by the pipette method (sand, silt and Clay = 60 %, 11 % and 29 %). After incubation of limestone and calcium silicate, fertilization was performed for macro and micro-nutrients following the recommendation of Novais et al. (1991) and Marques et al. (2014) adapted for experiments conducted in pots for corn crops.

The experiment was organized in a factorial scheme completely randomized with two doses of calcium silicate: 0 (absence) and 100% (presence) of calcium silicate indicated to soil liming at two irrigation depths: 30 and 100 % of necessary water replacement in this soil and two seed cultivars of *Zea mays* L., cv. BR-1010, considered sensitive and cv. DKB-390, tolerant to water stress, planted in 19 dm^{-3} pots. The study was composed of four repetitions.

The treatments comprised the application of 0 % (control) and 100 % (rec-recommended) calcium silicate and two water irrigation depths (30 % and 100 % of the recommended blade) and two seed cultivars of *Zea mays* L., cv. BR-1010, considered

sensitive and cv. DKB-390, tolerant to water stress. Calcium silicate and limestone doses were applied in the liming process to balance the amount of calcium silicate in the treatments. After application, the soil remained under incubation for 45 days (Table 1).

Table 1. Doses of calcium and limestone silicate applied to a 23 dm^{-3} pot.

Treatment	$CaSiO_3$	Treatment	$CaCO_3$
$CaSiO_3$	----g pot----	$CaCO_3$	----g pot----
0	0	100	23.3
100	27.02	0	0

We determined the soil water retention curve (Figure 1). Parameters of the soil water retention curve used in the irrigation blade quantification and irrigation management were obtained based on the model proposed by Genuchten (1980) with the aid of the solver application of Microsoft Office Excel® software ($\theta= 0.4215$ x [1+ (0.2040 x $|\Psi m|$)1.8757]-0.4669 + 0.2670). Field capacity was estimated using the equation proposed by Dexter (2004). The moisture value in field capacity was 0.3458 m^3 for voltage -40 kPa. Irrigation management was carried out based on the water retention curve in the soil and in Watermark readings (Soil Moisture Meter) installed at depth 0.15 m. Irrigation was performed whenever soil water stress reached -40 kPa in each treatment, as recommended by Guerra (1994). The readings were taken daily at 17h00. In addition, devices were installed to quantify the matrix potential at the greatest tensions 30 and 100 % of the ideal lamina.
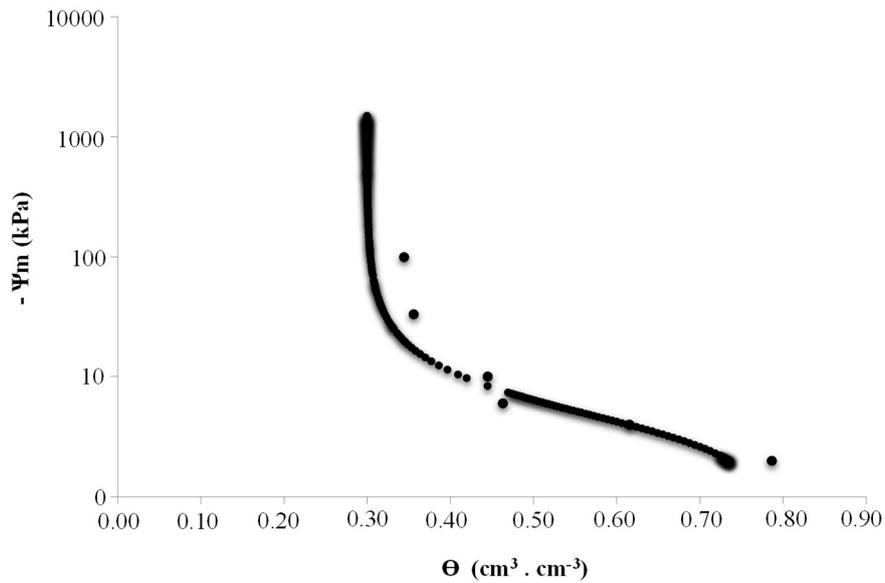
Figure 1. Water retention characteristic curve of Oxisol used in the research.

Irrigation was based on the water retention curve linked to soil and tensiometer measurements installed at depth 0.15 m. Irrigation was implemented when water tension in soil reached -40 kPa and at irrigation depth (30 and 100 % of necessary rate for water reposition in the soil). All measurements were carried daily, at 17h00, and soil moisture meters (Watermark, model 200SS-5) were installed to quantify the matric potential (Figure 2) only in two higher tensions (30 and 100% of ideal soil depth). The water volume applied to irrigation was calculated by equation: $V = (\theta_c - \theta_{treat.}) \times V_{soil}$, where V = water volume applied (mL), θc = humidity in yield capacity ($cm^3 . cm^{-3}$), θ_{treat} = humidity in treatment ($cm^3.cm^{-3}$), and V_{soil} = volume of soil (mL).

A drip irrigation system, with auto-compensating drippers and water flow of 4 L h^{-1}, was installed to ensure a precise application of depths. Flexible tubes of 80 cm long were used on the side lines, which were initiated at the distribution control, while water was pressurized by gravity. The uniformity coefficient linked to water flow in this study was measured by: CU = (q 25 % / q average) proposed by Bralts and Kesner (1982). Where, UC = uniformity coefficient, q 25 % = average of 25 % of minor flows (L h^{-1}), and q average = average total (L h^{-1}). In this study, the UC value was 0.93.

To determine the dry matter (DM) weight of corn plants, stems and leaves were collected. The leaves were separated from the stem by a plant cut and washed in running water. Leaf and stem were oven dried at 60° C with forced ventilation until a constant mass was reached and the mass was then weighed.

Transpiration rate, stomatal conductance and net photosynthetic rate were evaluated using an infra-red gas analyzer (LICOR, model LI-6400) in adaxial surface of fully expanded leaves. Photosynthetic water use efficiency was estimated according to Fischer and Maurer (1978). Gas exchange was evaluated between 9:00 and 12:00 h in all plants, and irradiance was kept at 1000 μmol m^{-2} s^{-1} during the measurements.

At the end of the study, corn production and weight of 100 corn seeds were measured.

Water use efficiency (WUE) was quantified considering the relationship between CO_2 assimilation rate and corn transpiration rate (FISCHER; MAURER, 1978). The infrared gas analyzer (IRGA) portable meter (Model - LI-6400) was used for this analysis.

Results were submitted to analysis of variance and, when there was a significant difference, the most appropriate test (Scott-Knout or t-test) was applied according to the theories recommended by Steel et al. (2006). In addition, standard deviations of all treatments were calculated and regression and correlation estimators (Pearson or Spearman) were applied using SISVAR® software (FERREIRA, 2014).

RESULTS AND DISCUSSION

Regardless of the absence or presence of calcium silicate, the highest production of leaf and stem dry matter of corn cultivars BRS-1010 (sensitive to water stress; Figures 2 A and C) and DKB-390 (tolerant to water stress; Figures 2 B and D) were obtained at 100% irrigation depth.

