

**SÃO PAULO STATE UNIVERSITY – UNESP
JABOTICABAL CAMPUS**

**SILICON ON C:N:P STOEQUIOMETRY AND NUTRITIONAL
EFFICIENCY OF SUGARCANE GROWN UNDER WATER
DEFICIT IN THREE TROPICAL SOILS**

Milton Garcia Costa
Agronomist engineer

2023

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Student: Milton Garcia Costa

Supervisor: Dr. Renato de Mello Prado

Co-supervisor: Dr. Luiz Fabiano Palaretti

Co-supervisor: Dr. Jonas Pereira de Souza Júnior

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EXPECTED IMPACT ON SOCIETY

It is expected that the findings achieved can contribute to the development of new practices for the use of silicon in sugarcane production, aiming to improve productivity and crop quality. The use of Si allows for a new path of research, enabling increased water use efficiency in sugarcane production systems.

IMPACTO ESPERADO NA SOCIEDADE

As descobertas desses estudos podem ser usadas para desenvolver práticas de manejo mais eficazes para a produção de cana-de-açúcar, com o objetivo de melhorar a produtividade e a qualidade do cultivo. O uso do Si permite abrir um novo caminho de pesquisa, permitindo aumentar a eficiência de uso de água nos sistemas de produção de cana-de-açúcar.

CERTIFICADO DE APROVAÇÃO

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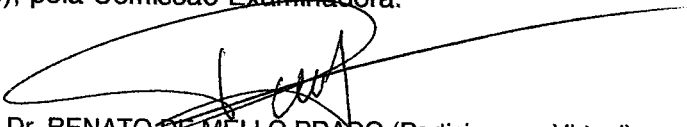
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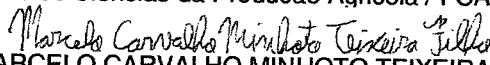
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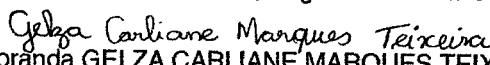
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Prof. Dr. RENATO DE MELLO PRADO (Participação Virtual)
Departamento de Ciências da Produção Agrícola / FCAV UNESP Jaboticabal



Prof. Dr. MARCELO CARVALHO MINHOTO TEIXEIRA FILHO (Participação Virtual)
Departamento de Fitossanidade, Engenharia Rural e Solos / FEIS UNESP Ilha Solteira -



Pós-doutoranda GELZA CARLIANE MARQUES TEIXEIRA (Participação Virtual)
Departamento de Ciências da Produção Agrícola / FCAV UNESP Jaboticabal

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AUTHOR'S BIOGRAPHY

MILTON GARCIA COSTA, was born in the city of Belém, state of Pará, Brazil, on October 2, 1997. Son of Lilian Garcia de Leão and Melque Dias Costa. He achieved the title of Technician in Forests (2016) by the Juscelino Kubitschek de Oliveira State School of Agroindustrial High School of the Network of Technological Schools of the State of Pará (EETEPa). During technical education, he participated as an internship at the Botany Department of the Brazilian Agricultural Research Corporation (Embrapa) – Eastern Amazon Unit, contributing to the computerization of the João Murça Pires herbarium. He achieved the title of Agronomist engineer (2021) from the Federal Rural University of the Amazon (UFRA), Capitão Poço Campus. During graduation, he was a scientific initiation scholarship by the National Council for Scientific and Technological Development (CNPq) from 2018 to 2020 and by the institutional scientific initiation program from 2020 to 2021, participating in several research projects with fertilization and nutrition of crops grown in the Amazon. In 2019 and 2020, he participated in the Academic Leveling teaching project, as a Mathematics tutor for initial undergraduate classes. Additionally, he was a member of the collegiate of the Agronomy course (2019-2021), a member of the University Council for Teaching, Research and Extension (CONSEPE; 2019-2020) and a member of the Higher University Council (CONSUN; 2019-2020) from UFRA. In August 2021, he started the master's degree in the Postgraduate Program in Agronomy (Soil Science) at the Faculty of Agrarian and Veterinary Sciences (FCAV) of the São Paulo State University (Unesp), developing research with the use of silicon via fertigation in sugarcane plants under water deficit in three tropical soils and the impacts on nutritional efficiency and homeostatic balance of carbon – nitrogen – phosphorus. In the master's degree, he participated in several research projects with the use of silicon as a stress attenuator in cultivated plants (such as sugarcane, corn, beans and cotton). He also participated as a member of judging committee of course conclusion works, co-supervised of scientific initiation and published scientific articles in high impact journals (JCR > 4). He is currently a member of the Study Group on Plant Nutrition at Unesp (Genplant).

“I will pursue everything that God has ever chosen for me
I will persist, and even in the marks of that pain
What's remains, I'll remember
And fulfill the most beautiful dream that God dreamed of.
In my place, waiting for a new one to arrive
I will persist, continue to hope and believe
And even when the vision is blurred and the heart just cries
But in the soul, there is certainty of victory”
(Celina Borges)

I dedicate this to my most beautiful flower, to my inspiration, to my strength, to my advisor, to my friend, who shared every dream and vibrated with every achievement and who taught me to seek the best of myself every day and always persist. My loved grandmother Maria Darti Dias Costa (*in memoriam*).

Dedicate

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SILICON ON C:N:P STOEQUIOMETRY AND NUTRITIONAL EFFICIENCY OF SUGARCANE GROWN UNDER WATER DEFICIT IN THREE TROPICAL SOILS

ABSTRACT

The benefit of silicon (Si) in the lives of the plants is undeniable, mainly the physiological and biochemical benefits, mainly in sugarcane plants in conditions of water deficit. However, little was understood about the impact of this beneficial element on modifying the homeostatic balance of carbon (C) – nitrogen (N) – phosphorus (P) and on the nutritional efficiency of sugarcane plants and whether these changes are enough to alter crop dry mass production under different soil conditions in the tropics. In order to broaden the understanding of the benefit of Si, the present study was carried out, aiming to evaluate the supply of Si, via fertirrigation, is sufficient to modify the homeostatic balance of C:N:P and increase the nutritional efficiency of sugarcane plants under water deficit in three tropical soils. For this, three experiments were carried out with pre-sprouted seedlings of sugarcane in three tropical soils (Dystrophic Red Latosol, Eutrophic Red Latosol and Quartzarenic) under controlled conditions in a greenhouse in two cycles of 150 days (1st cycle and 2nd cycle). Silicon was supplied via fertigation at a concentration of 1.8 mM every two days using the stabilized sodium silicate source with sorbitol. Biological losses caused by water deficit in sugarcane plants are related to the homeostatic imbalance of C:N:P, causing reductions in nutrient use efficiency and directly impacting dry mass biosynthesis. Silicon becomes a viable agronomic alternative in sugarcane crops with water restriction, reducing biological losses due to water deficit, modifying the homeostatic balance of C:N:P, improving the efficiency of use of these nutrients and improving the plant performance. The use of Si in sugarcane cultivation without stress was also efficient in improving plant performance, alternating the homeostatic nutritional balance, increasing the efficiency of use of C, N and P and increasing the production of dry mass of leaves and stems. The responses of sugarcane plants to Si application are limited depending on the type of cultivation soil, altering the intensity of responses to the benefits of the beneficial element. The strategic use of fertigation with Si in a water deficit regime becomes more advantageous in tropical soils with low availability of Si in the soil solution, such as the Quartzarenic Neosol. The perspective of the research is that Si can contribute to the sustainable cultivation of sugarcane in tropical soils in irrigated regions or under a regime of water deficit.

Keywords: *Saccharum officinarum* L., beneficial element, Si fertigation, homeostatic balance of C:N:P, water stress, abiotic stress.

SILÍCIO NA ESTEQUIOMETRIA C:N:P E NA EFICIÊNCIA NUTRICIONAL DA CANA-DE-AÇÚCAR CULTIVADA SOB DÉFICIT HÍDRICO EM TRÊS SOLOS TROPICAIS

RESUMO

O benefício do silício (Si) nas vidas das plantas é incontestável, principalmente os benefícios fisiológicos e bioquímicos, principalmente em plantas de cana-de-açúcar em condições de déficit hídrico. Entretanto, pouco se compreendia do impacto deste elemento benéfico em modificar o equilíbrio homeostático do carbono (C) – nitrogênio (N) – fósforo (P) e na eficiência nutricional das plantas de cana-de-açúcar e se essas alterações são o suficiente para alterar a produção de massa seca da cultura nas diferentes condições de solos nos trópicos. Para ampliar a compreensão do benefício do Si, realizou-se o presente estudo, objetivando-se avaliar o suprimento do Si, via fertirrigação, é suficiente para modificar o equilíbrio homeostático do C:N:P e incrementar a eficiência nutricional de plantas de cana-de-açúcar em déficit hídrico em três solos tropicais. Para isso, realizou-se a instalação de três experimentos com mudas pré-brotadas de cana-de-açúcar em três solos tropicais (Latossolo Vermelho Distrófico, Latossolo Vermelho Eutrófico e Neossolo Quartzarênico) em condições controladas em casa de vegetação em dois ciclos de 150 dias (1º ciclo e 2º ciclo). O silício foi fornecido por via fertirrigação na concentração de 1.8 mM a cada dois dias utilizando a fonte de silicato de sódio estabilizado com sorbitol. As perdas biológicas causadas pelo déficit hídrico nas plantas de cana-de-açúcar estão relacionadas ao desequilíbrio homeostático de C:N:P, causando reduções na eficiência de uso de nutrientes e impactando diretamente na biossíntese de massa seca. O silício torna-se uma alternativa agrônoma viável em cultivos de cana-de-açúcar com restrição hídrica, reduzindo as perdas biológicas por déficit hídrico, modificando o equilíbrio homeostático de C:N:P, melhorando a eficiência de uso desses nutrientes e melhorando o desempenho da planta. A utilização de Si no cultivo de cana-de-açúcar sem estresse também se mostrou eficiente em melhorar o desempenho das plantas, alternando o equilíbrio nutricional homeostático, aumentando a eficiência de uso de C, N e P e aumentando a produção de massa seca de folhas e caules. As respostas das plantas de cana-de-açúcar à aplicação de Si são limitadas dependendo do tipo de solo de cultivo, alterando a intensidade das respostas aos benefícios do elemento benéfico. O uso estratégico da fertirrigação com Si em regime de déficit hídrico torna-se mais vantajoso em solos tropicais com baixa disponibilidade de Si na solução do solo, como o Neossolo Quartzarênico. A perspectiva da pesquisa é que o Si pode contribuir para o cultivo sustentável da cana-de-açúcar em solos tropicais em regiões irrigadas ou sob regime de déficit hídrico.

Palavras-chave: *Saccharum officinarum* L., elemento benéfico, fertirrigação com Si, equilíbrio homeostático de C:N:P, estresse hídrico, estresse abiótico.

CHAPTER 1 - Innovative contribution of Si in the mitigation of abiotic stresses in plants from the modification of C:N:P homeostasis: a review of progress and perspectives¹

ABSTRACT

Different environmental stresses have altered C:N:P stoichiometry, resulting in biochemical and physiological changes in plants and decreasing crop yield. Silicon (Si) is a beneficial element that reduces plant stress, but most studies on this topic focus on physiological damage. Notwithstanding, recent studies indicate that stressed plants use Si strategically to maintain C:N:P homeostasis, reducing biomass loss. This can guarantee the sustainability of agricultural crops worldwide. In this scenario, this review addresses a new view on advances in the understanding of the impacts of environmental stresses on C:N:P homeostatic balance. It also discusses the role of Si in the homeostasis of these nutrients and its consequences in the attenuation of the deleterious biological damage of stress. The findings discussed in this review reinforce another significant benefit of Si in plants that correlates with C:N:P homeostasis, responsible for improving the nutritional efficiency of these vital nutrients, increasing crop yield, and mitigating stress. This review also highlights the need for further research that addresses the underlying mechanisms of Si in C:N:P stoichiometry.

Keywords: nutritional stoichiometry; elemental stoichiometry, beneficial element, environmental stresses, agricultural sustainability.

¹ This chapter corresponds to the article submitted to the journal BMC Plant Biology and is under evaluation for publication.

Contribuição inovadora do Si na mitigação de estresses abióticos em plantas a partir da modificação da homeostase C:N:P: uma revisão dos avanços e perspectivas

RESUMO

Diferentes estresses ambientais têm alterado a estequiometria C:N:P, resultando em alterações bioquímicas e fisiológicas nas plantas e diminuindo a produtividade das culturas. O silício (Si) é um elemento benéfico que reduz o estresse das plantas, mas a maioria dos estudos sobre esse tema foca nos danos fisiológicos. No entanto, estudos recentes indicam que plantas estressadas usam Si estrategicamente para manter a homeostase C:N:P, reduzindo a perda de biomassa. Isso pode garantir a sustentabilidade das culturas agrícolas em todo o mundo. Nesse cenário, esta revisão aborda uma nova visão sobre os avanços na compreensão dos impactos dos estresses ambientais no equilíbrio homeostático C:N:P. Discute também o papel do Si na homeostase desses nutrientes e suas consequências na atenuação dos danos biológicos deletérios do estresse. Reportou-se nesta revisão reforçam outro benefício significativo do Si nas plantas que se correlaciona com a homeostase C:N:P, responsável por melhorar a eficiência nutricional desses nutrientes vitais, aumentar o rendimento das culturas e mitigar o estresse. Esta revisão também destaca a necessidade de mais pesquisas que abordem os mecanismos subjacentes do Si na estequiometria C:N:P.

Palavras-chave: estequiometria nutricional; estequiometria elementar, elemento benéfico, estresses ambientais, sustentabilidade agrícola.

1 Introduction

Climate change has affected crop development and has become more frequent on a global scale, reducing crop yield by 51 to 82%, mainly due to abiotic stresses (Cooke and Leishman 2016a; Raza et al. 2022a). Crop yield decreases from physiological, biochemical, and molecular changes in plants, reflecting changes in water relations, uptake and assimilation of nutrients, loss of membrane integrity, and osmotic dysregulation (Mir et al. 2022). New reports have shown that abiotic stresses also alter the homeostatic balance between carbon (C), nitrogen (N), and phosphorus (P) (Hurtado et al. 2020; Rocha et al. 2022b, a), compromising the optimal ratio required for nutrient balance (Tian et al. 2019). Previous studies evidenced this fact in sugarcane plants cultivated under water stress (Costa et al. 2022; Oliveira Filho et al. 2021a, b; Teixeira et al. 2020, 2022). Thus, it is pertinent to emphasize the importance of C:N:P stoichiometric homeostasis due to its direct relationship with relative plant growth (Peng et al. 2011). Stressful conditions lead to C:N:P stoichiometric imbalance, disturbing plant metabolism. This affects the underlying physiological and genomic mechanisms and the evolutionary processes of plants (Urabe et al. 2010). Changes in C:N:P stoichiometry modify the metabolism of carbon, responsible for providing a structural basis for plants (Martin et al. 2018); nitrogen, a fundamental component for proteins (Yang et al. 2018); and phosphorus, responsible for cellular structures such as DNA and RNA components, in addition to increasing transpiration and C and N assimilation (Sardans et al. 2012).

In this scenario, strategies to mitigate stress damage to the nutritional balance of plants are important, and silicon (Si) stands as an option. Silicon is uptaken as H_4SiO_4 and accumulates in the leaves due to transpiration flow in the form of phytoliths; in this case C may be included (Alexandre et al. 1997). The scientific community has studied the importance of Si in plant biology for decades, showing its beneficial effects on plants (especially under stressful conditions) (Bansal et al. 2022a; Kim et al. 2017; Mir et al. 2022; Pavlovic et al. 2021; Raza et al. 2022a; Shivaraj et al. 2022) and no risk to the environment even at high doses (Etesami and Jeong 2018). However, review studies on Si indicate that this stress attenuating function in plants is due to the effect of Si on the physiological mechanisms of plants

(Bansal et al. 2022a; Mir et al. 2022; Tian et al. 2019) and little has been reported on changes in the elemental stoichiometry of C:N:P.

The strategy to reduce stress effects correlates with C:N:P homeostasis in plants, favoring the adaptive capacity of tolerance (Prado and Silva 2017). The first evidence of the role of silicon in elemental stoichiometry appeared in the 1980s (Raven 1983). The authors of that study discussed energy costs for SiO₂ assimilation in relation to other organic structural compounds. They observed that C incorporation requires 20 times more energy than SiO₂ incorporation for lignin formation, and 10 times more energy than SiO₂ incorporation for polysaccharide formation. However, only after the publication of the study of silica uptake in aquatic and wet macrophytes (Schoelynck et al. 2010), was the interest of Si researchers rekindled to better understand the benefits of Si in C:N:P elemental stoichiometry.