When the calcium silicate was applied, a 12% increase in values was obtained compared to the control group (absence) at both irrigations depths, for cv. BRS-1010 (Figures 2A and C) and cv. DKB-390 (Figures 2 B and D). Cv. DKB-390 produced 19 % more leaf dry matter than cv. BRS-1010 (Figures 2A and 2B). For dry matter stem, 30 % irrigation depth had significantly higher production in presence of calcium silicate. The net assimilation rate estimates photosynthetic efficiency of plants (SHIPLEY, 2006). This variable is directly related to the relative growth rate (GALMES et al., 2005). These two variables are therefore determinant to explain plant growth. They are also used in the evaluation of plant responses to water stress (SHAO et al., 2008). Marques et al. (2014) evaluated different irrigation depths in maize and concluded that the application of 100 % of calcium silicate increased the xylem water potential. In addition, calcium silicate

promoted beneficial effects on stomatal conductance, net photosynthesis rate and water use efficiency (MARQUES et al., 2016).
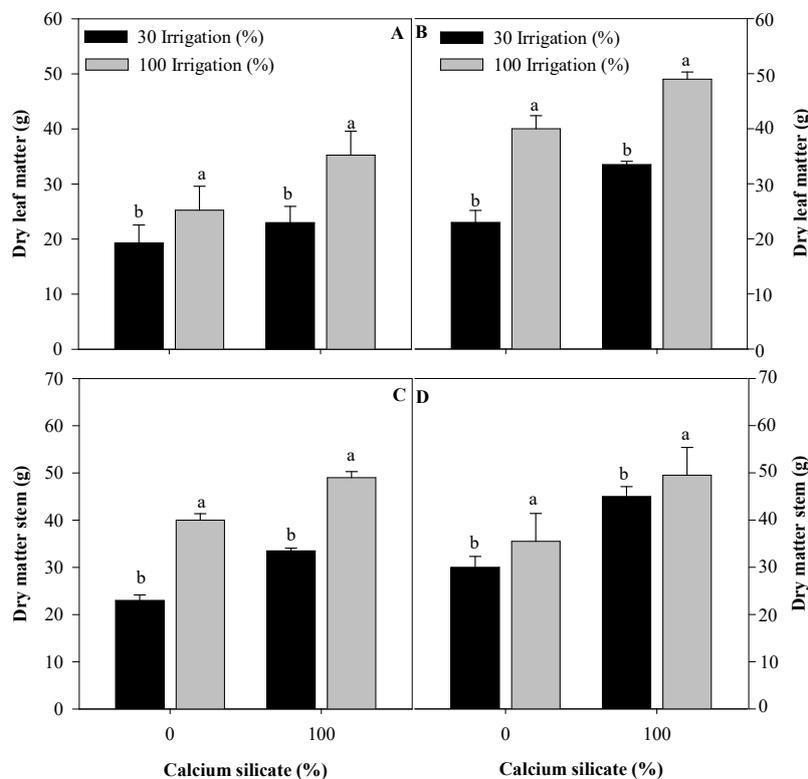

Figure 2. Dry matter of leaves and stem in *Zea mays* plants cv. BR-1010 (A and C) and DKB-390 (B and D) exposed to two calcium silicate levels (0 and 100 % of $CaSiO_3$ indicated by soil liming) and two irrigation depths (30 and 100 % of water necessity reposition in the soil). Means followed by the same letter to each irrigation depth are not significantly different by the Scott-Knott test at 5 % probability ($P > 0.05$). The bars represent the mean standard error.

In presence of calcium silicate (Figure 3A), cv. BRS-1010 (sensitive) showed a higher photosynthetic rate at 30% of irrigation depth, while for cv. DKB-390 (tolerant), the highest photosynthetic rate was in the presence of calcium silicate and at 100% irrigation depth (Figure 3 B), which showed photosynthetic rate 16% higher than cv. BRS-1010 did (Figure 3A).

The highest value of corn plants transpiration rate was observed for cv. DKB-390 (tolerant) and 100% irrigation depth, in presence of calcium silicate (Figure 3D). Figure 3C shows that cv. BRS-1010 (sensitive) had greater transpiration rate with the lowest water application (30 % irrigation depth).

The stomatal conductance in both cultivars was higher in presence of calcium silicate in cv. BRS-1010 (sensitive) and in cv. DKB-390 (tolerant), 30% of irrigation

depth (Figure 3 E) and 100% irrigation depth (Figure 3 F), respectively. Cv. DKB-390 showed the highest photosynthetic rate (16 %), stomatal conductance (17 %) and transpiration rate (22%) when compared to cv. BRS-1010. When water deficit occurs gradually, plants need acclimatization, which is possible due to changes in morphological and physiological characteristics, mainly in leaves and roots (CUTLER et al. 2011). The mechanisms used by plants in stress situations include the activation of enzymes involved in protection against oxidative stress, such as catalase, superoxide dismutase, peroxidases, and glutathione (SOUZA et al., 2013).

Water deficiency affects plant growth, which may be a reflection of changes in plant physiology, causing leaf area decrease, senescence acceleration, leaf abscission, reduction of intercellular spaces and mesophyll in cell size (GHANNOUM, 2009), decrease of intracellular CO_2 concentration, and reduced photosynthesis (MITTLER, 2002). Changes in photosynthetic reactions caused by water stress lead to the formation of reactive oxygen species (ROS), causing oxidative reactions (MITTLER, 2002); however, these ROS can be very important in defense responses in plants to water stress (SILVA et al., 2006). In addition, water stress promotes stomatal closure, reduces photosynthetic efficiency and limits nutrient absorption (ZARCO-PERELLÓ et al., 2005), causing losses to biomass and grain yields (RIBAUT et al., 2009).

Despite the high productive potential, corn cultivation presents great sensitivity to abiotic stresses and water deficit is the main cause of production losses. Thus, plant breeders have sought to develop genotypes with high yield under normal growing conditions and that are capable of maintaining good performance even under conditions of water scarcity, minimizing losses. In corn genotype cv. DKB-390 (drought tolerant), there is an increase in exoderm thickening, a greater number of metaxylem elements, a smaller diameter of the vessel elements and in leave, a greater number of stomata occurs and as well as a smaller distance between the vascular bundles (MAGALHÃES et al., 2012). Other studies have shown increases in internal carbon concentration (Ci) and concentration increases of abscisic acid (ABA) under water stress in corn genotypes cv. BRS-1010 (AVILA et al., 2015).

However, some acclimatization mechanisms can be activated when the plant is exposed to water stress (NILSEN; ORCUTT, 1996). The root system can increase the formation of adventitious roots with longitudinal interconnections of gas spaces called aerenchym (TAIZ; ZEIGER, 2006). Another mechanism of tolerance is stomata closure, which are responsible for transpiration control in plants (CUSHMAN, 2005). Closure

occurs when the mesophyll begins to suffer dehydration and is regulated by abscisic acid (ABA). At the cellular level, another response is the osmotic adjustment that decreases water potential by promoting water entry into the plant (LIANG et al., 2015). Physiological and anatomical changes can be adaptations of plants to reduce metabolic costs for soil growth and exploration, favoring survival in these environments.

All terrestrial plants contain Si in their tissues and Si concentration in the aerial part varies greatly between species (0.1 to 10% Si in dry weight), showing an extremely unequal distribution in plants (Kraus; Arduin, 1997). Studies on Si use in fertilization have shown innumerable benefits to plants, such as increasing plant tolerance to water stress. These data are relevant, as they highlight the benefit of Si as water stress enhancer in corn crops. These results show that in Brazil, silicon becomes part of essential micronutrients (OSMOND et al., 2008).