New studies with Si have unveiled the potential of this element to attenuate environmental stresses in agricultural crops, arousing the interest of agronomic use (Hurtado et al. 2020; Lata-Tenesaca et al. 2021; Rocha et al. 2021; Teixeira et al. 2022). The sugarcane crop has been the main object of study regarding the benefit of Si in C:N:P stoichiometric homeostasis (Costa et al. 2022; Frazão et al. 2020; Oliveira Filho et al. 2021a, b; Souza Júnior et al. 2022; Teixeira et al. 2020, 2022). However, researchers have also addressed other agricultural crops such as sorghum, sunflower (Hurtado et al. 2020), quinoa (Lata-Tenesaca et al. 2021) and forage plants (Hao et al. 2020; Rocha et al. 2021, 2022a). Research with Si has advanced a lot in recent years. The Scopus database presents great strides on this front, as searches for the terms “silicon and plants” retrieve about 12,000 papers. Notwithstanding, searches involving “silicon, plant, stoichiometry, and C:N:P” account for about only three dozen studies. Other databases such as the Web of Science also reflect this reality. In this scenario, this review proposes to approach a new view on the impacts of environmental stresses on C:N:P homeostatic balance. Furthermore, it discusses the role of Si in the homeostasis of these nutrients and its consequences in the attenuation of the deleterious biological damage of stress. We consider not only the restricted effect on elemental C:N:P stoichiometric changes, but also its implications on underlying mechanisms and its potential to reduce yield losses in agricultural crops, especially those grown under stress. In addition, new

approaches will be proposed to guide future research to advance the knowledge of this very promising line of research involving Si.

2 Silicon bioavailability in tropical soils and stoichiometric modifications in agroecosystems

2.1 Silicon bioavailability in tropical soils

The biogeochemistry of silicon (Si) in the soil involves the interaction of silicon with the biological, geological, and chemical components of the soil (Carey 2020). Silicon is the second most abundant element in the Earth's crust and is found in many minerals, including quartz and feldspar (Camargo and Keeping 2021). Silicon in soil is found in various forms, including silicate, amorphous silica, and biogenic silica (produced by living organisms) (Puppe et al. 2022).

Silicon is mainly found in soils in the form of silicon dioxide (SiO_2), which is insoluble in water (Tubaña and Heckman 2015). However, plants can absorb Si in the form of silicic acid ($\text{Si}(\text{OH})_4$), which is water-soluble and is formed by the dissolution of silicon dioxide (Schaller et al. 2021).

Silicon in the soil solution is found in the form of silicic acid for plant absorption, with its concentration in tropical soils ranging from 0.1 to 0.6 mM (Zargar et al. 2019). Silicon in soil can be released in a soluble form for plants through processes such as silicate dissolution by water and organic acids released by plant roots (Schaller et al. 2021). Furthermore, some bacteria can solubilize soil Si, making it available for plants (Raturi et al. 2021).

The availability of Si to plants can also be influenced by soil pH (Tubaña and Heckman 2015). In acidic soils, Si can bind to aluminum ions and become unavailable to plants, while in alkaline soils, Si can bind to calcium ions and become more available (Haynes 2014).

Plants can affect the Si dynamics in the soil solution through their root activity (Katz et al. 2021; Walker et al. 2003). Plant roots release organic compounds that can solubilize the Si present in the soil, increasing its concentration in the soil solution, such as organic acids and flavonoids (Gobler et al. 2011; Raturi et al. 2021). Furthermore, plant roots can absorb the silicon present in the soil solution and use it for growth and development.

The Si dynamics in the soil solution can also be influenced by the availability of other nutrients in the soil (Pavlovic et al. 2021; Sangster et al. 2001). For instance, the application of fertilizers containing calcium can increase the complexation of silicon with calcium, reducing its concentration in the soil solution (Zhou et al. 2013).

The availability of Si for plants can also be affected by polymerization, where chemical bonds of monosilicic acid are formed, creating longer chains that are therefore less easily absorbed by plant roots (Camargo and Keeping 2021). There are several factors that can influence the occurrence of polymerization, such as pH, Si concentration, soil type, temperature, humidity, time, and the availability of other elements in the soil (Schaller et al. 2021).

Hydrogen ion potential (pH) influences the Si polymerization in soil solution, since Si is more soluble at low pH (acidic) (Haynes 2019). In soils with lower pH, the Si solubility increases, which means that more Si is available in the soil solution to form polymers (Camargo and Keeping 2021). Furthermore, in low pH, the amount of hydrogen ions (H^+) in the soil solution increases, which can facilitate the formation of Si polymers (Tubaña and Heckman 2015). On the other hand, in soils with a more alkaline pH, the Si solubility is lower, which means that less Si is available in the soil solution to form polymers (Camargo and Keeping 2021). Additionally, at high pH, the amount of hydroxide ions (OH^-) in the soil solution increases, which can hinder the formation of silicon polymers (Haynes 2019).

Silicon concentration in the soil solution is also a crucial factor that influences polymerization. The higher the concentration of silicon in the soil solution, the higher the probability of silicon polymer formation (Tombeur et al. 2021a). This occurs because Si polymerization occurs when silicon molecules in the soil solution react with each other to form polymeric chains (Camargo and Keeping 2021). However, for these reactions to occur, it is necessary to have enough Si molecules in the soil solution.

Soil type can also influence Si polymerization due to its composition (Schaller et al. 2021). Soils rich in clay and organic matter tend to have a greater capacity for Si polymerization (Haynes 2014). Additionally, soils with lower Si concentration in the soil solution may decrease the rate of polymerization.

Temperature is one of the main environmental factors that can influence Si polymerization in soil solution. The Si polymerization is a chemical reaction that involves the formation of bonds between Si molecules, like most chemical reactions, and it increases with temperature (Haynes 2014). When the temperature increases, the kinetic energy of the molecules in the soil solution increases, which can increase the probability of collisions between Si molecules and, therefore, increase the rate of polymerization. In addition, the temperature increases can increase the Si solubility in the soil solution, which can also increase the rate of polymerization.

Soil moisture can also influence the Si polymerization in the soil solution in several ways (Camargo et al. 2021). The Si polymerization involves the formation of bonds between Si molecules, which occur in the presence of water (Camargo and Keeping 2021). Therefore, soil moisture can be an important factor for silicon polymerization. Additionally, reduced soil moisture can lead to an increase in Si concentration in the soil (>2 mmol), initiating the Si polymerization process (Zhu et al. 2019). Excessive moisture can also lead to Si leaching, which can limit the Si availability for polymerization (Bansal et al. 2022b).

Finally, some elements can react with Si during the polymerization process, forming insoluble compounds that hinder the formation of amorphous or crystalline silica, thereby reducing the availability of this beneficial element for plants (Haynes 2014). Understanding the process of Si polymerization in soils is essential for Si management in crop systems, as it reduces the availability of this beneficial element for plants and consequently decreases the efficiency of fertilizing agricultural crops.

2.2 Silicon adsorbed processes in tropical soils

Silicon can also be adsorbed on the surfaces of soil minerals through physical and chemical processes (Tubaña and Heckman 2015). Silicon uptake by soil minerals is important for its bioavailability to plants and its participation in nutrient cycling in agroecosystems (Wu and Ling 2019). Physical processes of Si adsorption by minerals are based on the attraction between Si and soil mineral particles, which is influenced by the surface charge and the charge of Si in solution (Kou L. et al. 2015). Silicon can be adsorbed by minerals with negative charges, such as Fe and Al

oxides. However, the physical adsorption of Si on minerals can be reversible depending on environmental conditions (Malik et al. 2021).

The chemical processes of Si adsorption on minerals occur through the formation of chemical bonds between Si and minerals, with this adsorption process being stronger than physical adsorption and influenced by mineral charges and the chemical properties of Si in solution (Liang et al. 2007). The Si can form chemical bonds with minerals that have positive charges, such as Fe and Al hydroxides, and generally the chemical adsorption process is irreversible.

The processes of Si adsorption occur on the surface of minerals, being directly influenced by the mineral's surface charge, specific surface area, and cation exchange capacity (Tubaña and Heckman 2015). Additionally, mineral characteristics such as mineralogical composition and geological age can also influence Si uptake (Carey 2020).

The hydrogen ion potential (pH) is also a factor capable of altering the rates of Si adsorption by minerals (Linden and Delvaux 2019). Silicon in solution is generally found in the form of silicate ions, which can be affected by soil acidity or alkalinity (Haynes 2019). In acidic soils, silicon can bind to aluminum and iron, while in alkaline soils, silicon can bind to calcium and magnesium (Haynes 2019).

In summary, the Si adsorption by soil minerals occurs through physical and chemical processes that involve the surface of minerals and the Si properties in solution. The adsorption of silicon by soil minerals is important for its availability to plants and its participation in nutrient cycling.

2.3 Silicon and its interaction in soil nutrient availability

The relationship between Si and soil nutrient availability is related to its ability to alter soil chemistry and influence the solubility and availability of nutrients for plants (Pavlovic et al. 2021). Silicon present in the soil can interact with other chemical elements, such as aluminum, iron, and phosphorus, altering their availability for plants (Haynes 2019). For example, Si can bind to aluminum in the soil and form insoluble compounds that reduce the availability of toxic aluminum for plants (Tubaña and Heckman 2015). This is particularly important in acidic soils, where high concentrations of aluminum can make the soil toxic to many plants.

Furthermore, Si can improve the availability of phosphorus in the soil, which is an important nutrient for plant growth (Schaller et al. 2019). Silicon can react with phosphorus in the soil and form water-soluble compounds that can be absorbed by plant roots (Hu et al. 2020a). This is especially important in soils with low availability of phosphorus, which can limit plant growth.

The presence of Si in the soil can also influence the availability of other nutrients, such as calcium, magnesium, and potassium, although the exact mechanisms are not yet fully understood (Araújo et al. 2022; Silva et al. 2021a; Zhou et al. 2013). One of the main ways that silicon increases nutrient availability is through improving soil structure (Tubana et al. 2016). Furthermore, Si can influence the biological activity of the soil, which can also increase the availability of calcium, potassium, and magnesium for plants (Walker et al. 2003).

2.4 The role of silicon in modifying the carbon (C): nitrogen (N): phosphorus (P) stoichiometry in the soil-plant system

Silicon (Si) plays an important role in altering the carbon (C), nitrogen (N), and phosphorus (P) stoichiometry in the soil-plant system (Carvalho et al. 2022; Costa et al. 2023). Stoichiometry refers to the relationship between different chemical elements in an organism or system. The presence of Si in the soil can affect the C:N:P ratio in plants, since Si can affect the availability and uptake of nutrients by soil organisms, including plants (Ågren and Weih 2020). Studies show that the addition of Si to the soil can increase the C:N ratio in plants, while decreasing the C:P ratio (Lata-Tenesaca et al. 2021; Teixeira et al. 2022).

The increase in the C:N ratio in plants can be explained by the fact that silicon can affect microbial activity in the soil, reducing the mineralization of organic nitrogen and, consequently, reducing the availability of nitrogen for plants (Brucker et al. 2020). Additionally, silicon can stimulate the synthesis of lignin compounds in plants, which are rich in carbon, thereby increasing the C:N ratio (Rivai et al. 2022). On the other hand, the decrease in the C:P ratio can be explained by the fact that Si can increase the availability of phosphorus for both plants and microorganisms (Brucker et al. 2020; Costa et al. 2023), once Si can affect the sorption of phosphorus by the soil and reduce the fixation of phosphorus in insoluble forms (Schaller et al. 2019).

Silicon also plays an important role in the biogeochemical cycle of carbon (Xia et al. 2020). The dissolved Si in the soil can react with atmospheric carbon dioxide to form calcium carbonate and silica (Song et al. 2018). This process can remove carbon dioxide from the atmosphere, which can help mitigate climate change.

Silicon can alter the activity of microorganisms involved in the decomposition of crop residues in soil (Marxen et al. 2016). The decomposition of organic matter is an important process that releases nutrients in the soil, making them available for plants. Studies show that the addition of Si can affect the microbial activity in the soil, thereby affecting the decomposition of crop residue (Brucker et al. 2020; Marxen et al. 2016).

Silicon causes changes in microbial activity in several ways, such as stimulating the growth of beneficial microorganisms and inhibiting the activity of pathogenic or low-quality decomposer microorganisms (Islam et al. 2020). Furthermore, Si can affect the synthesis of hydrolytic enzymes involved in the decomposition of the straw, such as cellulases and ligninases, stimulating the degradation of these compounds (Khaleghian et al. 2017).

In summary, Si can affect the C:N:P ratio in plants through its interactions with soil and soil organisms. Understanding these interactions can be important for optimizing fertilizer use and improving crop production in agricultural systems. However, more research is needed to fully understand these interactions and their effects on soil nutrient cycling.

3 Impacts of environmental stresses on carbon (C) : nitrogen (N) : phosphorus (P) homeostatic balance

Adverse conditions directly impact crop sustainability, decreasing yield and generating negative results in food production (Prado and Silva 2017). Changes in C:N:P stoichiometric ratios in plants indicate adverse conditions induced by environmental stresses. In this case, plants need to adjust their nutritional homeostatic balance to ensure their survival. It is thus necessary to advance in the understanding of the impacts of these stoichiometric changes on crop yield.

Stressful conditions induce a plant defense response to the detriment of crop yield (Teixeira et al. 2022), promoting gene transcription, protein modification and turnover, alternative splicing of mRNA precursors, and long-distance protein transport (Xu et al. 2022). Some types of stress can also affect soil nutrient availability, indicating that the incorporation of these elements in plant tissues depends on the soil nutrient ratio (Chen and Chen 2021; Hillebrand et al. 2014). Thus, plant nutrient content reflects C:N:P stoichiometry. Under greater nutrient availability, plants tend to increase investment in C-rich structures, increasing their competitiveness for light. This increases C:N and C:P stoichiometric ratios (Abbas et al. 2013), becoming a strategy for plants in natural conditions to increase their competitiveness. However, under cultivation conditions, this strategy may become uninteresting. This is because the plant increases its energy expenditure to incorporate C into organic compounds (Raven 1983), directing metabolic energy resources for crop production. If the crop is grown under stress, these stoichiometric ratios also change (Huang et al. 2018; Prado and Silva 2017).

Previous research shows that C:P and N:P stoichiometric ratios in plants may indicate photosynthetic C fixation capacity through N and P accumulation (Prado and Silva 2017). The N:P ratio also indicates plant nutrient limitation in different adverse growing conditions (Zhang et al. 2004). The reduction of C:P and N:P stoichiometric ratios in plants under optimal growth conditions indicates that assimilated C is directed to growth and energy supply for primary metabolism to the detriment of defense mechanisms or antistress systems associated with secondary metabolism (Rivas-Ubach et al. 2012). According to some authors, N:P stoichiometric ratios < 14 indicate N limitations while ratios greater than 14 suggest P limitations (Güsewell 2004). In turn, other authors mention optimal N:P ratios in the range of 10 to 20 (Koerselman and Meuleman 1996).

Thus, the level of modification of C, N, and P stoichiometric ratios translates into different responses in plants and depends on the type and level of stress and the species cultivated. Research on this topic is limited to a few stresses, especially the abiotic ones involving water, temperature, and salinity. These will be discussed later.

Water scarcity or excess reduce plant growth, altering the metabolism and harming the photosynthetic apparatus of plants, which respond with metabolic and

gene expression changes (Mostofa et al. 2018; Seleiman et al. 2021). The latter evidence indicates that water deficit also changes C:N:P homeostatic balance (Niu et al. 2019; Teixeira et al. 2020).

A study with “*Stylosanthes capitata* Vogel” under water deficit indicated a reduction in C:N ratio in the leaves and stem, along with an increase in C:P and N:P stoichiometric ratios in the leaves (Viciedo et al. 2021). The study evidenced that low water supply modifies C:N:P homeostatic balance in plants. A study with *Erica multiflora* grown under drought conditions had similar results, evidencing the increase of C:P and N:P stoichiometric ratios. The study showed a negative association between stoichiometric changes and plant growth rate (Rivas-Ubach et al. 2012). The authors associated the increase in stoichiometric ratios with reductions in sugar and amino acid concentrations, in addition to a decrease in metabolic activity.

Other authors observed similar results in sugarcane and first cycle energy cane, verifying that water deficit reduced C:N and C:P stoichiometric ratios and increased the N:P ratio, decreasing nutrient use efficiency (Teixeira et al. 2022). Resprouted sugarcane seedlings also presented a reduction in C:N and C:P stoichiometric ratios, which reduced nutrient use efficiency (Teixeira et al. 2020). A study carried out in different tropical soils showed that the nutritional stoichiometry responses of sugarcane plants can differ from case to case. The authors indicated an increase in the N:P stoichiometric ratio in plant stems in Quatzarenic Neosol and Eutroferric Red Latosol, while plants grown in Dystrophic Red Latosol showed no change in the N:P ratio (Costa et al. 2022). Furthermore, *Panicum maximum* plants grown in Quatzarenic Neosol under water deficit showed a reduction in the C:N stoichiometric ratio; however, the C:P ratio did not change in the first cycle (Rocha et al. 2022a) and in the regrowth (Rocha et al. 2022b). These results show that edaphic attributes can alter the responses of plants under water deficit, modifying the C:N:P homeostatic balance and opening a new path for research.