According to observations (SCHOLANDER, 1964) in corn plants under water stress, the presence of Si increased dry matter of the aerial, corroborating with the observed increased sorghum growth (*Sorghum bicolor*) submitted to water stress with increasing Si doses. On the other hand, OM production is monitored in the plant to elucidate or understand morphological processes linked to plant growth and their influence on plant productivity, characterized the quantitative analysis method (TURNER, 1988). The Si application as tolerance inducer in genotypes *Vigna unguiculata* shows that the genotypes assessed increased growth and development when cultivated under hydric stress of 50% and treated with Si, also reporting that the antioxidant activity of enzymes SOD, CAT and APX were boosted by the foliar application of Si (ARAUJO, 2017).
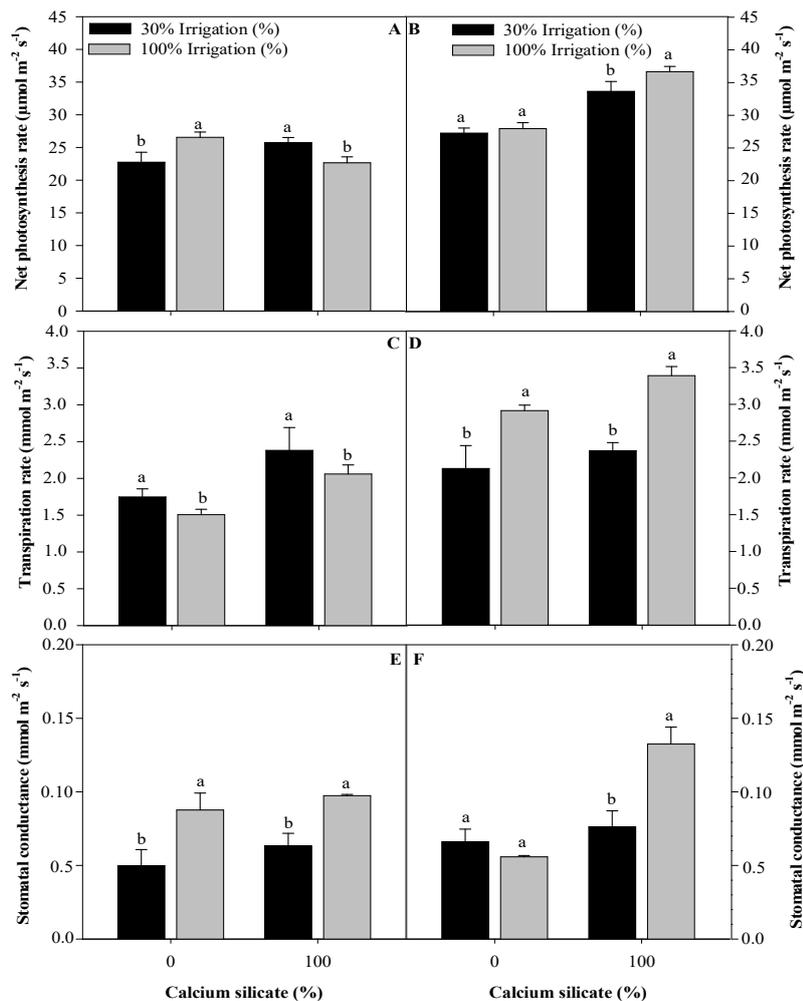
Figure 3. Net photosynthetic rate cv. BR-1010 (A) and cv. DKB-390 (B), transpiration rate cv. BR-1010 (C) and cv. DKB-390 (D), stomatal conductance cv. BR-1010 (E) and cv. DKB-390 (F) in *Zea mays* plants exposed to two calcium silicate levels (0 and 100 % of $CaSiO_3$ according to soil liming) and two irrigation depths (30 and 100 % of necessary water reposition in the soil). Means followed by the same letter to each irrigation depth are not significantly different by the Scott-Knott test at 5 % of probability (P > 0.05). The bars represent the mean standard error.

The highest weight obtained from 100 corn seeds (Figures 4A and 4B) and grain production (Figures 4C and 4D) was achieved using 100% irrigation depth, both in the presence or absence of calcium silicate. Cv. DKB-390 produced 15.6 % more grains than cv. BRS-1010 did. Plant species vary greatly in their ability to absorb and accumulate Si in tissues and may be classified, depending on percentages of SiO_2 in the dry matter, as: (a) accumulating plants, which include grasses, such as rice, containing more than 4 % SiO_2; B) intermediates, with SiO_2 contents ranging from 2 to 4 % (cereals, sugarcane and few dicots); C) non-accumulating plants, including most dicotyledons, with values lower than 2 % SiO_2, such as beans (HODSON et al., 2005).

Plant absorb water to meet their physiological needs and supply their nutrients, which are transported along water in the form of mass flow (BÄNZINGER et al., 2006). The technique of x-ray, microanalysis and mapping of Pozza et al. (2004) shows a uniform distribution of the element on all abaxial surface of coffee leaves.

Many studies have been developed for a better adaptation of crops to regions with water limitations and make them more tolerant to acidity (MARQUES et al., 2014). However, the production of most of the cultivated plants is impaired under stress conditions, especially maize that is sensitive to water deficit (RAIJ et al. 1998) and whose cultivation in semi-arid regions, such as the Brazilian northeast, is of great importance not only to directly supply food needs to the population, but also for the regional agro-industry. Si absorption benefits crops, such as increased lodging resistance and photosynthetic efficiency. Si is a chemical element involved in the physical functions of evapotranspiration regulation and is capable of forming a barrier of mechanical resistance to invasive fungi and bacteria into the plant, hindering insect pests attack (LUX et al., 2002).
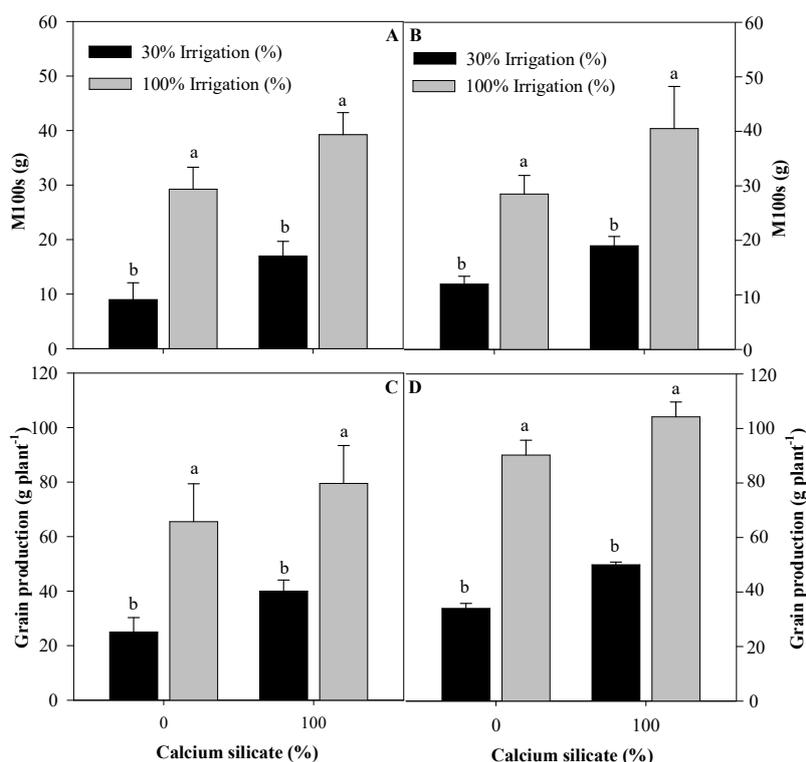

Figure 4. Weight of 100 corn seeds cv. BR-1010 (A) and cv. DKB-390 (B), and Grain production BR-1010 (C) and cv. DKB-390 (D) in *Zea mays* plants exposed to two calcium silicate levels (0 and 100 % of $CaSiO_3$ indicated to soil liming) and two irrigation depths (30 and 100 % of necessity for water reposition in this soil). Means followed by the same letter to each irrigation depth are not significantly

different by the Scott-Knott test at 5 % of probability (P > 0.05). The bars represent the mean standard error.

Water use efficiency (WUE) at different irrigation depths, using each proportion of calcium silicate, for both cultivars is shown in Figures 5A and 5B. Cv. BRS-1010 (Figure 5A) presented the highest WUE at 100 % irrigation depth in the absence of calcium silicate. However, in the presence of calcium silicate, this cultivar was more efficient at 30 % irrigation depth. For cv. DKB-390, the highest WUE was at 30 % irrigation depth in the presence of calcium silicate. Our results show that the use of calcium silicate favors higher WUE when soil moisture is a limiting factor, as at 30 % of irrigation depth. The use of WUE indicators is one way of analyzing crop response to different water availability conditions because it relates dry biomass production or commercial production to the amount of water applied or evapo-transpired by the crop (COSTA; MORAES, 2009). The effect of mechanical protection is mainly attributed to Si deposition in the form of amorphous silica ($SiO_2.nH_2O$) on cell wall (Feng, 2004). Si accumulation in the stomata forms a double layer of cuticle silica by reducing transpiration (DANTAS et al., 2011).