It is also noteworthy that the alteration of the C:N:P homeostatic balance in plants under water deficit usually decreased C:N and C:P ratios and increased the N:P stoichiometric ratio. Notwithstanding, the deleterious effects of water deficit do not only restrict nutritional stoichiometry (Figure 1), but also reduce C, N, and P use efficiency, thus affecting biomass production (Rocha et al. 2021; Teixeira et al. 2020,

2022). This evidences the deleterious effects of water deficit on C:N:P homeostatic balance. However, studies are restricted to a few species.

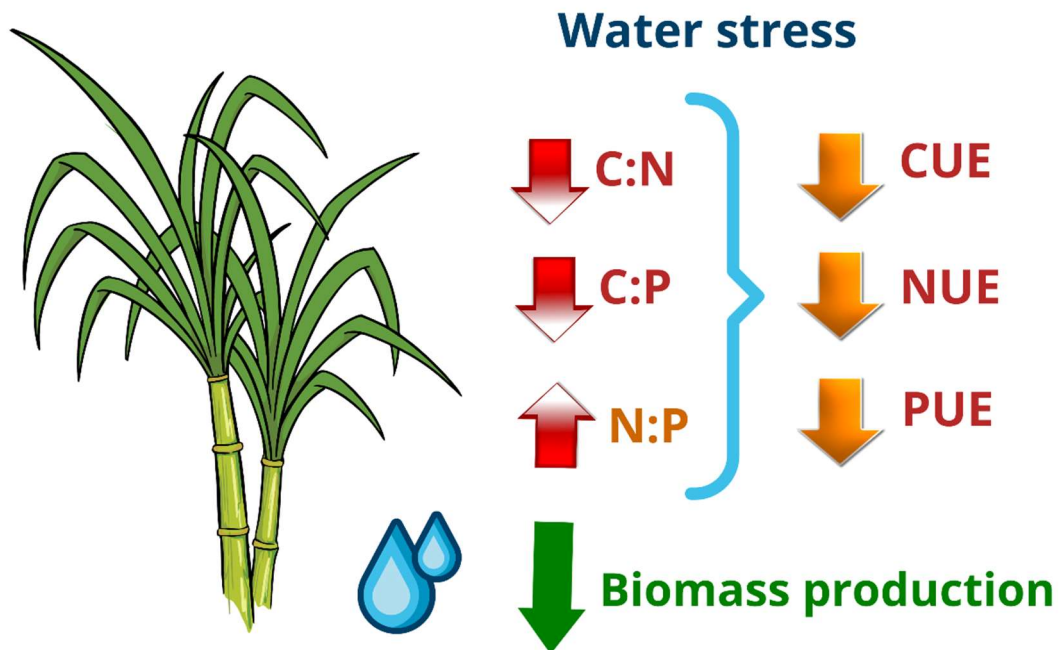


Figure 1. Modification of the C:N:P homeostatic balance in plants under water deficit. CUE: carbon use efficiency; NUE: nitrogen use efficiency; PUE: phosphorus use efficiency.

Stress from excess water decreased N:C and P:C ratios in the leaves, stems, and total biomass of swamp herbaceous plants (Sun et al. 2021). However, the authors of that study reported that the species showed changes of different intensities depending on their strategy of N and P uptake and their ability to store nutrients under stress.

Climate change has also had an impact on rising global temperatures (Jagadish et al. 2021), which can damage nutritional stoichiometry in plants and reduce crop yield. This increase in temperature in different ecosystems is increasing soil organic C mineralization rates and, consequently, atmospheric CO₂ concentration (Ferreira et al. 2010). Changes in atmospheric CO₂ concentrations and increasing temperatures alter the respiratory responses of plants at different intensities depending on the species (Atkin et al. 2005), affecting C:N:P homeostatic balance (Prado and Silva 2017).

Drought can cause a combined effect of increased soil temperature and water deficit, altering soil release and mobility, and consequently modifying plant nutrient

uptake rates (Zhang et al. 2019). These changes in soil nutrient dynamics, combined with changes in plant respiratory responses, alter C:N:P stoichiometric ratios.

The increase in warming and drought conditions and the increase in atmospheric CO₂ concentration have also impacted plant nutrient stoichiometry (Rivas-Ubach et al. 2012). The increase in CO₂ concentration itself can reduce plant transpiration due to increased C uptake, inducing stomatal closure (Pozo et al. 2007; Samarakoon and Gifford 1995).

Thermal stress caused by cold is important in several countries, but its effects on C:N:P elemental stoichiometry are still poorly understood, requiring further research efforts.

Cultivation areas with salinity problems are extensive and have increased worldwide (Ivushkin et al. 2019; Munir et al. 2022). In arid climate regions, halophytic plants tend to reduce C content and increase N content, while P content did not change under these conditions (Wang et al. 2015b). The authors of that study observed that woody and succulent plants tend to have higher C contents and lower N contents when grown in these arid environments, showing that groups of plants change their response mechanisms to adapt to adverse conditions. Pastures under saline stress showed similar results, in which C content decreased; however, C:N:P elemental stoichiometry did not change significantly (Wang et al. 2018).

Salt stress also affects C:N:P homeostatic balance (Hidri et al. 2019; Wang et al. 2015a, 2018) to the point of severely inhibiting plant growth, reducing crop yield (Hussain et al. 2016), as sunflower and sorghum.

A study with sunflower and sorghum indicated that salinization reduces C:N, C:P, and N:P stoichiometric ratios, decreasing biomass production (Hurtado et al. 2020). These alterations occur due to the reduction of C content in plants, as saline stress decreases photosynthetic rates, reducing C incorporation (Rios et al. 2017). However, a study with *Sulla carnosa*, a salinity-tolerant species, indicated that salt stress increased C:N and C:P stoichiometric ratios and reduced N:P ratio (Hidri et al. 2019). These results show that plants respond to salt stress adaptations through different mechanisms, modifying their balance as a function of their tolerance to environmental stresses. Current understanding of stoichiometric nutrient modifications in agricultural crops restricts to sorghum and sunflower crops (Hurtado

et al. 2020). Notwithstanding, this understanding cannot be extrapolated to other crops of great economic interest and, mainly, crops involved in food security.

Research thus evidences that the impacts of stress on stoichiometric changes vary with the species cultivated and with the nature of the stress. However, studies on this topic are few. This is worrisome due to the little attention given to the damage of these stresses to the stoichiometric homeostasis of nutrients vital for optimal plant metabolism and physiological processes. Plants under stress cannot maintain nutritional balance, which can be the primary cause of biological damage. Therefore, strategies that contribute to reversing or attenuating these effects are fundamental for agricultural sustainability. In this sense, one of the strategies without environmental risk that can contribute to stoichiometric homeostasis in plants under stress would be the use of Si. Notwithstanding, it is important to know and discuss the mechanisms involved in this process.

4 Biological role of silicon in carbon (C) : nitrogen (N) : phosphorus (P) homeostasis in stressed plants

Plant roots uptake silicon, which is then transported with the transpiration current and deposited as hydrated amorphous silica ($\text{SiO}_2 \cdot n\text{H}_2\text{O}$) in cell walls, filling cell lumens and intercellular spaces (Prychid et al. 2003). This element deposited in epidermal cell walls forms Si-cuticle double layers and Si-cellulose double layers (Kido et al. 2015). Silicon has a direct role in modifying the composition of plant cell walls, altering the bonds of noncellulosic polymers and lignin (Głazowska et al. 2018). This beneficial element improves structural stability during cell expansion and division. Its concentration in the cell wall is high, being three times higher than in the whole cell (He et al. 2013).

Organic hydroxyl groups can also be cross-linked with monosilicic acid (Williams 2007), ensuring silicon cross-linking in cell walls by the hydroxyl groups of polysaccharides such as lignin and tannin (Sheng and Chen 2020). Additionally, some authors state that monosilicic acid shares similar chemical properties with boron (B), as silicon (Si) belongs to neighboring groups in the periodic table, especially when boric acid is converted to tetrahydroxyborate (Sheng and Chen

2020). These authors suggest that possible patterns of Si binding to the cell wall include the complexation between monosilicic acid and polysaccharide cis-diols or lignin phenols due to the similarity of Si-O-C and borate-diol ester bonds in cell walls.

Other authors proposed that mixed-linkage glucans interact with Si in the cell wall and contribute as a deposition template for the beneficial element (Fry et al. 2008; Kido et al. 2015). In addition, mixed-linkage glucans strengthened the cell wall of rice plants in the presence of Si (Kido et al. 2015).

A study with *Brachypodium distachyon* showed that under greater availability of Si, this beneficial element predominated in the form of phytoliths, with only 9% of the element occurring in the form of amorphous Si and cell wall-bound Si. However, in plants with low Si supply, the amount of phytoliths decreased in all cell components, but polysaccharide-bound Si had priority (Głazowska et al. 2018).

Raven (1983) also pointed out that silicon has a biological role similar to that of lignin in the cell wall. Lignin shares similar characteristics with pyrocatechol, which has the ability to form Si-lignin complexes (Sheng and Chen 2020). The literature points to a great diversity of polysaccharides and phenolic units of lignin capable of interacting and forming Si-sugar and Si-phenol complexes in plant cell walls. Therefore, the plant reduces the metabolic pathway for the synthesis of lignin, which is a compound that requires high energy expenditure for its synthesis (Schoelynck et al. 2010). This mechanism may thus reduce lignin synthesis (Klotzbücher et al. 2018; Schaller et al. 2012a; Suzuki et al. 2012).

Notwithstanding, silicon can activate systems involved in lignin synthesis (Hussain et al. 2021b). Evidence indicates that increased uptake of Si applied in the form of nanosilica increases foliar lignin content in rice plants (Alvarez et al. 2018). The two mechanisms that involve Si and the deposition (or not) of lignin in the cell wall are likely to occur simultaneously in the plant, but the intensity of each one depends on the species and the element content in the culture medium. One can assume that the increase in leaf Si content can decrease lignin synthesis in a given species, but at low concentrations of the element the plant activates the lignin synthesis pathway. Notwithstanding, this hypothesis requires further research.

The importance of Si usually stands out, specifically in cell walls to the detriment of cell membranes and organelles. This benefit of Si in cell walls is vital for

plants, as these structures not only have the biological role of supporting plant growth, but also play the role of a defense barrier against stress (Franck et al. 2018; Hématy et al. 2009; Sheng and Chen 2020).

Silicon supply to plants may attenuate abiotic stresses and mitigate plant damage by improving C, N, and P stoichiometric homeostasis from the increase in the uptake of these nutrients and in C assimilation. This would increase the use efficiency of these nutrients in plant metabolism, improving crop yield. We will discuss these factors based on current knowledge.

4.1 Silicon in improving nitrogen and phosphorus uptake and stoichiometric ratios

The understanding of the beneficial effect of Si on N and P uptake is relatively recent, with reports of an increase in N (Gou et al. 2020; Haddad et al. 2018; Wu et al. 2017) and P (Greger et al. 2018; Mehrabanjoubani et al. 2015) uptake by plants.

Under stress conditions, depending on the species and genotype, plants tend to change their uptake preference for NO_3^- and NH_4^+ , modifying the strategy to ensure their survival in stressful environments (Esteban et al. 2016). Optimal plant growth occurs with 40% of N in the ammoniacal form and the rest in the nitrate form (Silva Júnior et al. 2020), but this varies with genotype. Ammonium can accumulate in flooded soils and/or irrigated areas and can cause damage from ammonia toxicity. According to the literature, Si mitigates ammonia toxicity in plants (Barreto et al. 2016, 2022; Campos et al. 2016, 2020; Ferreira Barreto et al. 2017; Leal et al. 2021; Silva et al. 2020; Silva Júnior et al. 2019; Souza Junior et al. 2021; Viciado et al. 2019a). Furthermore, when studying conditions of low availability of N, several authors reported an increase in the concentrations of this nutrient in the presence of Si. This indicates the synergistic effect of these two elements (Cuong et al. 2017; Deus et al. 2020; Mabagala et al. 2020; Mali and Aery 2008; Pati et al. 2016), pointing to the attenuation of N deficiency in different crops (Araújo et al. 2022; Sales et al. 2021). This effect of Si also reflects crop quality due to the increase in the protein content of forage plants (Buchelt et al. 2021) and in plant vitamin C content (Garcia Neto et al. 2022; Santos et al. 2022). In quinoa, the role of Si in controlling C flux increased N and P concentrations (Lata-Tenesaca et al. 2021).

The synergism between N and Si has to do both with the potential of the beneficial element to modify the transcriptional regulation of genes related to N uptake (Haddad et al. 2018) and with the improvement of transport of this nutrient by plants under stress conditions (Sheng et al. 2018). Studies on *Brassica napus* plants mention the upregulation of genes involved in coding NO_3^- transporters (BnaNTR2.1; BnaNTR1.1), with increased efficiency of NH_4^+ transporters (Sheng et al. 2018). Among the underlying mechanisms of Si in maintaining C:N:P homeostatic balance is the improvement of N status in stressed plants. This improvement increases the uptake of this nutrient and the efficiency of its transport, thus modifying N metabolism in plants. The beneficial effects of Si under nitrogen deficiency in rice plants are due to the stoichiometric shift of C with Si and increased lignin synthesis (Deus et al. 2020).

In fact, several reports indicate the beneficial effect of Si in increasing P content in stressed plants (Costa et al. 2022; Hu et al. 2020a; Pavlovic et al. 2021). Evidence indicates that Si improves P uptake either by increasing the biosynthesis of exudates such as malate and citrate, which compete with P for adsorption sites, or by forming Al and Fe complexes, increasing P availability in the soil solution (Hu et al. 2020a; Kostic et al. 2017). Studies also suggest that silicic acid competes with phosphates for bonds on mineral surfaces, ensuring greater mobility of P in the soil and increasing P availability for plants (Schaller and Puppe 2022). There is a system in the soil that feeds itself, indicating a strong interaction between Si and P. Plants can increase silicon uptake even in soils with low phosphorus availability (Silva Júnior et al. 2019) probably due to the increase in carboxylate release, which induces silicon dissolution from Si-containing minerals (Tian et al. 2021).

The benefits of Si in the dynamics of N and P uptake by plants by altering tissue nutrient contents naturally reflect N:P stoichiometric ratios.

In plants, the N:P ratio indicates P status, in which ratios greater than 20 would be limiting for this nutrient, decreasing plant growth (Yan et al. 2017). Silicon reduced the biological losses of P deficiency in sorghum plants from the increase in P uptake and use efficiency (Silva and Prado 2021). Another study also mentioned the positive effect of Si on the regulation of inorganic phosphorus (Pi) transporters in wheat plants (TaPHT1;1 and TaPHT1;2) (Kostic et al. 2017). Under conditions of

excess P, Si also alters the regulation of transporter genes (OsPHT1;6) in a negative way, reducing P uptake by plants (Hu et al. 2018). Furthermore, Si can improve root growth by increasing the area of uptake of water and nutrients (Schaller and Puppe 2022), mainly low-mobility ions such as P. In this context, Si acts directly on P balance in the metabolism of plants under stress, improving its uptake by plants and reducing the biological damage caused by its lack or excess.

Some authors reported a decrease in C content and in C:Si ratio in plants from an increase in Si (Fernandes et al. 2021; Frazão et al. 2020; Souza Júnior et al. 2022; Teixeira et al. 2020, 2022). This possibly occurred because plants could partially replace carbon compounds with silicon compounds (Schaller et al. 2016), a fact that will be discussed later.

Another study showed the beneficial role of Si in modifying C:N:P stoichiometry in *Holcus lanatus* under N and P nutritional stress. The study evidenced the role of this beneficial element in altering the C:Si ratio by reducing Si content (Minden et al. 2021). Similar results occurred under saline stress conditions (Hurtado et al. 2019), indicating the role of Si in reducing C:N:P homeostatic balance loss under stress conditions. However, motivated by the hypothesis that stressful conditions reduce C in plants, researchers have criticized the role of Si in stoichiometry (Hodson and Guppy 2022). Still, this hypothesis calls for further studies since there is evidence of the same effects occurring in plants in the absence of stress (Alvarez et al. 2018; Frazão et al. 2020; Souza Júnior et al. 2022).

Although most studies focus on stressful conditions, some studies address the absence of stress, indicating that the role of Si in maintaining C:N:P stoichiometry is not restricted to stressful conditions (Frazão et al. 2020; Mantovani et al. 2018; Neu et al. 2017; Schaller et al. 2012b; Souza Júnior et al. 2022). Two studies with sugarcane assessed the role of Si in reducing C content, improving N and P uptake, and changing C:N:P homeostatic balance (Frazão et al. 2020; Souza Júnior et al. 2022). In orchid plants, increasing doses of Si altered C:N:P stoichiometric ratios (Mantovani et al. 2018). The different studies mentioned above took place under optimal conditions, in the absence of stress, indicating that the biological role of replacing C is not restricted to stressful conditions, but a benefit in plants with efficient Si uptake.