Si increased photon capture, increasing excitation energy absorption to centers aimed at photochemical reactions, in addition to increasing efficiency of plastoquinone (FENG, 2004) and electron transport rates through the photosystems (LUX et al., 2002). Si is a beneficial element for plants (BRAGA et al. 2010) and is the second most common mineral in the soil (HODSON et al., 2005), occurring in the form of Si or silicate, which can be combined with various metals (POZZA et al., 2004). Si can be absorbed by the roots in the form of silicic acid [$Si(OH)_4$] and transported to the shoot via xylem (MA; YAMAJ 2006). The contents of this element in the shoot of the plant range between 0.1 and 10 % dry matter (RAIJ et al., 1988). Si mitigates biotic and abiotic stresses (SILVA et al., 1984) in corn (MARQUES et al., 2014), such as infection caused by a pathogen (CAO et al., 2015), saline stress, and drought stress (PUPPALA et al., 2005), besides increasing plant tolerance to metal toxicity, such as Al in *Zea mays* (CHEN et al., 2005).
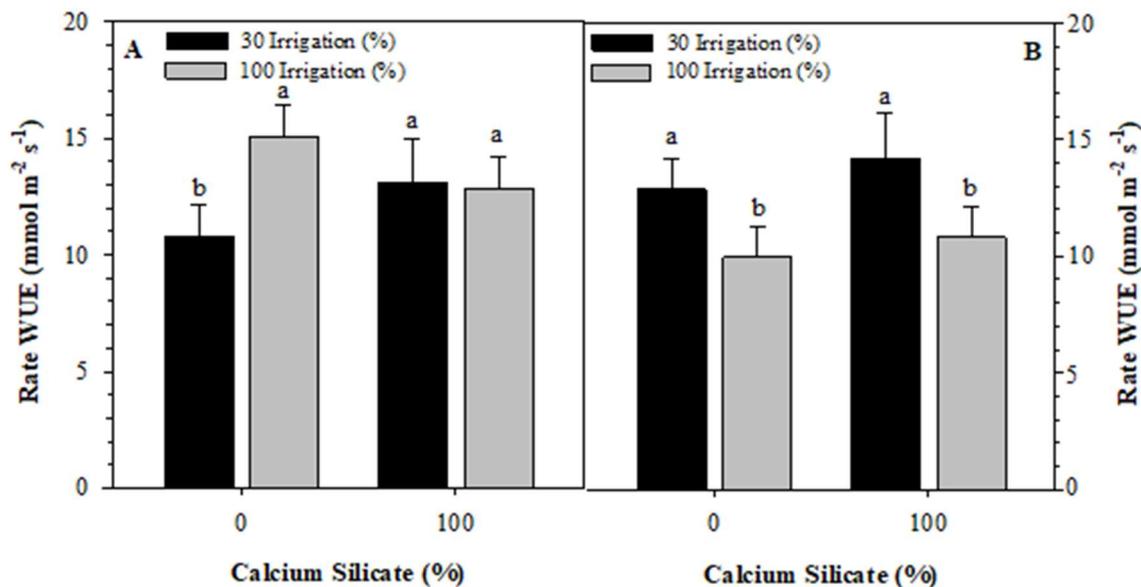
Figure 5. WUE in cv.BR-1010 (A) and DKB-390 (B) in *Zea mays* plants exposed to two calcium silicate levels (0 and 100 % of $CaSiO_3$ indicated to soil liming) and two irrigation depths (30 and 100 % of necessary water replacement in the soil). Means followed by the same letter to each irrigation depth are not significantly different by the Scott-Knott test at 5 % of probability ($P > 0.05$). The bars represent the mean standard error.

CONCLUSION

The two corn cultivars studied, cv. BRS-1010 water-stress sensitive, and cv. DKB-390 water-stress tolerant, presented higher production in the presence of calcium silicate, when the smallest water layer was applied. The highest efficiency in water use was obtained in the treatment with calcium silicate, with the application of a 30% lamina irrigation. cv. DKB 390 was the most productive, with greater tolerance to water defict.

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RESUMO: O silício (Si) desempenha funções específicas na agricultura, sendo considerado um elemento benéfico, pois se acumula em quantidades elevadas no tecido da planta. O acúmulo de Si nas paredes celulares reduz a perda de água pela transpiração e pode ser um fator de adaptação ao estresse hídrico. Este estudo avaliou a eficiência de

diferentes cultivares de milho utilizando o silicato de cálcio como amenizador do estresse hídrico. O experimento foi organizado em esquema fatorial, inteiramente casualizado, com duas doses de silicato de cálcio (0 e 100% de acordo com a calagem do solo), com duas lâminas de irrigação (30 e 100% de reposição de água necessária no solo) e duas cultivares de milho: a (cv. BRS-1010) considerada sensível ao estresse hídrico e a (cv. DKB-390) tolerante ao estresse hídrico, com quatro repetições. Estudamos a produção de matéria seca em folhas e caule, o peso de 1000 sementes e o rendimento da cultura. Medimos a eficiência das trocas gasosas e do uso da água para comparar os diferentes tratamentos. Os resultados para matéria seca do caule e das folhas foram melhores em ambas as cultivares, quando utilizadas o silicato de cálcio, independente da lâmina de irrigação. As duas cultivares de milho estudadas, cv. BRS-1010 sensível ao estresse hídrico e DKB-390 tolerante ao estresse hídrico apresentaram maior produção na presença de silicato de cálcio, quando a menor lâmina de água foi aplicada. A maior eficiência no uso da água foi obtida no tratamento com silicato de cálcio, utilizando 30% de irrigação. A cv. DKB 390 foi a mais produtiva, com maior tolerância ao déficit hídrico.

PALAVRAS-CHAVE: *Zea mays* L. Irrigação. Matéria seca. Produção. Híbridos.

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CHAPTER 3

ORIGINAL ARTICLE 2: Gas exchange and putrescine content as drought stress indicators in maize cultivars fertilized with calcium silicate

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Gas exchange and putrescine content as drought stress indicators in maize cultivars fertilized with silicon

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Abstract

The effects of drought stress on maize have been extensively reported in tropical and subtropical areas, including morphological changes in plant and reduction in the grain yield. The aim of this study was to evaluate the effect of silicon fertilization in two irrigation blades, on gas exchange, putrescine content, quantification of Ca, K, Zn and Fe by neutron activation and grain yield in two maize cultivars, tolerant and sensitive to drought stress. Two experiments were conducted, the first using BR-1010 (sensitive to drought stress) and the second using DKB-390 (tolerant to drought stress), in 19 dm^{-3} pots with one plant in each pot. The experiments were organized in a completely randomized design, combinations of two irrigation blades (30 % and 100 % of necessary water replacement) and two silicon conditions per pots: control (-Si), and 27g Si (+Si) using calcium silicate (10.5 % Si) with four replicates. The contents of putrescine, Ca, K, Zn and Fe, as well as transpiration rate, stomatal conductance and net photosynthetic contents were quantified. At the end of the study, corn yield was measured. It was concluded that supplementation with Si contributes to a 12% increase in yield for BR-1010 (drought stress sensitive) and 14% for DKB-390 (drought stress tolerant). Si increased the net photosynthetic rate, transpiration rate, stomatal conductance in DKB 390. The content of putrescine increased in plants submitted to drought stress. The leaf contents of Ca, K, Zn and Fe varied according to the cultivars and water blade studied.