The recent results revealed that the role of Si in C:N:P stoichiometry reflects the improvement of vital physiological processes of plants, improving gas exchange and increasing plant defense mechanisms (Carvalho et al. 2022; Frazão et al. 2020; Rocha et al. 2022b, a).

4.2 Silicon in improving carbon assimilation

The improvement of the photosynthetic apparatus of plants under stress conditions has directly impacted gas exchange, reducing damage in C assimilation (Bukhari et al. 2021; Moraes et al. 2020; Santos Sarah et al. 2022).

Silicon has a direct impact on the photosynthetic apparatus of stressed plants, ensuring the integrity of chloroplast thylakoids (Feng et al. 2010; Song et al. 2014). Several studies have shown a decrease in chlorophyll degradation under stress conditions in the presence of Si (Gou et al. 2020; Hussain et al. 2021a; Mustafa et al. 2021). This occurs due to the activation of defense mechanisms that decreases the content of reactive oxygen species (ROS) (Kim et al. 2017; Mostofa et al. 2021) responsible for the oxidation of photosynthetic pigments and other organic compounds such as membranes. Other authors also evidence the role of Si in maintaining redox status and ion homeostasis in plant cells, inducing genes encoding enzymes such as peroxidase (Farouk et al. 2020). Furthermore, Si improves the efficiency of photosystem II, benefiting chlorophyll *a* fluorescence (Bari et al. 2020; Hu et al. 2020b; Hussain et al. 2021a; Khattab et al. 2021).

Silicon has shown its beneficial effect in improving C assimilation by maintaining pigment integrity, consequently improving the photosynthetic efficiency of stressed plants, which implies stoichiometric modifications of C in C:N:P homeostatic balance.

A study evidenced that the role of Si in improving C incorporation in plants is not restricted to stress conditions, it can also occur in plants grown under optimal conditions such as rice plants (Alvarez et al. 2018). In this sense, the authors overturn the theory of Hodson and Guppy (2022), that the beneficial effect of Si on C:N:P stoichiometry would occur due to stress reducing C incorporation. Alvarez et al. (2018) also reported that Si improves C incorporation in plants without stress. Moreover, Frazão et al. (2020) observed the same results in sugarcane plants in the

absence of stress. These studies evidence that Si reduces C content, especially restricted to cell walls, not because of the reduction in C, but probably because of the increase of C use efficiency by the plants.

4.3 Silicon in improving carbon, nitrogen, and phosphorus use efficiency

Some authors reported the role of Si in improving C, N, and P use efficiency (CUE, NUE e PUE) (Costa et al. 2022; Neu et al. 2017; Oliveira Filho et al. 2021a, b; Parecido et al. 2022). Greater efficiency in the use of C, N, and P in plants directly implies the use of nutrients from senescent tissues for the formation of new tissues, increasing biomass production (Prado 2021). Under stress conditions, greater nutrient use efficiency helps to reduce biomass loss, attenuating biological losses in crop yield.

The presence of Si improved N use efficiency in several studies (Buchelt et al. 2020; Hurtado et al. 2019; Mohanty et al. 2020; Parecido et al. 2022), indicating the role of this beneficial element in improving N status in plants. The role of Si in improving N use efficiency may have to do with the increase in amino acid biosynthesis, promoting N remobilization by amino acids from reservoirs of vegetative organs to reproductive organs such as grains, therefore increasing crop yield (Tegeder and Masclaux-Daubresse 2018). In addition, by increasing the activity of enzymes such as nitrate reductase in the N assimilation pathway, Si may favor N metabolism (Silva et al. 2021b). Silicon is likely to have a multiple effect on N metabolism. However, this statement needs further elucidation.

Another study also evidenced the benefit of Si in improving nutrient uptake and use efficiency in sorghum and sunflower plants, improving nutritional efficiency (Hurtado et al. 2019). In wheat plants, silicon improves phosphate nutrition, with a possible allocation of P to reproductive organs to the detriment of vegetative organs, consequently increasing grain production (Neu et al. 2017) and P use efficiency. This is due to Si replacing parts of C compounds (Schaller et al. 2012a), allowing allocation of energy resources.

The presence of Si alters C use efficiency in stressed plants, evidencing the role of this beneficial element in modifying C metabolism in plants (Costa et al. 2022; Frazão et al. 2020; Souza Júnior et al. 2022) while benefiting plant growth. The

benefit of Si stems from the fact that it reduces the demand for C to produce 1 g of dry matter, consequently reducing C content (Costa et al. 2022; Neu et al. 2017; Rocha et al. 2022b; Schaller et al. 2012b; Souza Júnior et al. 2022; Teixeira et al. 2020).

The first author to propose this modification of C allocation patterns by Si was Raven (1983). The author reported that the stoichiometry of Si uptake and incorporation in cell walls requires only one adenosine triphosphate (ATP), making this element more advantageous than lignin and polysaccharides, which require 20 and 10 times more energy, respectively. This author also calculated that each gram of glucose invested in lignin incorporation would be equivalent to incorporating 12.7 g of SiO₂. Added to this is the fact that although Si incorporation is energetically cheaper, metabolically it is less versatile for organic compounds such as lignin (Raven 1983). The author emphasizes that the lower versatility correlates with disadvantages in relation to the biological functions of organic compounds. These include cellular pH regulation, which may impair the regulation of excess H⁺ or OH⁻, leaving the alternative more expensive in terms of energy due to the loss of OH⁻ by cell sheath or other metabolic pathways. Therefore, the process of “trade-offs” of Si and C occurs in small scales, not having this total replacement in cell walls, but enough to generate a beneficial energy balance for the plants (Figure 2). Added to this is the fact that silicon having higher molar mass and density than C would increase plant dry matter and thus crop yield (Raven 1983), especially in Si-accumulating species. Schaller et al. (2012) complement that the increase of Si in grasses decreases cellulose content in stabilization tissues (stem) and increases cellulose content in tissues of lesser importance for stabilization such as leaves. In other words, increases in Si content affect the cellulose/Si ratio in all tissues.

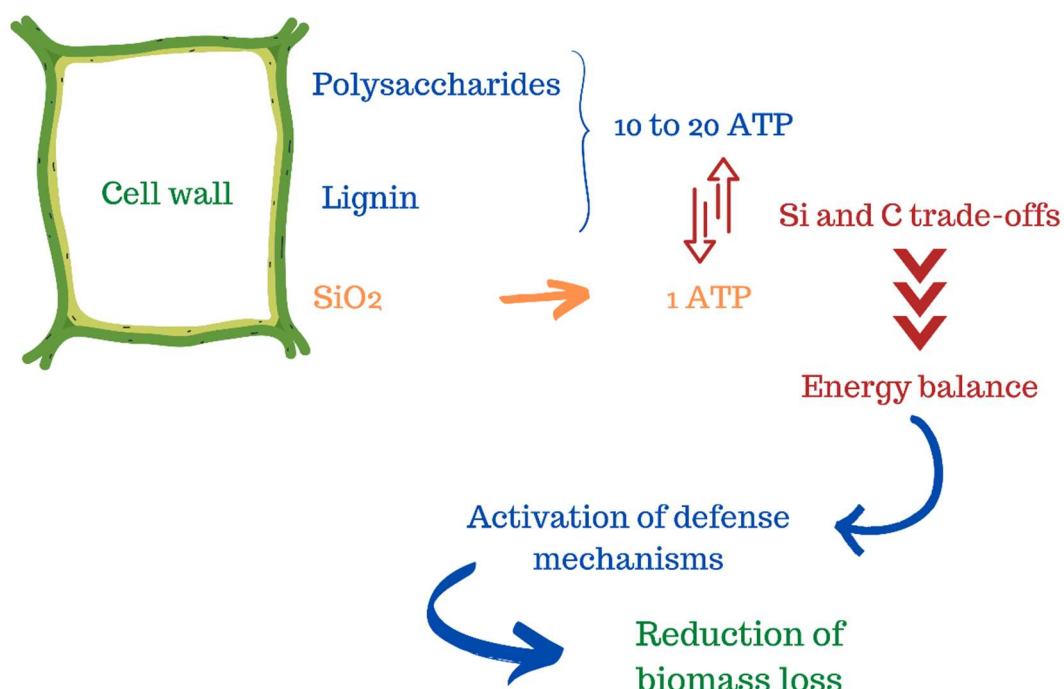


Figure 2. Raven's (1983) principle of Si and C trade-offs in stressed plants.

These benefits of Si in C metabolism are likely to occur in plants with or without stress. However, under stress conditions, the plant needs to activate defense mechanisms to reduce biological damage and ensure its survival in the stressful environment (Khare et al. 2020) so it can benefit more from Si. This makes interesting the trade-offs of Si and C in stressed plants, as these plants tend to reduce metabolic energy in biomass formation, therefore reducing crop yield loss (Figure 3). Evidence also points out that plants in more weathered soils with lower nutrient availability tend to stimulate Si uptake and increase its concentration in plant tissues. This constitutes a strategy to reduce energy costs for certain metabolic pathways, as the plant can use the energy balance for other metabolic processes such as reproduction (Tombeur et al. 2021b). Increased incorporation of C by gas exchange in the presence of Si – discussed earlier – increases C use efficiency. This is because Si preserves the integrity of photosynthetic pigments (Feng et al. 2010; Song et al. 2014) and improves C assimilation rate in plants (Frazão et al. 2020; Teixeira et al. 2020), ensuring greater synthesis of organic compounds and, consequently, of dry matter.

Silicon usually modifies the dynamics of nutrients from the process of uptake and radial transport and by improving nutrient use, decreasing plant biomass loss, and ensuring better plant performance (Figure 3). One can thus infer that the origin of the benefits of Si in plant physiology, much reported in the literature for many species, is due to its effect on the maintenance of C:N:P homeostatic balance. These nutrients have a structural function, participating in hundreds of organic compounds vital for excellent metabolic performance as well as in crop development and productivity, ensuring agricultural sustainability.

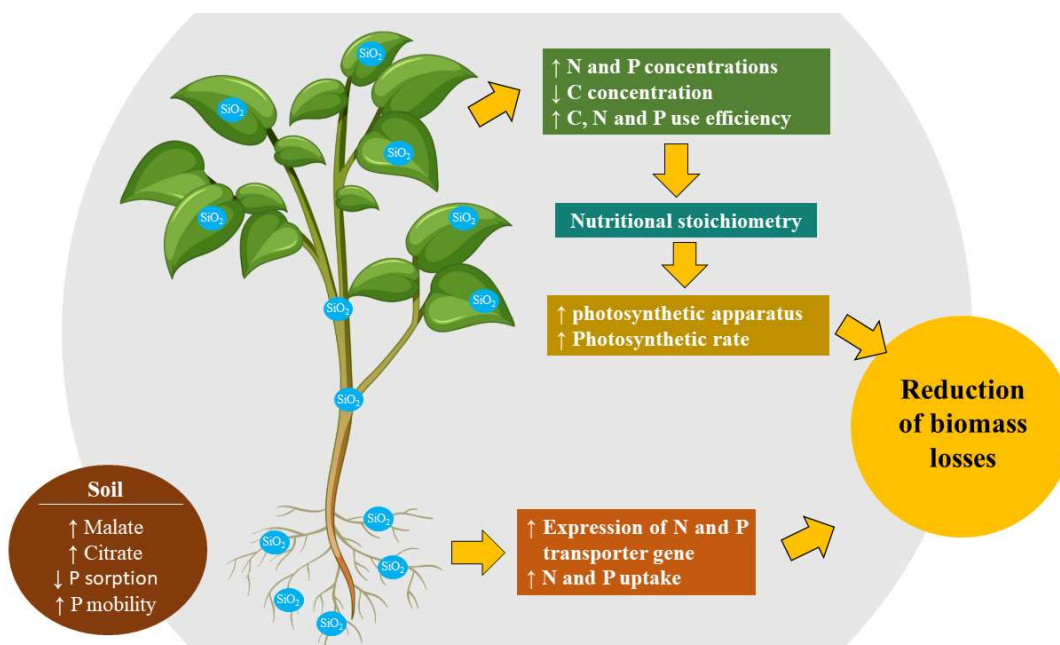


Figure 3. Summary of the main mechanisms of Si attenuation to reduce biomass losses in plants grown under abiotic stress.

5 Conclusions and perspectives

This research evidenced that stressful cultivation conditions naturally impact the nutritional balance of plants, that is, C:N:P stoichiometry. In turn, Si causes the opposite effect, improving nutritional performance and crop production, which can impact food security. The underlying mechanisms of Si in plant mineral nutrition should be considered in most studies that seek to better understand the benefits of this element in plant life, whether cultivated with or without abiotic stress.

Despite the advances in the understanding of Si in C:N:P stoichiometry, limitations still occur. This opens the way for further research, in which new

approaches are important. Firstly, studies involving the beneficial effects of Si on plants at the cellular level are restricted to the cell wall, requiring further research at the subcellular level in cell organelles. Secondly, by increasing nutritional efficiency, silicon is likely to affect genes associated with C, N, and P metabolism; therefore, multidisciplinary studies involving proteomics and plant mineral nutrition are important. Thirdly, research is lacking on the optimal concentration of Si available in the soil and in the leaf, as well as on the best sources and modes of Si application in cultivated plants. This knowledge is even more important for stressed plants, as it can potentiate the benefits of silicon in C:N:P stoichiometry. However, these studies did not establish a critical level of the element in leaves and soil. Fourthly, it is important to evaluate the effects of Si on elemental stoichiometric homeostasis in multistress conditions, since it is common to have more than one stress at the same time during field cultivation. Fifthly, studies are lacking on species with different mechanisms of Si uptake (accumulators and nonaccumulators of Si) and its effects on C:N:P homeostasis and, consequently, on stress mitigation. Sixthly, the increase in N supply intensifies P limitation and while favoring the dissolution of Si from soil phytoliths and its uptake by the plant. This may be a plant strategy to use Si to maintain N:P homeostasis without harming plant growth. However, this hypothesis needs further validation. Seventhly, there is a need to unravel, in agricultural or nonagricultural areas (such as native forests that have greater tolerance to adverse climatic conditions), silicon release from soil phytoliths in relation to biogenic silica, which consists of hydrated silica ($\text{SiO}_2 \cdot n\text{H}_2\text{O}$). Further analysis should compare these sources for silicon uptake by plants and its benefits in elemental stoichiometric homeostasis.

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CHAPTER 2 - Impact of silicon on carbon, nitrogen, and phosphorus stoichiometric homeostasis favors nutrition and stem dry mass accumulation in sugarcane cultivated in tropical soils with different water regimes²

ABSTRACT

Studies with silicon (Si) in sugarcane indicate a greater response in productivity in plants under stress, and the underlying mechanisms of Si in the crop are poorly reported. In this context, the benefits of Si in the crop's stem production are expected to occur at the C:N:P stoichiometry level in plant tissues, benefiting plants with and without stress. However, the extension of this response may vary in different soils. Thus, this research aimed to evaluate if fertigation with Si modifies the C:N:P stoichiometry and if it can increase sugarcane's nutritional efficiency and vegetative and productive parameters. Therefore, three experiments were installed using pre-sprouted seedlings to cultivate sugarcane in tropical soils belonging to the Quartzarenic Neosol, Eutrophic Red Latosol, and Dystrophic Red Latosol classes. The treatments comprised a 2 × 2 factorial scheme in each soil. The first factor was composed without water restriction (water retention = 70%; AWD) and with water restriction (water retention = 35%; PWD). The second factor presented Si (sorbitol-stabilized sodium silicate) concentrations (0 mM and 1.8 mM) arranged in randomized blocks with five replications. Fertigation with Si increases the Si and P concentration, the C and N efficiency, the C:N ratio, and the dry mass production. However, it decreases the C and N concentration and the C:P, C:Si, and N:P ratios in sugarcane leaves and stems regardless of the water regime adopted in the three tropical soils. Cluster and principal components analysis indicated that the intensity of the beneficial effects of Si fertigation on sugarcane plants varies depending on the cultivation soil and water conditions. We found that Si can be used in sugarcane with and without water stress. It changes the C:N:P homeostasis enough to improve the nutritional efficiency of C, P, N, and, consequently, the dry mass accumulation on the stems, with variation in the different cultivated soils.

Keywords: beneficial element, water deficit, abiotic stress, fertigation with silicon (Si), *Saccharum officinarum* L.