Keywords: Calcium Silicate, Neutron activation analysis, Polyamines, Stress Tolerance, Water use efficiency, *Zea mays* L.

Abbreviations: Ca, calcium; Fe, iron; K, potassium; PAs, polyamines; Put, putrescine; ROS, reactive oxygen species; Si, silicon; Zn, zinc.

Introduction

Drought stress caused by water scarcity is one of the critical factors that limits maize yields in most maize production regions worldwide (Cooper et al., 2014). In tropical and subtropical regions, the irregular distribution of rainfall favors water stress, which affects several physiological and biochemical processes, reducing the development of cultivated plants. Fertilization with silicon (Si) may be a viable alternative to attenuate the harmful consequences of water stress in plants of the Poaceae family, such as corn (Rao, 2017). The application of Si in soils with limited moisture increases the growth and yield of corn hybrids due to the improvement in photosynthetic rate, higher osmotic adjustment, increase in water content and decrease in transpiration (Amin et al., 2018). The main mechanism for the relief of abiotic stress by Si is its deposition on the cuticles, which prevents water loss through evapotranspiration, protecting plants that face water deficit (Ma et al., 2015). Under drought stress conditions, Si-mediated mechanisms that are involved in water consumption by the plant root include increasing the osmotic motive force via active adjustment; the improvement in the transport activity of aquaporins at the transcriptional and post-transcriptional levels, the modification in root growth and the increase in the root/shoot ratio (Chen et al., 2016).

To understand the physiological parameters in plant response to drought stress, it is necessary to evaluate a set of metabolites, especially polyamines (PAs), which are aliphatic organic bases belonging to low molecular weight bioactive amines, essential for cell growth and functions, interacting with many macromolecules. As a consequence of these various forms of interaction, PAs trigger a series of cellular effects, acting as inactivating enzymes of reactive oxygen species (ROS), coenzymes and also as regulatory molecules (Leite et al., 2012). They are also an effective cross-protection mechanism against biotic threats, providing a link between abiotic and biotic stress responses (Arbona et al., 2013). Among the PAs found in plants, the most abundant are diamine putrescine, triamine spermidine and tetramine spermine.

Studies have shown that Si may change plant tolerance to drought stress. Plants grown with Si has altered responses in nutrient uptake have reduced toxic accumulation of iron and manganese and other heavy metals, like aluminium, and increased phosphorus uptake (Zhu et al., 2004). Si application increased the uptake of transcellularly transported elements like K, P, Zn and Fe. In contrast, Ca uptake which occurred via both apoplastic

and transcellular pathways was decreased by Si application, possibly through reduction of apoplastic uptake (Mehrabanjoubani et al., 2015).

The nutrients that have been taken up by plants under stress can be quantified by several methods. Among them, the multi-elemental technique, neutron activation analysis, k_0 method (INAA- k_0), that has been successfully applied in the determination of the elemental concentration of soils, plants and fertilizers (Menezes and Jacimovic, 2011). The principle of this technique is to irradiate a sample by neutron flux in a nuclear reactor in order to produce radionuclides and, then, to measure gamma emissions, determining several chemical elements.

Therefore, this study evaluated the effect of silicon fertilization in two irrigation blades, on gas exchange, putrescine content, quantification of Ca, K, Zn and Fe by neutron activation and grain yield in two maize cultivars, tolerant and sensitive to drought stress.

Results and Discussion

The net photosynthetic rate of BR-1010 (sensitive) with 30% irrigation blade with +Si (Fig. 1A). DKB-390 (tolerant) +Si increased the net photosynthetic rate in the 100% irrigation blade (Fig. 1B). This result demonstrates that Si-treated plants exhibit higher photosynthesis, once they have more stable chloroplasts due to better hydration and greater stomatal conductance (Figs. 1D and 1F). Drought stress directly affects photosynthesis rates, limiting CO_2 diffusion to the substomatic chamber. The oxidative stress resulting from abiotic and biotic stress affects photosynthesis, affecting the main enzymes of the Calvin cycle and the photosynthetic electron transport chain (Gong and Chen, 2012). In the leaves, Si fills the interfibrillar spaces and reduces the movement of water through the cell wall, which conserves the water and can reduce the transpiration rate (Marafon and Endres, 2013).

Maize cultivars studied presented a different behavior in relation to transpiration rate (Figs. 1C and 1D). The highest values were observed in BR-1010 (sensitive) +Si under drought stress conditions (30% irrigation). On the other hand, for DKB-390 (tolerant), the highest values were observed +Si no drought stress. Therefore +Si increased the transpiration rates, which favored the net photosynthesis rate (Figs. 1A and 1B). Si supplementation may not affect maize cuticular transpiration of the leaf, but it significantly reduces stomatal transpiration (Gao et al., 2006). In this case, not only may increase drought tolerance be associated with leaf transpiration, but also with root water

absorption, since the reduction in water loss by transpiration is not the only mechanism mediated by Si in plants (Shi et al., 2016). Some plants, after the addition of Si, transpiration increases (Chen et al., 2011); in others, transpiration is reduced (Gao et al., 2006), or no change in transpiration is observed (Hattori et al., 2008), indicating different strategies among species to balance water absorption and loss on the leaf surface.

+Si increases stomatal conductivity in two cultivars studied (Figs. 1E and 1F), indicating that Si has influence on the stomatal movement of plants. To prevent the leaf water potential from falling below critical levels for the stability of the water transport system, stomatal conductance is decreased (Oren et al., 1999). Silicon supplementation may increase the photosynthetic rate, being associated with positive effects on stomatal conductance and transpiration under stress conditions (Yao et al., 2011). Si does not always decrease plant transpiration. Hattori et al. (2005) observed an increase in stomatal conductance and transpiration rate of leaves in potted sorghum by supply of Si under drought stress. Similar results were also observed in drought-stressed wheat (Gong et al., 2008) and rice (Chen et al., 2011).
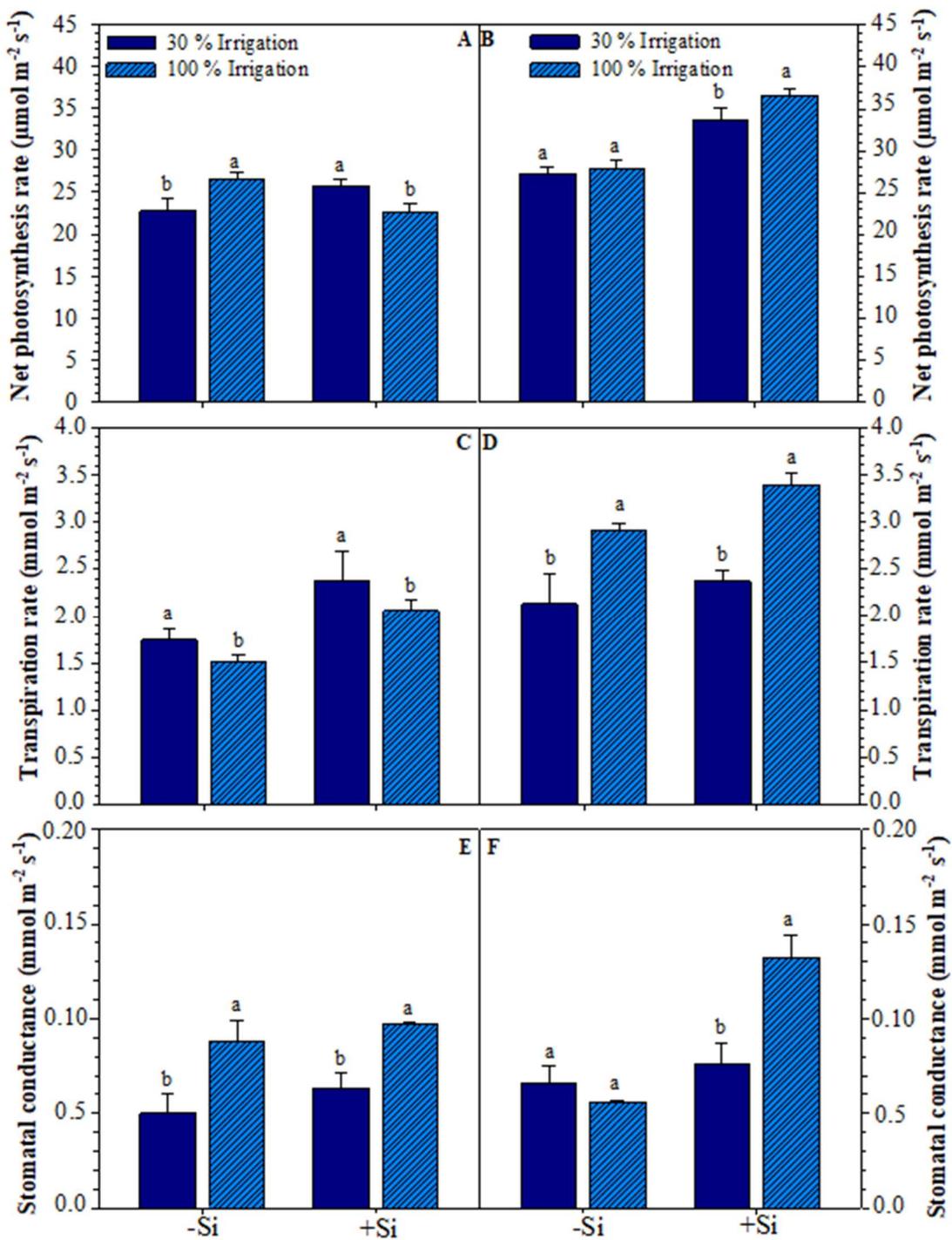
Figure 1. Net photosynthetic rate, transpiration rate and stomatal conductance in BR-1010 (A, C, E) and DKB-390 (B, D, F) in maize exposed to -Si and +Si and two irrigation blades (30 and 100 % of necessary water reposition). Means followed by the same letter are not significantly different by the Tukey test at 5% of probability. The bars represent the mean standard error.