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Impacto do silício na homeostase estequiométrica de carbono, nitrogênio e fósforo favorece a nutrição e o acúmulo de massa seca do colmo em cana-de-açúcar cultivada em solos tropicais com diferentes regimes hídricos

RESUMO

Estudos com silício (Si) em cana-de-açúcar indicam uma maior resposta na produtividade em plantas sob estresse, e os mecanismos subjacentes do Si na cultura são pouco relatados. Nesse contexto, espera-se que os benefícios do Si na produção de colmos da cultura ocorram ao nível da estequiometria C:N:P nos tecidos vegetais, beneficiando plantas com e sem estresse. No entanto, a extensão desta resposta pode variar em diferentes solos. Assim, esta pesquisa teve como objetivo avaliar se a fertirrigação com Si modifica a estequiometria C:N:P e se pode aumentar a eficiência nutricional e os parâmetros vegetativos e produtivos da cana-de-açúcar. Para tanto, foram instalados três experimentos utilizando mudas pré-brotadas para o cultivo de cana-de-açúcar em solos tropicais pertencentes às classes Neossolo Quartzarênico, Latossolo Vermelho Eutrófico e Latossolo Vermelho Distrófico. Os tratamentos foram em esquema fatorial 2×2 em cada solo. O primeiro fator foi composto sem restrição hídrica (retenção hídrica = 70%; AWD) e com restrição hídrica (retenção hídrica = 35%; PWD). O segundo fator apresentou concentrações de Si (0 mM e 1,8 mM) arranjadas em blocos casualizados com cinco repetições. A fertirrigação com Si aumenta a concentração de Si e P, a eficiência de C e N, a relação C:N e a produção de massa seca. No entanto, diminui a concentração de C e N e as relações C:P, C:Si e N:P nas folhas e caules da cana-de-açúcar independentemente do regime hídrico adotado nos três solos tropicais. A análise de agrupamento e componentes principais indicou que a intensidade dos efeitos benéficos da fertirrigação com Si nas plantas de cana-de-açúcar varia dependendo das condições do solo e da água de cultivo. Constatamos que o Si pode ser utilizado na cana-de-açúcar com e sem estresse hídrico. Altera a homeostase C:N:P o suficiente para melhorar a eficiência nutricional de C, P, N e, consequentemente, o acúmulo de massa seca nas hastes, com variação nos diferentes solos cultivados.

Palavras-chave: elemento benéfico, déficit hídrico, estresse abiótico, fertirrigação com silício (Si), *Saccharum officinarum* L.

1 Introduction

In tropical soils, the available silicon (Si) concentration in the soil solution is limited mainly by the high degree of weathering, low pH, and high desilication rate resulting from intense leaching (Keeping, 2017), even in high Si concentration on the ground. Tropical soils are predominantly Oxisols, Ultisols, and Entisols, with a predominance of kaolinite in the mineralogical composition (Poppiel et al., 2018) and consequently low available Si content ($\leq 20 \text{ mg kg}^{-1}$ of Si) (0.01 M CaCl_2 extractor) (Haynes, 2014). On the other hand, the levels of available Si can decrease until the polymerization process, forming dimers and short linear oligomers (polysilicic acid) and evolving to the formation of a silica gel ($\text{SiO}_2 \cdot n\text{H}_2\text{O}$), which is unavailable for root absorption (Schaller et al., 2021). Silicon mobility is aggravated in sandy textured soils, such as Quartzarenic Neosol, so the chemical and physical attributes influence the Si dynamics in the soil and its availability to plants.

Evidence indicates greater Si use from the soil solution by Si-accumulating plants, such as sugarcane (*Saccharum officinarum* L.) (Teixeira et al., 2021, 2022), as they have efficient carriers for Si absorption (LSi1, LSi2, and LS6) (Yamaji and Jian Feng, 2009). However, studies on this species and most crops focus on plants grown under abiotic (Verma et al., 2020b; Sousa Junior et al., 2021; Teixeira et al., 2021) and biotic stress conditions (Tomaz et al., 2021). There are indications that the beneficial element modifies the C:N:P stoichiometry, guaranteeing productivity gains, which was observed in forage plants cultivated in Quartzarenic Neosol (Rocha et al., 2021, 2022) and young sugarcane plants cultivated for only 30 days (Teixeira et al., 2020) and 80 days (Oliveira Filho et al., 2021). However, it is unknown whether these effects could reflect in a later growth stage of the crop's stems. Although this line of investigation is starting in sugarcane, it can be very promising since there may be potential for Si to promote changes in the elemental stoichiometry of C, N, and P, improving the plant's nutritional processes. It is possible to consider that the Si in plant tissues predominates in the cell wall and has a lower assimilation cost than C (Schaller et al., 2012), which could impact the homeostasis of plant structural elements and consequently the nutritional efficiency of the plant and the production of stems. However, it may also depend on the soil's Si balance, which needs to be better understood before being proven.

In sugarcane, water deficit is a limiting factor for growth and development. It leads to a productivity drop, which has become more recurrent in recent years (Teixeira et al., 2021; Verma et al., 2021). However, Si use can mitigate the deleterious effects of this water deficit by acting on biochemical and physiological processes already elucidated in the literature (Marchiori et al., 2017; Yan et al., 2018; Jain et al., 2019). On the other hand, most research results were obtained using Si in the form of calcium silicate, which is characteristically insoluble in water (0.01% at 20 °C) (Camargo and Keeping, 2021). Therefore, it implies high doses in Entisol and Spodosol soils from the United States (McCray and Ji, 2018), Rhodic Hapludox and Quartzarenic Neosol soils from Brazil (Camargo et al., 2019, 2021a, 2021b), and clayey-sandy soils without a defined class from China (Verma et al., 2020a, b).

Currently, researchers aim to reduce the amount of Si in crops using soluble sources via fertigation, favoring ion-root contact, increasing the plant's Si absorption efficiency (Shukla et al., 2018), and providing greater sugarcane productivity (Dingre and Gorantiwar, 2021; Singh et al., 2021). This trend is based on the greater solubility of the source used, which reduces the risk of Si polymerization in the soil since the element concentrations in the solution applied to the soil are lower than the limit (3 mM of Si) in which it starts the polymerization process (Schaller et al., 2012).

In this context, using soluble sources of Si applied via irrigation systems is a promising technique, and fertigation can improve the decrease in the polymerization rate and crop yield under water deficit conditions. According to Frazão et al. (2020), it can even improve sugarcane growth without stress in soilless cultivation using Si solution. However, there is a lack of research on these sources. In addition, it is essential to better understand Si effects in alleviating water stress, knowing the underlying mechanisms involved, since most studies restrict gas exchange assessments (Bezerra et al., 2019; Teixeira et al., 2021), and very few studies delve deeper into the nutritional study.

In this scenario, it is pertinent to evaluate two hypotheses: first, that Si applied via fertigation is efficient and, after absorbed, is sufficient to modify the stoichiometric homeostasis of C, N, and P; and whether it is sufficient to increase nutritional efficiency and, consequently, if it would alleviate the losses in the dry mass production of leaves and stems of sugarcane cultivated under water deficit, or

enhance the dry mass production of leaves and stems in the irrigated crop without water deficit, in different types of soil.

If these hypotheses are accepted, it will be proven for the first time that the Si effect via fertigation on the C:N:P elemental stoichiometry is relevant. It favors not only the initial growth but also a more advanced stage in sugarcane. In other words, until stem production achieving agronomic importance. This finding should strengthen the Si agricultural use for the sustainable cultivation of sugarcane in tropical soils, in marginal regions with water restriction, and improve production in irrigated areas (without water restriction), where the cultivation of both sugarcane producing regions is growing in the world. Therefore, this research was carried out to evaluate whether Si fertigation can modify the C:N:P stoichiometry and whether this can increase nutritional efficiency and, consequently, the biomass production of leaves and especially stems of sugarcane cultivated with and without water deficit, depending on the soil.

2 Material and methods

2.1 Experimental areas

The study comprised three experiments with the sugarcane variety RB 962860 in a greenhouse at the Universidade Estadual Paulista “Júlio Mesquita Filho” (UNESP), Jaboticabal Campus, Brazil. The three experiments were independent and included three soil types: Quartzarenic Neosol (NQ); Eutrophic Red Latosol (Oxisol) (LVe); and Dystrophic Red Latosol (Oxisol) (LVd). The temperature and relative humidity inside the greenhouse were recorded using a thermo-hygrometer, showing a maximum average temperature of $45.6 \pm 1.3^{\circ}\text{C}$, minimum of $26.8 \pm 2.5^{\circ}\text{C}$, and relative humidity of $63.1 \pm 6.3\%$ (Figure 1).

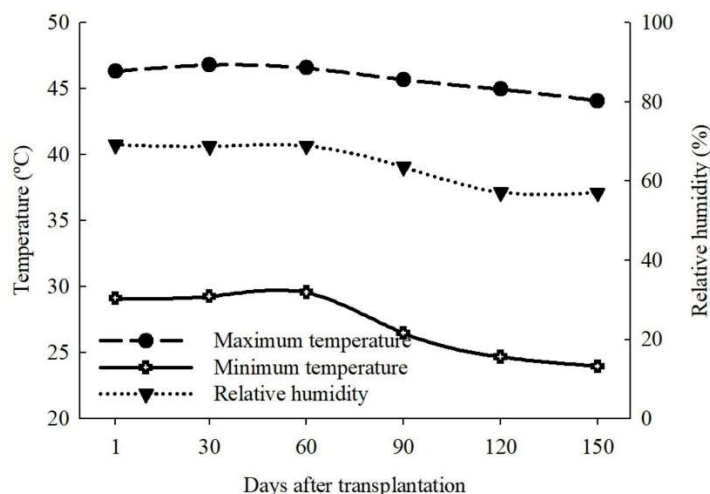


Figure 1. Temperature and relative humidity of the air during the experimental period of cultivation with absence (0.0 mM) and presence of fertigated Si (1.8 mM) and two water conditions (35 and 70%) in three tropical soils (Quartzarenic Neosol; Eutroferric Red Latosol; and Dystrophic Red Latosol).

2.2 Experimental design

The experimental design used in the three experiments was in randomized blocks, in a 2×2 factorial scheme, with two water conditions: without water restriction (water retention = 70%; AWD) and with water restriction (water retention = 35%; PWD); combined with Si absence (0 mM) and presence (1.8 mM), in five repetitions. The experimental plot comprised a pre-sprouted seedling aged 60 days after the bud emergence in a 20 L polypropylene pot containing 18 L of soil sample during a 150-day cycle. After transplanting, the seedlings were pruned at 0.3 ± 0.02 m from the soil surface, to avoid water loss.

2.3. Installations of experimental plots

The three experiments carried out the collection of soils from the surface layer of a native vegetation area. Then, the soil samples were dried in the open air and sieved with sieves (2 mm). Next, chemical analysis was performed for soil fertility using the method described by Raij et al. (2001). After that, an analysis of the Si concentration was conducted following the method described by Korndorfer et al. (2004). Finally, a granulometric analysis was carried out according to the method

indicated by Donagema et al. (2011) (Table 1). The used soils presented sandy, clayey, and sandy loamy textures in Quartzarenic Neosol, Eutrophic Red Latosol, and Dystrophic Red Latosol, respectively.

Table 1. Chemical characteristics of Quartzipsamments (NQ), Eutroferic Red Latosol (LVe), and Dystrophic Red Latosol (LVd)

Soil	pH	MO	P	S	K	Ca	Mg	Al	H+Al	CTC	V	m	Si	Clay	Silt	Sand
	CaCl ₂	g dm ⁻³	mg dm ⁻³			-----	mmol _c dm ⁻³	-----			%		mg kg ⁻¹		g kg ⁻¹	
NQ	4.3	9	2	6	0.3	3	1	0	16	20.0	21	0	1	50	10	940
Lve	6.2	8	8	8	1.0	16	5	0	17	38.6	57	0	5	550	240	210
LVd	5.2	9	20	7	1.2	14	6	0	22	44.2	49	0	3	300	40	660

pH: CaCl₂ by potentiometry; H+Al: SMP buffer by potentiometry; M.O: by spectrophotometry; P: in resin by spectrophotometry; S: by turbidimetry; K, Ca, and Mg: atomic absorption spectrometry; Si: 0.01 mol L⁻¹ calcium chloride.

Soil acidity was corrected 45 days before transplanting, correcting base saturation to 60% (PRNT = 125%; CaO: 48%; MgO: 16%). Nutrient supply was performed via fertigation from phosphate fertilization 30 days after liming, nitrogen, potassium, and nitrogen fertilization of micronutrients in transplanting, and the topdressing at 76 days after transplanting N and K. For phosphate fertilization, a dose of 90, 70, and 50 P₂O₅ mg dm⁻³ was used for Quartzarenic Neosol, Eutrophic Red Latosol, and Dystrophic Red Latosol, respectively. The dose used for nitrogen fertilization was 15 mg N dm⁻³ (Urea) and, for K fertilization, 100 mg K₂O dm⁻³ (potassium chloride). As for the micronutrients, 2 mg B dm⁻³ (Boric acid) and 5 mg Zn dm⁻³ (zinc sulfate) were used.

2.4 Water retention in the soil

The soil water retention capacity was determined for each soil by filling the pots (lysimeters) (20 L) with soil (18 L), with three replications and, later, placing them in a water tank filled with water (2/3 of the height of the pots) for a period of 24 h. Then, the pots were covered with plastic film, drained freely, and their mass was measured at 0, 24, 36, 48, 60, and 72 h after saturation. After draining the excess water, the water replacement capacity was determined through the difference between the wet and dry soil masses. Finally, the treatments' gravimetric and

volumetric moisture, soil density, and gross irrigation depths were calculated (Bernardo et al., 2019).

In each experiment, two lysimeters were installed, one for each level of water retention in the soil (35 and 70%). The daily mass variation of the lysimeters was measured using load cells (model GL 50; Alfa Instruments Electronics S.A.) with a 0.57 mm precision. Data were stored in a data logger (CR10X Campbell Sci., Logan – United States) by connecting a differential channel multiplexer data acquisition system (AM 416 Relay Multiplexer, Campbell Sci., Logan, UT, United States). Data logger data were extracted using the PC200W software interface. Every fifteen days, the measurement of the masses of the lysimeters was performed using a digital scale to adjust possible variations.

The maintenance of soil moisture retention levels lost by evapotranspiration was performed manually every two days for 16–18 h. At 30 days after transplanting, the water retention level in the soil was maintained at 70% in all treatments. Then, two retention levels (35 and 70%) were installed. The installation of the 35% water retention was gradual, first reducing to 50% and, after seven days, to 35% of the soil's water retention capacity.

2.5 Silicon fertigation

Silicon fertigation was performed every two days using a source of sodium-potassium silicate stabilized with sorbitol at a concentration of 1.8 mM ($113.4 \text{ g Si L}^{-1}$, $18.9 \text{ g K}_2\text{O L}^{-1}$, $100 \text{ mL sorbitol L}^{-1}$, and pH 11.8) (Frazão et al., 2020). The pH value of the silicate solution was adjusted to 6.0 ± 0.5 using HCl 1 mM. Finally, potassium balance was performed using KCl fertigation (8.43 mg K L^{-1}) in treatments without Si fertigation.

2.6 Analysis

2.6.1 Biomass partition

At the end of the cultivation cycle, the cut was carried out at 0.1 m from the soil surface of the sugarcane's aerial part. After cutting the plants, the samples were

separated into leaves and stems and washed with deionized water, detergent solution (0.1% v/v), HCl solution (0.3% v/v), and deionized water, respectively. Then, the samples were dried in an oven with forced air circulation ($65 \pm 5^\circ\text{C}$) until reaching constant mass, and, finally, the leaf dry mass (LDM) and stem dry mass (SDM) were determined.

2.6.2 C, N, P, and Si concentrations in leaves and stems

The determinations of C and N concentrations were carried out from the dry combustion ($1,000^\circ\text{C}$) of the LDM and SDM using the elemental analyzer (LECO truspec CHNS), calibrated with the LECO 502-278 standard (C = 45.0%). The P concentration was determined from the nitric-perchloric digestion and the spectrophotometer reading (Carmo et al., 2000). The Si concentration was determined from the alkaline digestion (H_2O_2 and NaOH) and the reading of the colorimetric reaction with ammonium molybdate using the spectrophotometer (Korndorfer et al., 2004).

2.6.3 Stoichiometric ratios and content of C, N, P, and Si

Carbon, Nitrogen, Phosphorus, and Silicon concentrations from leaves and stems were used to establish the C:N, C:P, N:P, and C:Si stoichiometric ratios. The C, N, P, and Si content were estimated for the leaves and stems from the product of the nutrient concentration and the dry mass of the studied organ.

2.6.4 C, N, and P use efficiency

The C, N, and P use efficiencies in leaves and stems were estimated from the quotient of the square of dry matter and nutrient content (g of accumulated nutrient) (Siddiqi and Glass, 2008).

$$C \text{ use efficiency } (g^2 g^{-1}) = \frac{\text{Dry matter}^2}{C \text{ content}} \quad (\text{Eq. 1})$$

$$N \text{ use efficiency } (g^2 g^{-1}) = \frac{\text{Dry matter}^2}{N \text{ content}} \quad (\text{Eq. 2})$$

$$P \text{ use efficiency } (g^2 g^{-1}) = \frac{\text{Dry matter}^2}{P \text{ content}} \text{ (Eq. 3)}$$

2.7 Statistical analysis

Data were submitted to preposition tests (Shapiro–Wilk normality and Levene homogeneity) (Royston, 1995; Gastwirth et al., 2009) and, later, analysis of variance ($p < 0.05$) and, when significant, the comparison test of Tukey mean ($p < 0.05$). In addition, a hierarchical cluster analysis was performed using the Euclidean distance as the similarity coefficient and the single linkage method as the group connection algorithm. Furthermore, principal components analysis (PCA) was performed using the correlation matrix. Finally, statistical analyzes were performed using the Python programming language (version 3.9.7; Python Software Foundation).

3 Results

3.1 Carbon, nitrogen, phosphorus, and silicon concentrations

The water deficit did not change the Si concentration in the leaves in the three tropical soils in the absence of fertigation with Si. However, there was a decrease in the stems of sugarcane plants cultivated in Quartzarenic Neosol and Eutrophic Red Latosol (Table 2). Regarding its absence, Si fertigation was efficient in increasing the Si concentration in leaves and stems of plants in treatments with water deficit (PWD) and without water deficit (AWD) in the three tropical soils (Table 2).

The C concentration in the leaves increased with the water deficit in sugarcane plants without fertigation with Si in Eutrophic Red Latosol. At the same time, there was a decrease in the C concentration in the stems in Dystrophic Red Latosol under PWD with the absence of fertigation with Si (Table 2). Regarding its absence in sugarcane cultivation, Si fertigation decreased the foliar concentration of C in PWD in Quartzarenic Neosol and Dystrophic Red Latosol. While in Eutrophic Red Latosol, there was no difference (Table 2). On the other hand, under AWD conditions, Si fertigation decreased the foliar concentration of C in plants cultivated in the three tropical soils (Table 2). In turn, the C concentration in the stems also

decreased with Si fertigation only in Dystrophic Red Latosol and in both water retention capacities (PWD and AWD) (Table 2).

Table 02. C, N, P, and Si concentrations in the leaves and stems of sugarcane cultivated with absence (0.0 mM) and presence of fertigated Si (1.8 mM) and two water conditions (without – AWD and with water deficit - PWD) in three tropical soils (Quartzarenic Neosol; Eutroferic Red Latosol; and Dystrophic Red Latosol)

Quartzarenic Neosol, Eutrophic Red Latosol, and Dystrophic Red Latosol							
Water condition	Si	Quartzarenic Neosol		Eutrophic Red Latosol		Dystrophic Red Latosol	
		Leaf	Stem	Leaf	Stem	Leaf	Stem
C (g kg ⁻¹)							
PWD	without	444.55 Aa	410.38 Aa	433.78 Aa	408.62 Aa	437.75 Aa	402.38 Ba
	with	421.12 Ab	407.36 Aa	430.08 Aa	402.58 Ba	426.18 Ab	396.84 Ab
AWD	without	442.40 Aa	408.01 Aa	429.58 Ba	411.20 Aa	434.36 Aa	406.04 Aa
	with	418.12 Ab	407.35 Aa	422.00 Bb	410.68 Aa	421.84 Bb	399.20 Ab
MSD (5%)		7.49	5.57	4.12	6.49	3.95	3.01
N (g kg ⁻¹)							
PWD	without	5.62 Aa	3.38 Aa	5.06 Ba	7.03 Aa	4.08 Aa	5.58 Aa
	with	5.18 Ab	2.13 Bb	4.56 Bb	4.75 Ab	3.34 Ab	4.93 Aa
WD	without	5.86 Aa	2.80 Ba	6.12 Aa	3.62 Ba	3.00 Ba	5.38 Aa
	with	5.12 Ab	2.58 Aa	5.34 Ab	2.78 Bb	2.42 Bb	3.92 Bb
MSD (5%)		0.31	0.32	0.37	0.47	0.45	0.66
P (g kg ⁻¹)							
PWD	without	0.42 Bb	0.48 Bb	0.20 Ba	0.14 Aa	0.59 Ba	0.74 Aa
	with	0.51 Ba	0.68 Ba	0.21 Ba	0.16 Aa	0.61 Ba	0.77 Ba
AWD	without	0.65 Aa	0.71Aa	0.33 Aa	0.15 Aa	0.66 Ab	0.64 Bb
	with	0.66 Aa	0.75 Aa	0.34 Aa	0.15 Aa	0.76 Aa	0.93 Aa
MSD (5%)		0.022	0.054	0.024	0.022	0.070	0.058
Si (g kg ⁻¹)							
PWD	without	2.48 Ab	0.44 Bb	1.26 Ab	0.57 Bb	3.29 Ab	0.52 Ab
	with	7.65 Aa	2.32 Ba	6.90 Ba	4.21 Aa	6.79 Ba	1.63 Ba
AWD	without	2.43 Ab	1.42 Ab	3.14 Ab	1.08 Ab	3.16 Ab	0.42 Ab
	with	11.78 Aa	3.26 Aa	12.24 Aa	4.21 Aa	11.22 Aa	2.88 Aa
MSD (5%)		4.68	0.49	2.50	0.50	1.93	0.28

* Different uppercase letters indicate differences in water conditions and different lowercase letters indicate differences in Si fertigation by Tukey test ($p < 0.05$); MSD: Minimum significant difference.

The water deficit decreased the N concentration in the plant's leaves in the absence of fertigation with Si in Eutrophic Red Latosol. While in Dystrophic Red Latosol, there was an increase in this nutrient's concentration (Table 2). Regarding the stems, there was an increase in the N concentration with the absence of fertigation with Si in sugarcane plants cultivated in Quartzarenic Neosol and

Eutrophic Red Latosol (Table 2). However, the N concentration in the leaves decreased with the Si fertigation regarding its absence in the plants cultivated in two water conditions and the three tropical soils (Table 2). In the stem, it was verified that the Si fertigation regarding its absence in PWD caused a decrease in the N concentration in the stems of plants in the cultures carried out in Eutrophic Red Latosol and Dystrophic Red Latosol. However, there were no differences in Quartzarenic Neosol. In addition, plants grown in AWD and fertigated with Si decreased stem N concentration only in Eutrophic Red Latosol (Table 2).

Phosphorus concentration in leaves and stems decreased with the water deficit in sugarcane plants without Si fertigation in Quartzarenic Neosol and Eutrophic Red Latosol. However, there was an increase in the P concentration in Dystrophic Red Latosol (Table 2). The increase in the P concentration in leaves and stems was observed in PWD fertigated with Si regarding its absence in sugarcane cultivation only in Quartzarenic Neosol (Table 2). Meanwhile, there was an increase in the P concentration in the leaves and stems of plants under AWD conditions promoted by the fertigation of Si, regarding its absence, but only in plants cultivated in Dystrophic Red Latosol (Table 2).

3.2 Stoichiometric ratios of C:N, C:P, C:Si, and N:P

The C:N ratio in leaves increased with the water deficit in sugarcane plants without Si fertigation in Eutrophic Red Latosol. However, there was a decrease in this ratio in plants cultivated in Dystrophic Red Latosol (Figure 2A). Additionally, there was a decrease in the C:N ratio in the leaves of plants grown in the absence of fertigation with Si in Quartzarenic Neosol and Eutrophic Red Latosol (Figure 2B). On the other hand, Si fertigation increased the C:N stoichiometric ratio in the plants' leaves in the two water conditions and the three tropical soils, except for the PWD plant grown in Quartzarenic Neosol (Figure 2A). This stoichiometric alteration was also observed in stems, with similar behavior in the plant's leaves, except for PWD in Dystrophic Red Latosol cultivation and AWD in Quartzarenic Neosol cultivation (Figure 2B).

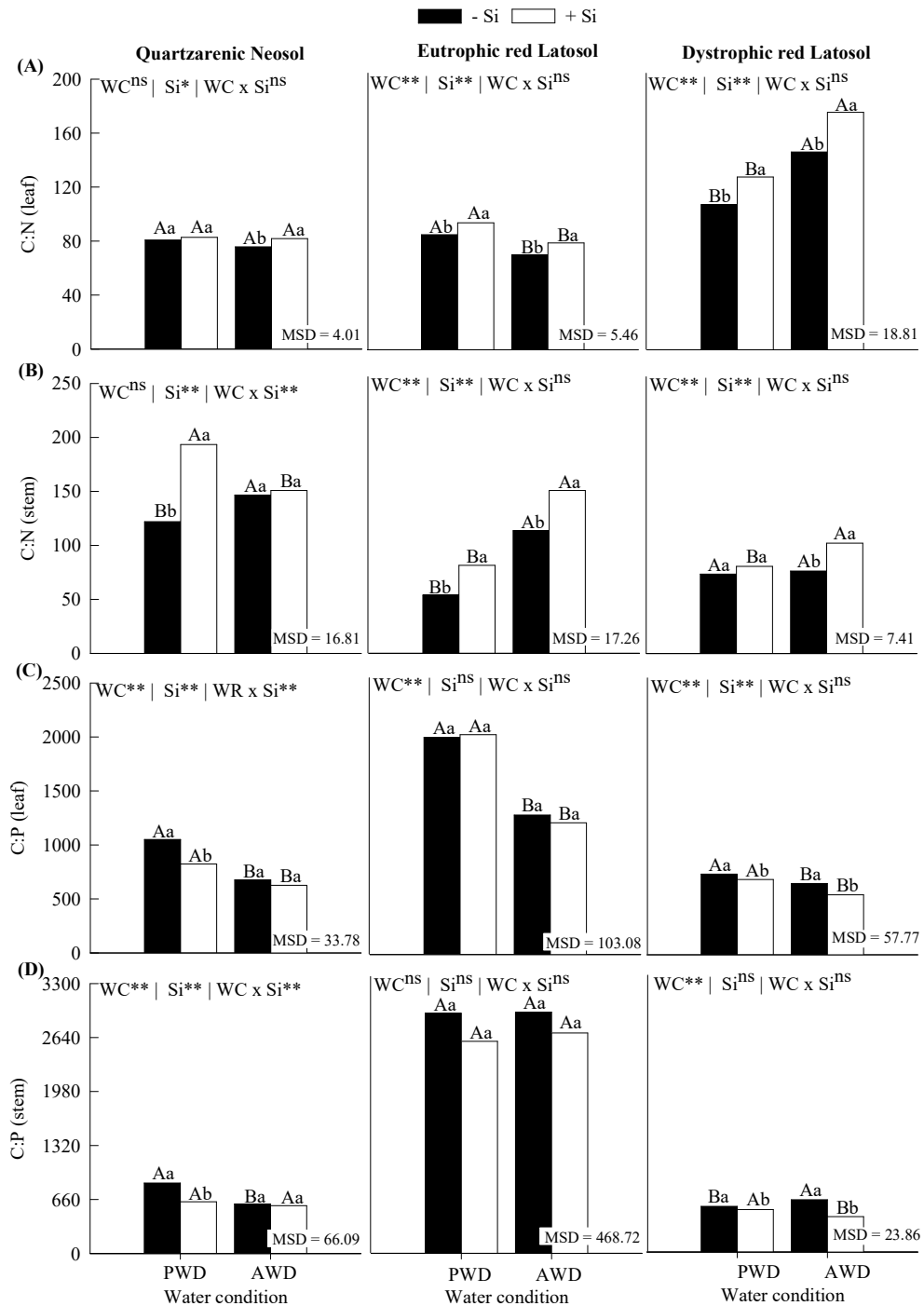


Figure 2. Stoichiometric ratios of C:N (A,B) and C:P (C,D) in leaves and stems of sugarcane cultivated with absence (0.0 mM) and presence of fertigated Si (1.8 mM) and two water conditions (without—AWD and with water deficit—PWD) in three tropical soils (Quartzarenic Neosol; Eutrophic Red Latosol; and Dystrophic Red Latosol). WC, water condition; MSD, minimum significant difference; ** and *: significant at 1 and 5% probability, respectively; NS = not significant at 5% probability. Different uppercase letters indicate differences in water conditions and different lowercase letters indicate differences in Si fertiligation by Tukey's test ($p < 0.05$).

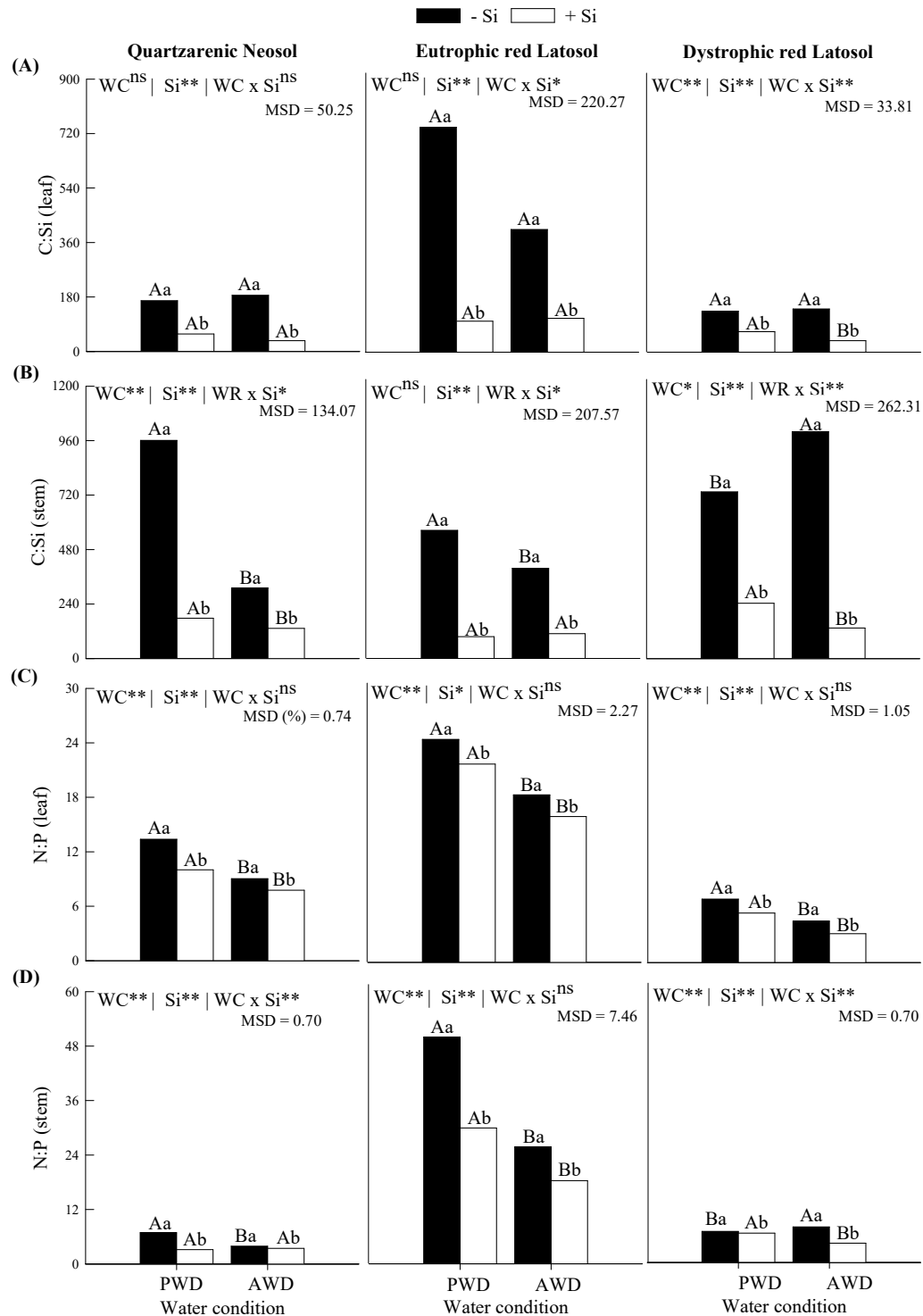


Figure 3. Stoichiometric ratios of C:Si (A,B) and N:P (C,D) in leaves and stems of sugarcane cultivated with absence (0.0 mM) and presence of fertigated Si (1.8 mM) and two water conditions (without—AWD and with water deficit—PWD) in three tropical soils (Quartzarenic Neosol; Eutroferic Red Latosol; and Dystrophic Red Latosol). WC, water condition; MSD, minimum significant difference; ** and *: significant at 1 and 5% probability, respectively; NS, not significant at 5% probability. Different uppercase letters indicate differences in water conditions and different lowercase letters indicate differences in Si fertilization by Tukey's test ($p < 0.05$).

The water deficit increased the C:P ratio in the leaves of plants cultivated in the three tropical soils without Si fertigation (Figure 2C). There was also an increase and decrease in this ratio in this organ on the crops cultivated in Quartzarenic Neosol and Dystrophic Red Latosol, respectively (Figure 2D). Furthermore, Si application decreased the C:P stoichiometric ratio in leaves and stems of sugarcane cultivated under PWD in Quartzarenic Neosol and under PWD and AWD in Dystrophic Red Latosol (Figures 2C, D).