Put concentration was higher under drought stress in both cultivars (Figs. 2A and 2B). + Si increased Put in BRS-1010 (sensitive) and decreased in DKB-390 (tolerant). However, when there is no drought stress (100% irrigation) the levels of Put in the two cultivars had the lowest values on + Si. Plants under stress conditions accumulate several osmolytes, such as PAs, especially Put, which is one of the most abundant (Leite et al., 2012). PAs have metabolic pathways interconnected with different routes in the formation of molecules and metabolites that signal plant responses to stress (Farriduddin et al., 2013). The PA-mediated regulation in response to water stress suggests that they are potentially useful in overcoming the damaging effects of drought, stabilizing the cytoplasmic membrane, as well as acting as a free radical scavenger (Monteiro et al., 2014). Many studies have shown that foliar application of Put at an appropriate level can trigger physiological processes and induce the biosynthesis of osmotic adjustment substances, such as free amino acids, soluble sugars, and proline. This may compensate for the negative impacts of drought stress on plant biomass and increase the quality and quantity of certain bioactive substances (Sánchezrodríguez et al., 2016; Mohammadi et al., 2018).
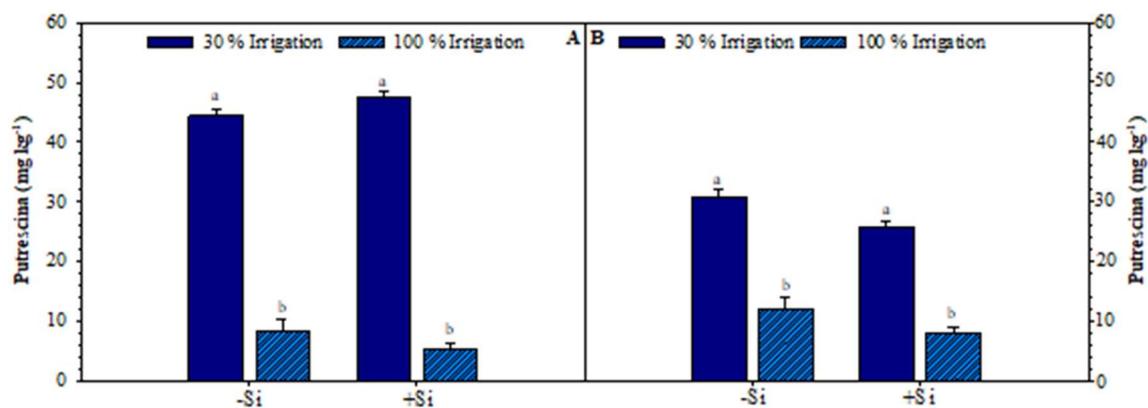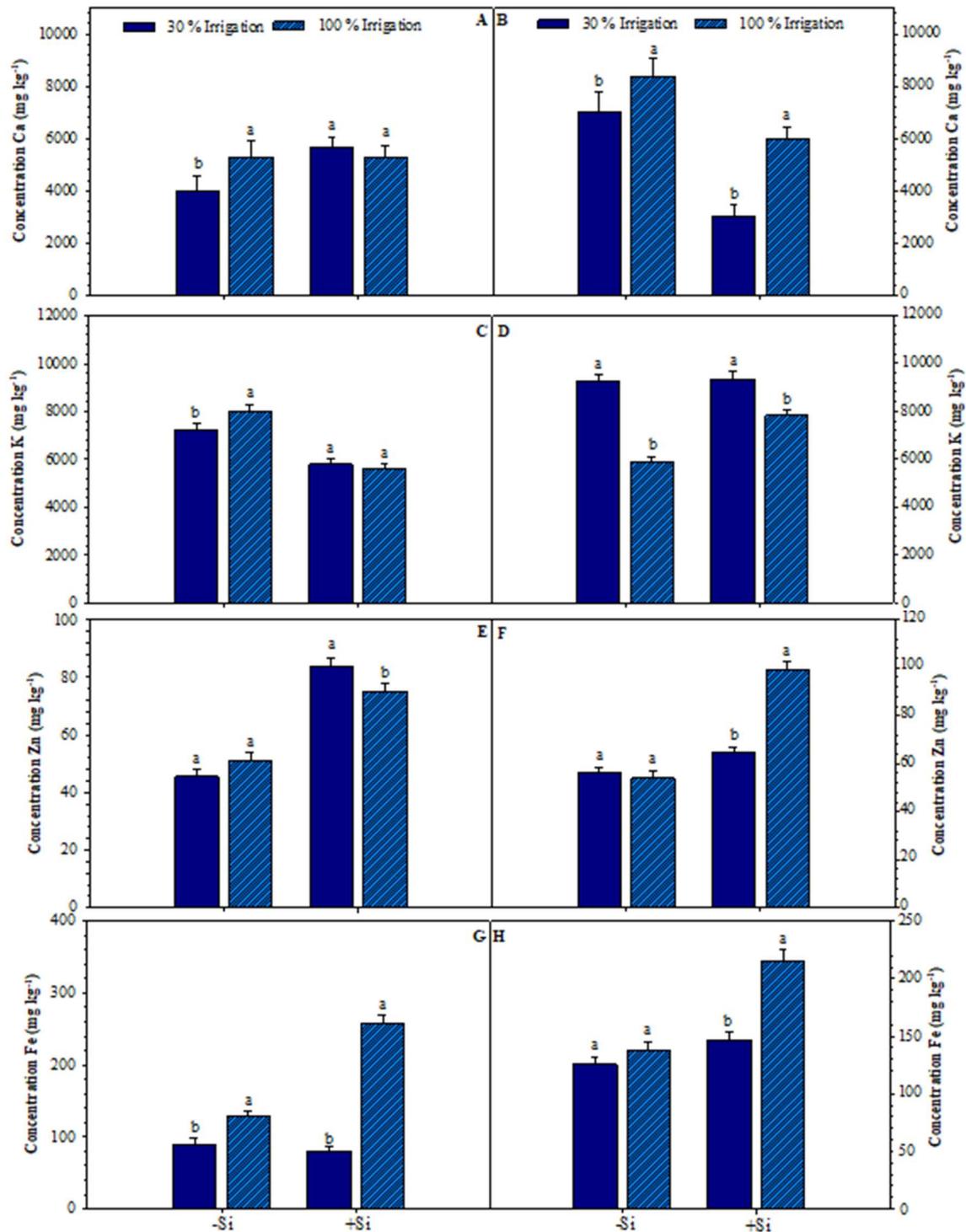