The water deficit did not change the C:Si ratio in the leaves of sugarcane plants without Si fertigation in the three tropical soils (Figure 3A). However, there was an increase in the C:Si ratio in Quartzarenic Neosol and a decrease in this ratio in Eutrophic Red Latosol and Dystrophic Red Latosol (Figure 3B). Silicon use decreased the C:Si stoichiometric ratio in leaves and stems of sugarcane cultivated under PWD and AWD in the three tropical soils (Figures 3A,B).

There was an increase in the N:P ratio in leaves and stems with the water deficit in plants without Si fertigation in the three tropical soils (Figures 3C,D), except for sugarcane stems cultivated in Dystrophic Red Latosol (Figure 3D). Moreover, there was also a decrease in the leaf stoichiometric ratio of N:P in the plant, with the fertigation of Si in the two water conditions and two soils (Quartzarenic Neosol and Dystrophic Red Latosol) (Figure 3C). This ratio's stoichiometric ratio in the stem decreased in PWD in plants grown in Quartzarenic Neosol and Eutrophic Red Latosol. It also decreased in the AWD condition of the culture grown in the two Latosols (Figure 3D).

3.3 Si, C, N, and P contents

Water deficit decreased Si content in leaves and stems in sugarcane plants without Si fertigation in the three tropical soils, except for plants cultivated in Dystrophic Red Latosol (Table 3). Conversely, Si fertigation increased Si content in leaves and stems in the two water conditions studied and the three tropical soils (Table 3).

Carbon content in leaves and stems decreased with the water deficit in the three tropical soils without Si fertigation (Table 3). Additionally, Si supply increased

leaf C content in the PWD plant grown in Eutrophic Red Latosol. However, it decreased in the plant grown in Quartzarenic Neosol and Dystrophic Red Latosol (Table 3). In AWD, there was an increase in leaf C content by Si fertigation only in cultivation with Dystrophic Red Latosol, with no difference in this variable in the other soil types (Table 3). The C content in the plant stem increased in PWD fertigated with Si in the three tropical soils. In contrast, in AWD, the increase was observed only in the cultivation of Quartzarenic Neosol and Eutrophic Red Latosol (Table 3).

Table 03. C, N, P, and Si content in leaves and stems of sugarcane cultivated with absence (0.0 mM) and presence of fertigated Si (1.8 mM) and two water conditions (with and without water deficit) in three tropical soils (Quartzarenic Neosol; Eutroferic Red Latosol; and Dystrophic Red Latosol)

Water condition		Si	Quartzarenic Neosol		Eutrophic Red Latosol		Dystrophic Red Latosol	
			Leaf	Stem	Leaf	Stem	Leaf	Stem
C (mg per plant)								
PWD	without	15437 Ba	6503.9 Bb	7506.4 Bb	4461.5 Bb	11396 Ba	5574.2 Bb	
	with	15789 Ba	9563.8 Ba	7819.8 Ba	5911.9 Ba	12100 Ba	6070.0 Ba	
AWD	without	16820 Aa	9899.8 Ab	10255 Aa	6769.8 Ab	15030 Ab	8390.1 Aa	
	with	16458 Aa	12567 Aa	10729 Aa	7604.8 Aa	16845 Aa	8674.3 Aa	
MSD (5%)		440.03	1104.14	250.13	310.58	730.53	372.37	
N (mg per plant)								
PWD	without	193.36 Ba	53.205 Ba	88.825 Ba	74.606 Aa	102.90 Aa	78.100 Ba	
	with	192.46 Aa	49.854 Ba	83.721 Ba	67.644 Ab	94.725 Aa	75.562 Aa	
APW	without	224.42 Aa	67.663 Ab	146.37 Aa	55.626 Ba	102.95 Aa	114.76 Aa	
	with	204.41 Ab	81.817 Aa	138.68 Aa	46.574 Bb	93.494 Aa	85.525 Ab	
MSD (5%)		12.36	9.05	8.63	5.29	11.97	10.15	
P (mg per plant)								
PWD	without	14.47 Bb	7.579 Bb	3.65 Ba	1.56 Bb	14.85 Bb	10.15 Ba	
	with	18.90 Ba	15.69 Ba	3.85 Ba	2.31 Ba	17.43 Ba	11.71 Ba	
AWD	without	24.68 Aa	17.23 Ab	7.87 Aa	2.44 Aa	22.64 Ab	13.08 Ab	
	with	26.11 Aa	22.50 Aa	8.70 Aa	2.95 Aa	30.30 Aa	19.40 Aa	
MSD (5%)		0.98	2.40	0.89	0.56	2.27	1.77	
Si (mg per plant)								
PWD	without	80.02 Bb	7.02 Bb	47.82 Bb	7.71 Bb	84.20 Ab	7.21 Ab	
	with	411.73 Ba	47.77 Ba	167.04 Ba	61.42 Ba	192.61 Ba	24.92 Ba	
AWD	without	113.21 Ab	28.86 Ab	117.58 Ab	17.69 Ab	118.15 Ab	7.51 Ab	
	with	471.12 Aa	91.42 Aa	474.51 Aa	86.0 Aa	467.88 Aa	65.86 Aa	
MSD (5%)		26.60	4.34	25.42	9.44	44.21	4.04	

* Different uppercase letters indicate differences in water conditions and different lowercase letters indicate differences in Si fertigation by Tukey test ($p < 0.05$); MSD: Minimum significant difference.

Water deficit also decreased the N content in leaves and stems in sugarcane plants without Si fertigation in the three tropical soils, except for stems in plants cultivated in Eutrophic Red Latosol and leaves in plants cultivated in Dystrophic Red Latosol (Table 3). On the other hand, Si fertigation did not change leaf N content in the two water retention capacities in the three tropical soils, except for Quartzarenic Neosol, where there was a decrease in N content in PWD (Table 3). Additionally, the N content in the stem decreased in PWD fertigated with Si in Eutrophic Red Latosol, while in AWD, there was an increase in this variable in Quartzarenic Neosol and a decrease in Dystrophic Red Latosol (Table 3).

Phosphorus content in leaves and stems of plants was reduced with the water deficit in sugarcane without Si fertigation (Table 3). Furthermore, leaf P content was increased in the plant with Si fertigation in PWD in Quartzarenic Neosol and Dystrophic Red Latosol, and in AWD in Dystrophic Red Latosol (Table 3). Moreover, the P content in the stem was increased as a function of Si fertigation in the plant cultivated in PWD in Dystrophic Red Latosol and Quartzarenic Neosol, and in AWD in Dystrophic Red Latosol (Table 3).

3.4 Carbon, nitrogen, and phosphorus use efficiency and biomass partition

The water deficit reduced the C use efficiency in the leaves and stems of plants grown in the three tropical soils without Si fertigation (Figures 4A, B). Additionally, the C use efficiency in the leaves (Figure 4) and in the stems (Figure 4), and the N use efficiency in the stems (Figure 4), were increased in the plant with Si fertigation in the two water conditions, and the three tropical soils (Figures 4A, B).

The N use efficiency decreased with the water deficit in sugarcane plants without Si fertigation in the three tropical soils, except for leaves cultivated in Quartzarenic Neosol and Eutrophic Red Latosol (Figures 4C,D). Silicon fertigation also increased the efficiency of N foliar use in plants cultivated in the two water conditions and the three evaluated soils, except for Eutrophic Red Latosol cultivated in PWD (Figure 4C).

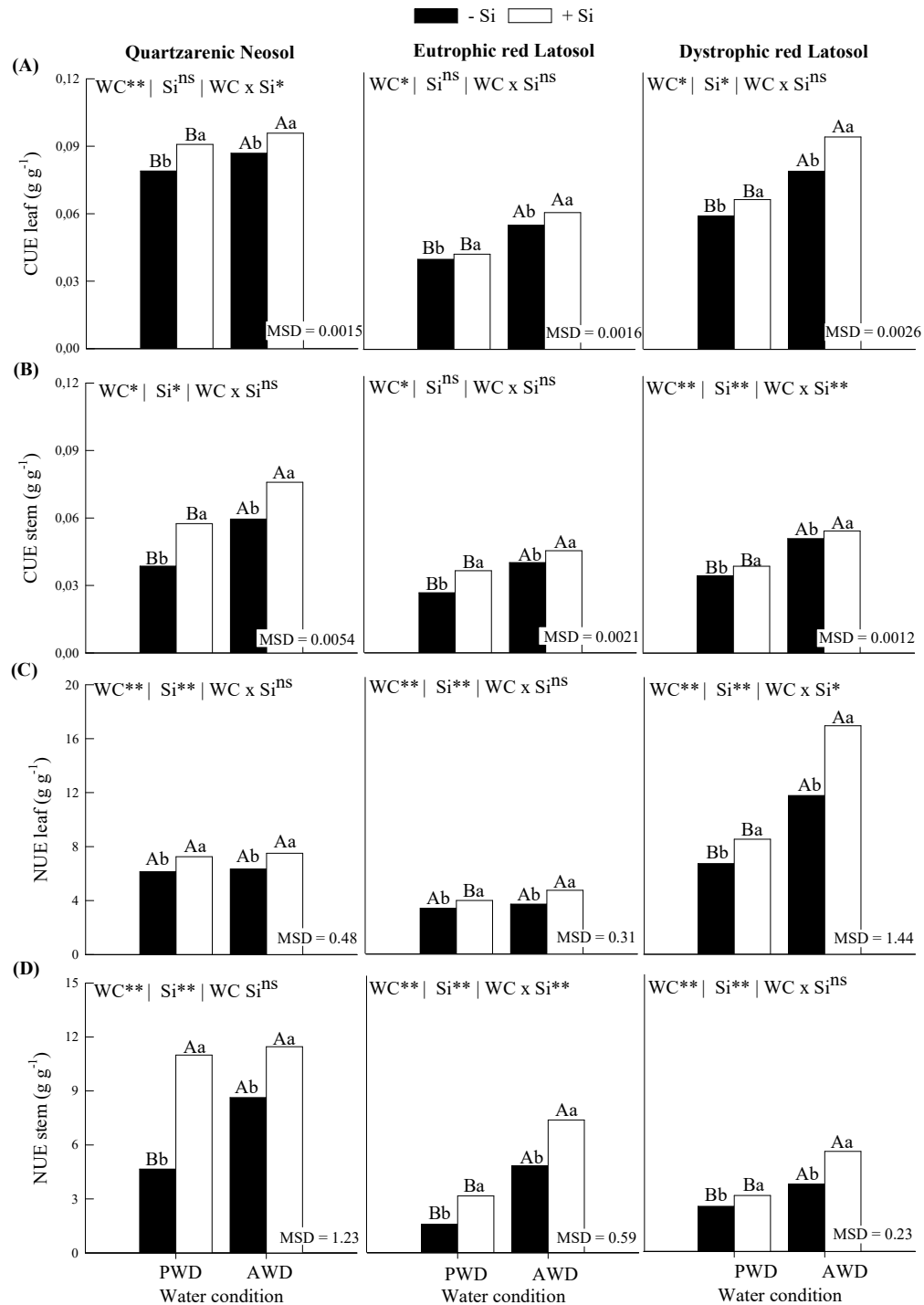


Figure 4. Use efficiencies of Carbon (A,B) and Nitrogen (C,D) in leaves and stems of sugarcane cultivated with absence (0.0 mM) and presence of fertigated Si (1.8 mM) and two water conditions (without—AWD and with water deficit—PWD) in three tropical soils (Quartzarenic Neosol; Eutroferic Red Latosol; and Dystrophic Red Latosol). CUE, C use efficiency; NUE, N use efficiency; WC, water condition; MSD, minimum significant difference; ** and *: significant at 1 and 5% probability, respectively; NS, not significant at 5% probability. Different uppercase letters indicate differences in water conditions and different lowercase letters indicate differences in Si fertilization by Tukey's test ($p < 0.05$).

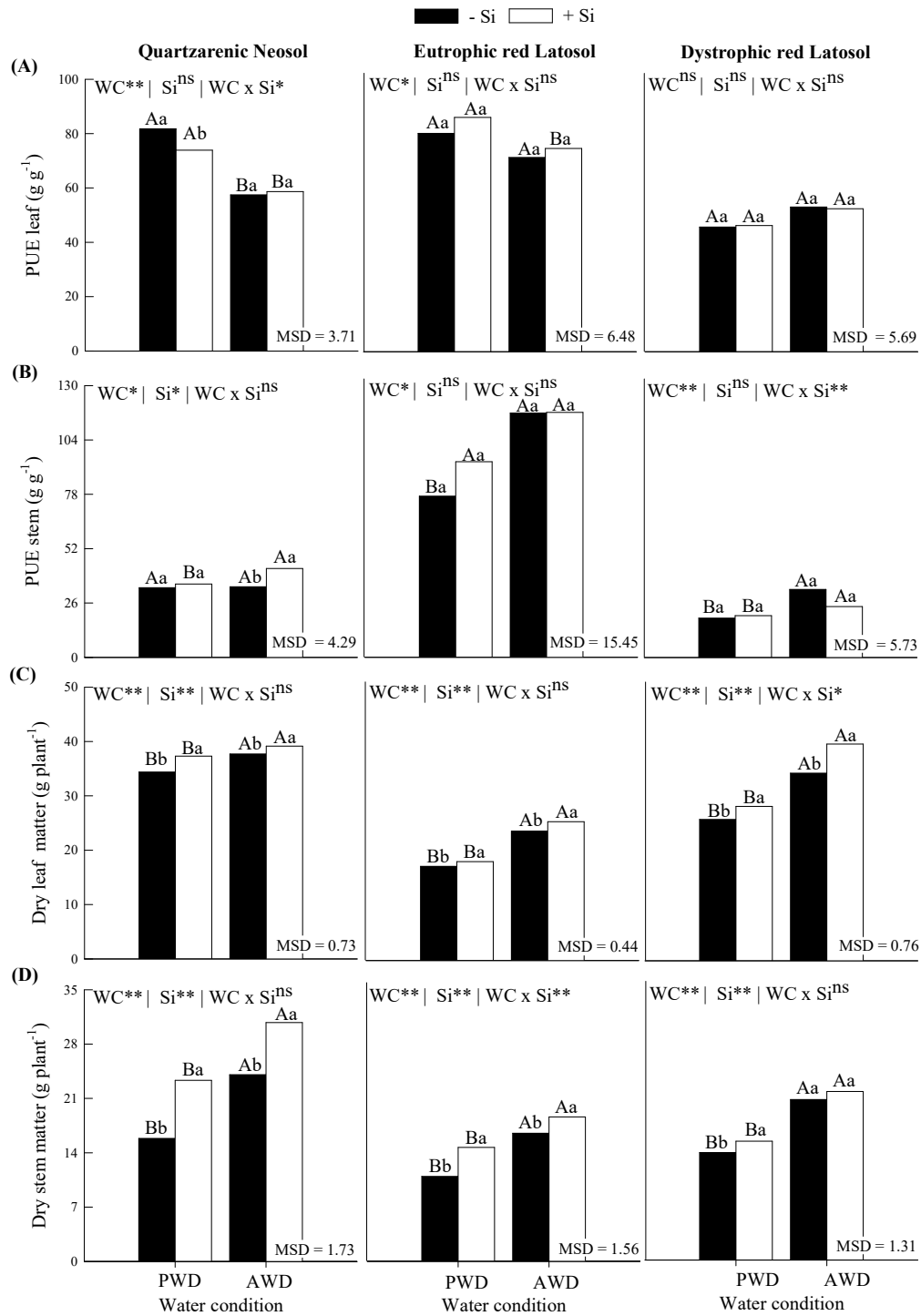


Figure 5. Phosphorus use efficiencies (A,B) and dry mass partition (C,D) in leaves and stems of sugarcane cultivated with absence (0.0 mM) and presence of fertigated Si (1.8 mM) and two water conditions (without—AWD and with water deficit—PWD) in three tropical soils (Quartzarenic Neosol; Eutroferic Red Latosol; and Dystrophic Red Latosol). PUE, P use efficiency; WC, water condition; MSD, Minimum significant difference; ** and *: significant at 1 and 5% probability, respectively; NS, not significant at 5% probability. Different uppercase letters indicate differences in water conditions and different lowercase letters indicate differences in Si fertigation by Tukey's test (p < 0.05).

Water deficit increased P use efficiency in sugarcane plants without Si fertigation in Quartzarenic Neosol. However, there was decreased P use efficiency in stems in Eutrophic Red Latosol and Dystrophic Red Latosol (Figure 5A). In PWD, there was a decrease in the P use efficiency in leaves in sugarcane fertigated with Si and cultivated in Quartzarenic Neosol. At the same time, there were no differences in this variable in plants cultivated in other soils (Figure 5A). Finally, in the stem, the P use efficiency increased in the plant cultivated in AWD condition in Quartzarenic Neosol. However, this variable did not differ in the other soils (Figure 5B).