Figure 2. Concentration of putrescine in maize leafs BR-1010 (A) and DKB-390 (B) exposed to -Si and +Si and two irrigation blades (30 and 100 % of water necessity reposition). Means followed by the same letter are not significantly different by the Tukey test at 5% of probability. The bars represent the mean standard error.

Significant differences in nutrient contents were found between cultivars and as a function of irrigation blades, being that different metabolic activities can explain the absorption rate of the cultivars in function of the studied variables. In BR-1010 (sensitive), +Si

increased 50% and 110%, respectively, the contents of Ca and Zn (Figs. 3A and 3E) in drought stress (30% irrigation). Reduction in contents of Ca and increased Zn in the leaves of DKB-390 when +Si was used (Figs 3B and 3F). Si application prevented certain symptoms of Zn and Mn deficiency (necrotic spots), most probably due to its indirect effect by enhancing antioxidant defense capacity in plant tissues (Bityutskii et al., 2014). Uptake and transport of Zn in maize are significantly decreased by the incorporation of Si (Kaya et al., 2009). On the contrary, in rice another study with addition of Si considerably increased root Zn concentrations in both cultivars to different degrees (Song et al., 2011). The increase in Ca uptake observed in BR-1010, at the drought stress (30% irrigation) may be ascribed to a diminution in plasma membrane penetrability and an increase in the movement of plasma membrane H+-ATPase due to the addition of Si (Kaya et al. 2006). Plants with different Si accumulation capacities may respond differentially, if the apoplastic pathway is prevented by Si deposition, the uptake of some elements such as Ca^{2+} might be decreased (Brackhage et al. 2013; Mehrabanjoubani et al. 2015).

On the other hand, K had a different behavior between the two cultivars studied (Figs. 3 C and 3D), being absorbed in greater quantity when +Si and –Si, under conditions of drought stress (30% irrigation) in DKB-390 (tolerant), indicating that the application of Si can affect soil K availability and nutrient content in plants (Chen et al., 2016). There was no significant difference between the levels of K in cultivar BRS-1010 (sensitive) when + Si and -Si.

Fe was absorbed in greater quantity with + Si, mainly in DKB-390 (Fig. 3 H), which could be a result of the increase the apoplastic Fe pool, together with the enhanced expression of genes involved in biosynthesis of Fe-mobilizing compounds in roots. Si can also increase the absorption of Fe as a function of its distribution in the plant and increase Fe transport from root to shoot (Fu et al., 2012, You-Qiang et al., 2012). Plants fertilized with Si display both greater short- and long-term Fe uptake than the plants without Si (Mali and Aery, 2009).

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Figure 3. Concentration of Ca, K, Zn and Fe in maize leafs BR-1010 (A, C, E and G) and DKB-390 (B, D, F and H) exposed to -Si and +Si and two irrigation blades (30 and 100 % of water necessity reposition). Means followed by the same letter are not significantly different by the Tukey test at 5% of probability. The bars represent the mean standard error.

+Si contributes to a 12% increase in yield for BR-1010 (sensitive) and 14% for DKB-390 (tolerant) (Figs. 4A and 4B). The drought stress reduced grain yield, but supplementation with Si favored an increase in corn yield, reducing negative effects. The deleterious effects of drought are minimized by Si nutrition due to several physiological changes, such as the increase in photosynthetic rate (Kurdali et al., 2013), maintenance of photosynthetic mechanisms (Chutipaijit et al., 2012) and higher water retention in plants (Ahmed et al., 2013).
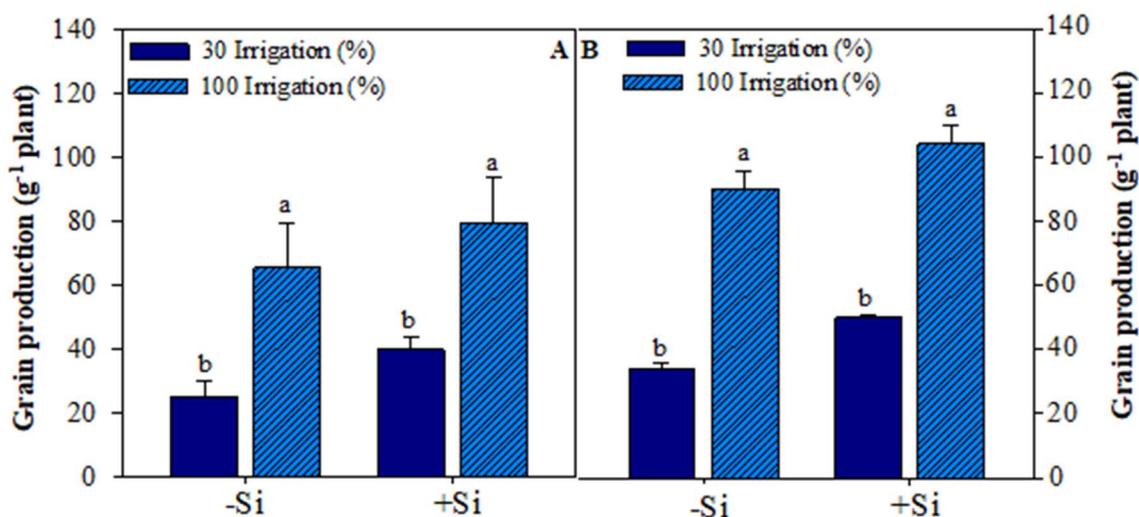

Figure 4. Grain production BR-1010 (A) and DKB-390 (B) in maize exposed to -Si and +Si and two irrigation depths (30 and 100 % of water necessity reposition). Means followed by the same letter are not significantly different by the Tukey test at 5% of probability. The bars represent the mean standard error.

It was concluded that supplementation with Si contributes to a 12% increase in yield for BR-1010 (drought stress sensitive) and 14% for DKB-390 (drought stress tolerant). Si increased the net photosynthetic rate, transpiration rate, stomatal conductance in DKB 390. The content of putrescine increased in plants submitted to drought stress. The leaf contents of Ca, K, Zn and Fe varied according to the cultivars and water blade studied.

Material and Methods

Study site and plant material

The experiment was conducted during 2018 under greenhouse conditions. Two contrasting maize cultivars were used, distinct in terms of drought tolerance, more specifically DKB-390 (tolerant) and BRS-1010 (sensitive). When compared with BRS-1010 (sensitive), the DKB-390 (tolerant) has an increase in exoderm thickening, a greater number of metaxylem elements, a smaller diameter of the vessel elements and in leave, a greater number of stomata occurs and as well as a smaller distance between the vascular bundles. The seeds were obtained from EMBRAPA Maize and Sorghum, Brazil.

Chemical and physical soil analysis

The soil was classified as Oxisol (Embrapa, 2013) and samples were collected at a blade of 0-20 cm. The samples were placed to dry, crushed through a 5-mm sieve and mixed to describe the chemical and physical compositions. After application of limestone and calcium silicate, the soil remained under incubation for 45 days. Fertilization was performed for macro- and micronutrients, following the recommendation of Marques et al. (2014), adapted for experiments conducted in pots for maize crops.

Experimental Design

Two experiments were conducted, the first using BR-1010 (sensitive to drought stress) and the second using DKB-390 (tolerant to drought stress), planted in 19 dm^{-3} pots with one plant in each pot. The experiments were organized in a completely randomized design, combinations of two irrigation blades (30 % and 100 % of necessary water replacement) and two silicon conditions per pots: control (-Si), and 27g Si (+Si) using calcium silicate (10.5 % Si, 25,0 % Ca) in four replicates.

Equipment and irrigation management

Parameters of the soil water retention curve used in the irrigation blade quantification and irrigation management (Fig. 5) were obtained based on the model proposed by Genuchten (1980). The moisture value in field capacity was 0.3458 m^3 for voltage -30 kPa. Irrigation management was carried out based on the water retention curve in the soil and in Watermark readings (Soil Moisture Meter) installed at a blade of 0.15 m. Irrigation was performed whenever soil water stress reached -30 kPa in each treatment, as recommended by Guerra (1994). Readings were taken daily at 5 p.m. In addition, devices were installed to quantify the matrix potential at the greatest tensions, 30 and 100 % of the ideal blade. Irrigation was based on the water retention curve linked to soil and tensiometer measurements, installed at a blade of 0.15 m. Irrigation was implemented when water tension in soil reached -30 kPa and at irrigation blade (30 and 100 % of necessary rate for water recovery in the soil). All measurements were carried out daily, at 5 p.m., and soil

moisture meters (Watermark, 200SS-5) were installed to quantify the matrix potential only at two higher tensions (30 and 100% of the ideal soil blade).
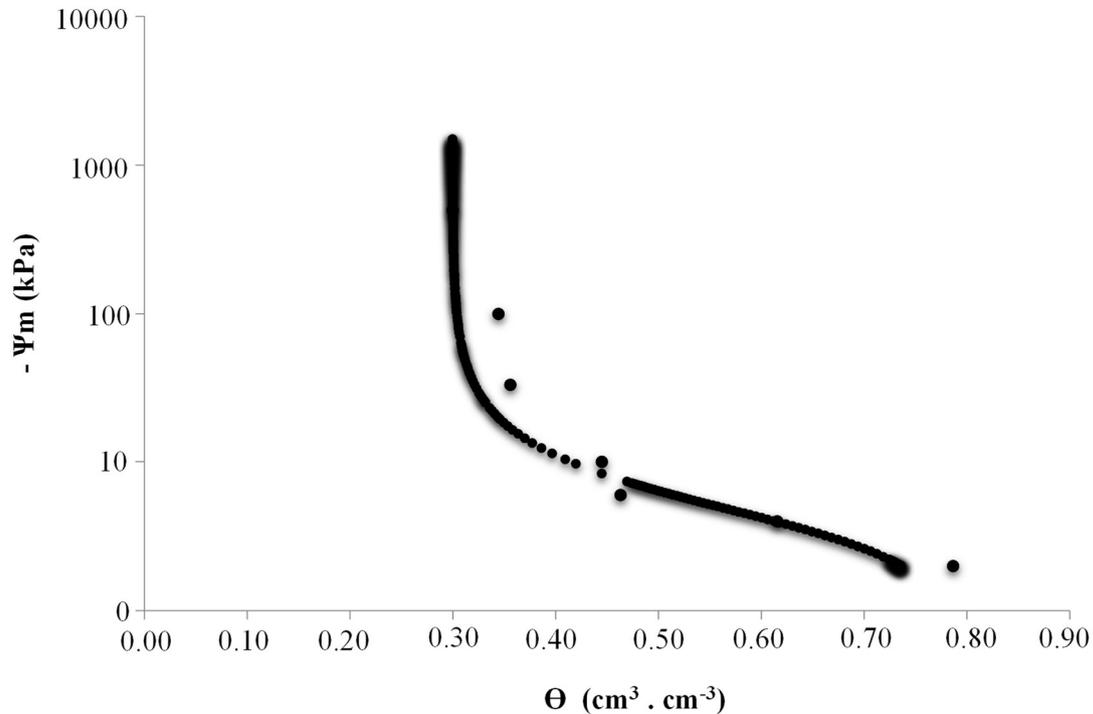

Figure 5. Water retention characteristic curve of the Oxisol used in the research

Neutron activation analysis, standardized k_0 method

The elemental concentration determinations of Ca, K, Zn and Fe in plant leaves tissues were carried out by neutron activation analysis, k_0-method (Menezes et al., 2014) at the Nuclear Technology Development Centre, located in Belo Horizonte, MG. Irradiations were carried out in the TRIGA MARK I IPR-R1 nuclear research reactor. Other essential elements were not quantified since they did not have suitable nuclear characteristics to be analyzed by this technique.

Physiological aspects

Transpiration rate, stomatal conductance and net photosynthetic rate was measured by Infrared Gas Analyzer (IRGA, model LI-6400) in the adaxial surface of fully expanded leaves. Photosynthetic water use efficiency was estimated according to Fischer and Maurer (1978). Gas exchange was evaluated between 9 a.m. and 12 o'clock in all plants, and irradiance was kept at 1000 μmol m^{-2} s^{-1} during the measurements.

Determination of putrescine.

The Put was determined according to Gloria et al. (2005). The extraction was done from samples (1 g) with 7 mL of 50 g/L trichloroacetic acid (TCA). After agitation for 10 min in a vortex mixer, the slurry was centrifuged at $10000g$ at 4 °C, and the supernatant was collected. The solid residue was extracted twice with volumes of 7 and 6 mL of TCA. Supernatants were combined and filtered through a 0.45 im pore size filter. The PUT was separated by ion-pair reverse phase HPLC and quantified by fluorescence after postcolumn derivatization with o-phthalaldehyde.

Liquid chromatography was performed with an LC-10AD system connected to a RF-551 spectrofluorometric detector at 340 and 445 nm of excitation and emission, respectively, and to a CBM-10AD controller (Shimadzu, Kyoto, Japan). A reversed-phase μBondapak C18 column, 300 x 3.9 mm i.d., 10 μm, was used with a μBondapak C18 Guard-pak insert (Waters, Milford, MA). The mobile phases were (A) a solution of 0.2 M sodium acetate and 10 mM 1-octanesulfonic acid sodium salt adjusted to pH 4.9 with acetic acid and (B) acetonitrile. The flow rate was set at 0.8 mL/min and the gradient was as follows: 13 min at 11% B, 19 min at 30%, 24 min at 11%, and 45 min at 11%. The postcolumn derivatization reagent was delivered at 0.4 mL/min. It consisted of 1.5 mL of Brij-35, 1.5 mL of mercaptoethanol, and 0.2 g of o-phthalaldehyde dissolved in a 500 mL solution of 25 g of boric acid and 22 g of KOH (pH adjusted to 10.5 with 30 g/L KOH). The column and postcolumn reaction apparatuses were kept at 23 ±1 °C.

The identification of the putrescine was performed by comparison of to those of standard solution. Quantification was accomplished by direct interpolation in the standard curves ($R2 \geq 0.9926$). The determination limits for putrescine was 0.02 mg/100 gm.

Agronomic measurements

At the end of the study grain maize yield in each treatment was measured at harvest in g plant^{-1}.

Statistical analysis

Data were subjected to variance analysis (ANOVA) and when significant differences occurred; Tukey test at 5% level of error probability ($p \leq 0.05$) was applied. All statistical procedures were carried out with the SISVAR® software (Ferreira, 2014).

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