The water deficit also decreased dry mass in leaves and stems in the three tropical soils cultivated without Si fertigation (Figures 5C, D). Additionally, leaf dry mass production increased in plants cultivated with Si fertigation in both water conditions and the studied soils (Figure 5C). There was also an increase in dry mass production regarding the plant stem using Si fertigation in both water conditions, except for the AWD plant cultivated in Dystrophic Red Latosol, where there was no effect of Si application for this variable (Figure 5D).

3.5 Hierarchical cluster analysis

The hierarchical cluster analysis for leaves indicated that under water restriction conditions, without Si fertigation, there was greater dissimilarity from the other conditions evaluated in Quartzarenic Neosol. On the other hand, in Eutrophic Red Latosol, two groups were formed, dividing the two water conditions. In Dystrophic Red Latosol, the greatest dissimilarity was observed in the AWD treatment with Si fertigation (Figures 6A, C, E).

There were similar groups in leaves and stems for response variables, however, with a difference in the groups' composition for tropical soils. For Quartzarenic Neosol, two groups were formed in leaves and stems: the first group comprised the subgroup of N and C concentrations and the C:Si ratio; and the second group comprised the P use efficiency and the C:P and N:P ratios. The second group also comprised two subgroups: the first subgroup comprising the content of C, N, P, the dry mass production, and the P concentration; and the second subgroup comprising the C:N ratio, the efficiency of C and N use, and the Si

concentration and content, except for the P use efficiency, which was grouped in the second group in stems (Figures 6A,B).

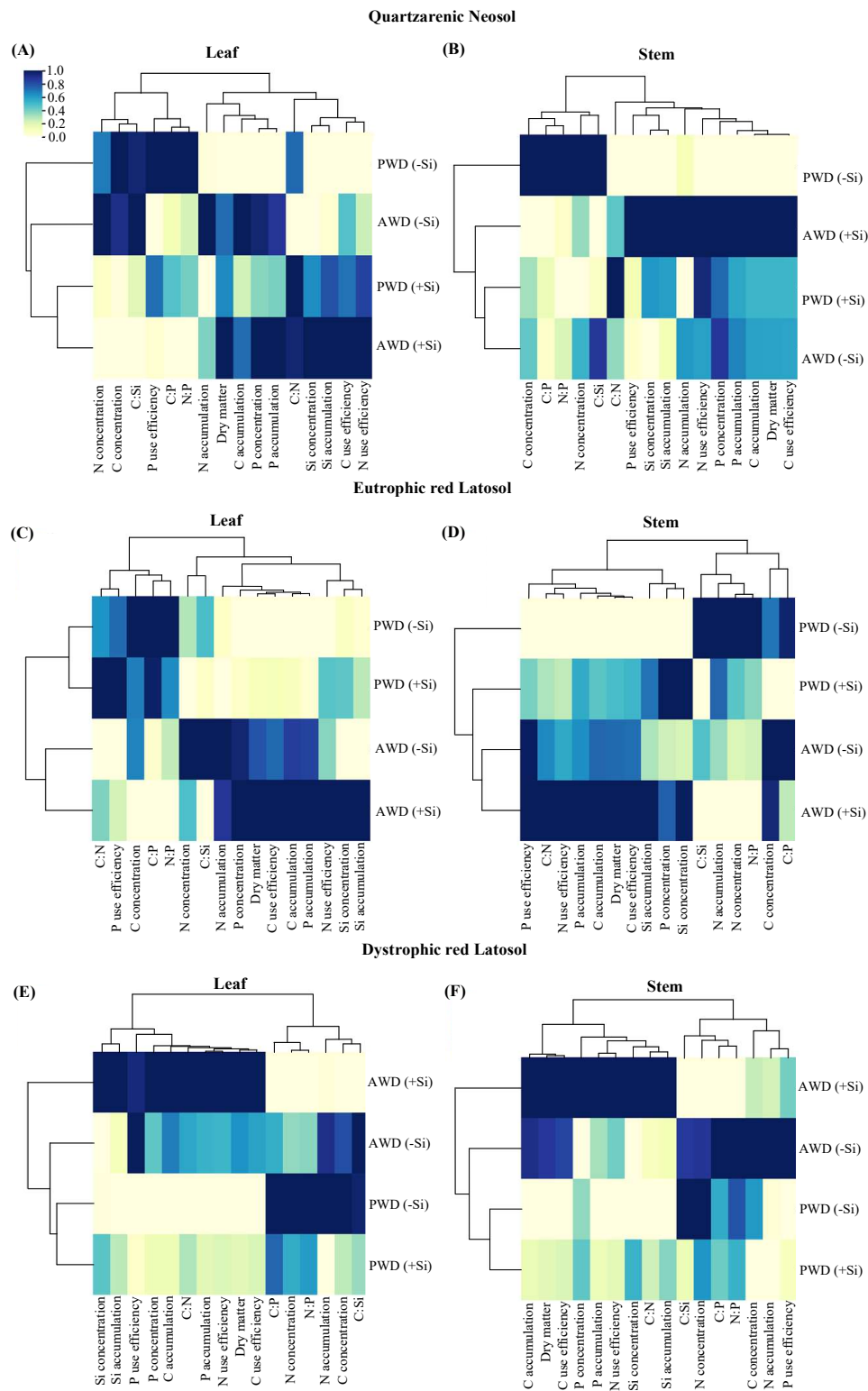


Figure 6. Heat map of hierarchical clustering of variables of concentrations and accumulations of C, N, P, and Si, stoichiometric ratios of C:N:P:Si, use efficiencies of C, N, and P, and dry mass partition in the leaf (A,C,E) and in the stem (B,D,F) of

sugarcane cultivated with absence (0.0 mM) and presence of fertigated Si (1.8 mM) and two water conditions (without—AWD and with water deficit—PWD) in three tropical soils (Quartzarenic Neosol; Eutroferric Red Latosol; and Dystrophic Red Latosol).

In Eutrophic Red Latosol, there were two groups for leaves and stems: the first group indicated greater similarity between the C:N, C:P, and N:P ratios, the P use efficiency, and the C concentration; the second group comprised two subgroups, one with the N concentration and the C:Si ratio, and the second with the P and Si concentrations and the C, N, P, and Si contents, due to the C and N use efficiency and the dry mass production. However, there was a change in the C:N stoichiometric ratio and the P use efficiency for the second group in stems (Figures 6C,D). For Dystrophic Red Latosol, the hierarchical grouping analysis of the variables in leaves showed the formation of two groups: the first group indicated greater similarity of the Si concentration and content with the dry mass production, C, N, and P use efficiency, the P concentration, C and P content, and the C:N stoichiometric ratio; the second group comprised the C:P, N:P, and C:Si ratios and the C and N concentrations. However, there was a change in the P use efficiency for the first group in stems (Figures 6E, F).

The hierarchical cluster analysis indicated a greater dry mass production similarity with AWD treatment fertilized with Si in leaves and stems in the three tropical soils. It also found that Si fertigation in PWD showed similar results under AWD conditions in leaves and stems in Quartzarenic Neosol, and stems in Eutrophic Red Latosol (Figure 6). The C and N use efficiency and the P and Si concentration and content are highly related to the AWD treatment with Si fertigation on leaves and stems in the three tropical soils (Figure 6).

The stoichiometric ratios C:Si, C:P, and N:P are inversely proportional to the dry mass production, which showed high similarity with AWD treatment fertilized with Si in leaves and stems in tropical soils (Figure 6). The P use efficiency in the leaves is inversely related to the AWD treatment fertilized with Si in the three tropical soils due to the increase in foliar P concentration (Figure 6). On the other hand, the P use efficiency and concentration in stems showed high similarity with AWD treatment fertilized with Si (Figure 6C).

3.6 Principal component analysis

Principal component analysis (PCA) in leaves and stems explained 99.3 and 92.4, 98.6 and 98.2, and 98.1 and 96.9% of the variable responses of sugarcane cultivated in Quartzarenic Neosol, Eutrophic Red Latosol, and Dystrophic Red Latosol, respectively (Figure 6). In the stem, PCA explained 92.4, 98.2, and 96.9% of the response variables of sugarcane cultivated in Quartzarenic Neosol, Eutrophic Red Latosol, and Dystrophic Red Latosol, respectively (Figure 7). Given the importance of stems in crop productivity, we will highlight the PCA analysis in this organ.

In sugarcane cultivation in Quartzarenic Neosol, the C concentration is associated with the PWD treatment without Si fertigation and the C:N ratio with the PWD treatment with Si fertigation (Figure 7B). The N use efficiency, the Si concentration, and the C, P, and Si content were associated with the two water treatments fertigated with Si, and the C and P use efficiency, the N content, and the dry mass production were associated with AWD treatment fertigated with Si (Figure 7B). In addition, PCA indicated that the increase in the C:Si, C:P, and N:P stoichiometric ratios and the N concentration are associated with treatments that were not fertigated with Si in the two water conditions studied (Figure 7B).

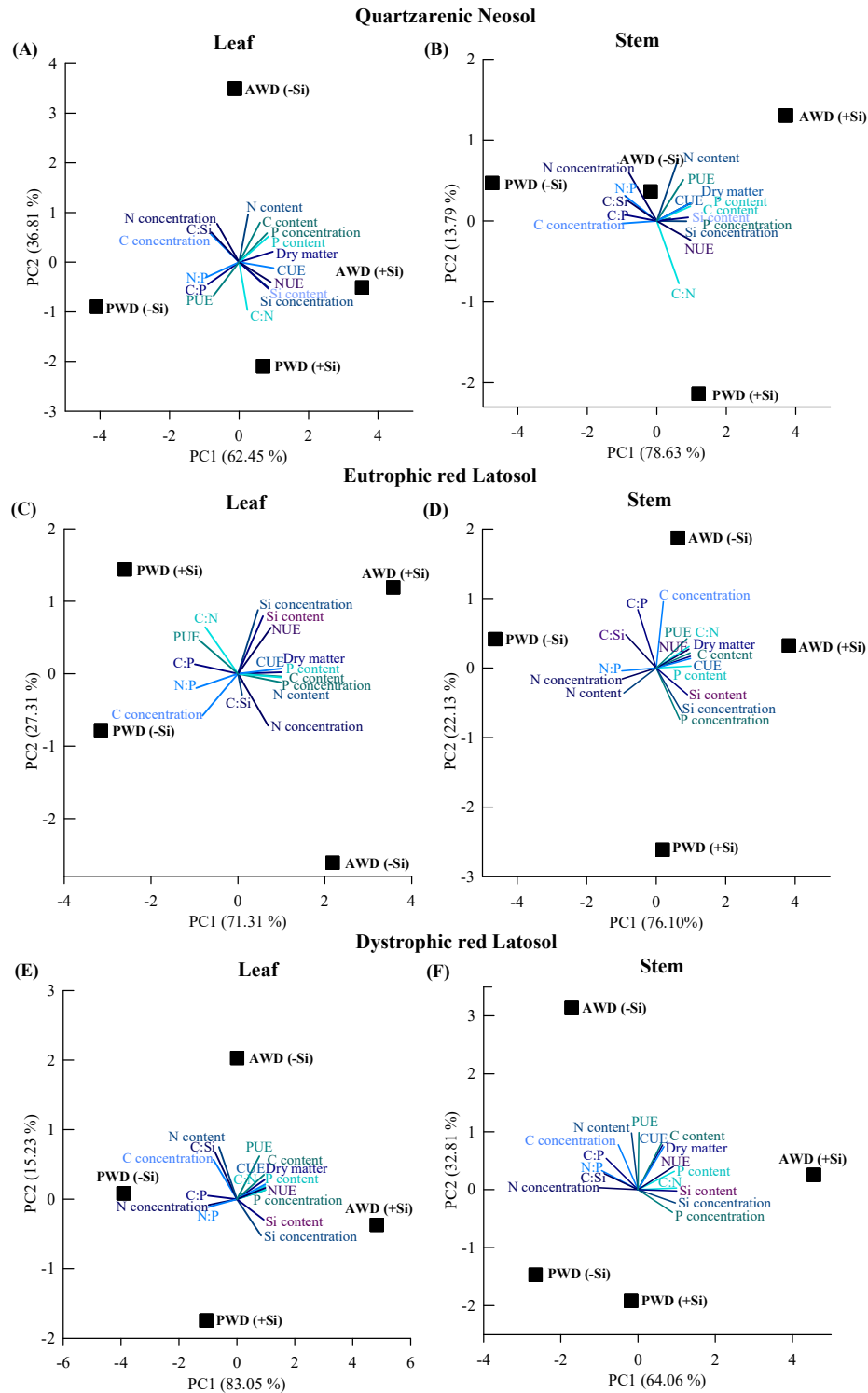


Figure 7. Principal component analysis of the variables of concentrations and accumulations of C, N, P, and Si, stoichiometric ratios of C:N:P:Si, use efficiencies of C, N, and P, and dry mass partition in the leaf (A,C,E) and in the stem (B,D,F) of sugarcane cultivated with absence (0.0 mM) and presence of fertigated Si (1.8 mM) and two water conditions (without—AWD and with water deficit—PWD) in three tropical soils (Quartzarenic Neosol; Eutroferic Red Latosol; and Dystrophic Red Latosol). CUE, C use efficiency; NUE, N use efficiency; PUE, P efficiency use.

For Eutrophic Red Latosol, there was an association of the C:Si and C:P stoichiometric ratios with the treatments not fertigated with Si in the two water conditions studied, while the Si and P concentration and the Si content are associated with the fertigated treatments in the two water conditions (Figure 7D). Furthermore, carbon concentration was associated with PWD treatment without Si fertigation, and the N:P ratio and N concentration and content were associated with PWD treatment without Si fertigation (Figure 7D). Moreover, there was an association between the C, N, and P use efficiency, the C:N ratio, the C and P content, and the dry mass production with the AWD treatment fertigated with Si (Figure 7D).

For the sugarcane stem cultivated in Dystrophic Red Latosol, PCA indicated an association of increased N concentration and C:Si, N:P, and C:P stoichiometric ratios with treatments without Si fertigation. However, N use efficiency, P and Si concentration, P and Si content, and the C:N stoichiometric ratio were associated with treatments fertigated with Si in both water conditions (Figure 7F). Carbon and Nitrogen concentrations and P use efficiency were associated with PWD treatment without Si fertigation, and C use efficiency, C content, and dry mass production were associated with AWD treatment (Figure 7F).

4 Discussion

There is a predominance of studies regarding water deficit in sugarcane crops without Si supply. They have reported losses in crop productivity, which is generally explained by damage to the plant's physiological aspects (Bezerra et al., 2019; Camargo et al., 2019; Teixeira et al., 2021). These water deficit losses in the production of sugarcane stems were also verified in the three soils studied. However, we found that the water deficit caused these losses because there was a change in the C:N, C:P, and N:P stoichiometric ratios, which varied according to the plant's organ and soil. These effects on these ratios resulted in a decrease in the use efficiencies of C and N in leaves and C and N in stems in Eutrophic Red Latosol and Quartzarenic Neosol. Furthermore, there was a reduction in the C and N use efficiency in leaves and stems in Dystrophic Red Latosol (Figures 2–4), which explains the decrease in the production of sugarcane stems. Therefore, the

underlying damage of water deficit is associated with the instability of stoichiometric homeostasis, which causes a decrease in nutritional efficiency and, consequently, in the production of stems. It is not only restricted to losses in gas exchange, as reported by other authors (Marchiori et al., 2017; Bezerra et al., 2019; Camargo et al., 2019; Teixeira et al., 2021). Our results present implications for researchers who study biological damage from water deficit in sugarcane and other species that normally neglect stoichiometric nutrient homeostasis assessments. These facts make it difficult to better understand the nutritional component of crop productivity. Thus, further research is required.

Silicon use is a known alternative to alleviate the water deficit in sugarcane crops, but this may depend on the crop's ability to absorb this element. This fact favors sugarcane because it is classified as a plant that accumulates Si, having specific transporters in the roots and high efficiency in absorbing this beneficial element (Wang et al., 2021). Additionally, Si is absorbed by LSi influx channels and transported to other tissues and organs by efflux channels, and the cooperative influx and efflux system regulates plant accumulation patterns (Trejo-Téllez et al., 2022). However, soil mineralogy can alter the availability of Si in the soil solution, with greater adsorption of monosilicic acid to the mineral's hematite, goethite, magnetite, lepidocrocite, akaganeite, ferroxhyte, ferrihydrite and amorphous iron hydroxide, predominant in tropical soils (Dietzel, 2002; Schaller et al., 2021). Under these conditions, the availability of Si in the soil solution is low, reducing plant uptake and, consequently, its benefits (Schaller et al., 2021).

In order to ensure adequate silicate nutrition for the crop, most studies have evaluated its effects on stem production using Si in solid form with sources of very low solubility in water (calcium silicate), implying the use of the element in high doses (Camargo et al., 2017, 2019, 2020; Clemente et al., 2019). However, there were doubts whether fertigation with Si in concentrations diluted with soluble sources. In other words, using relatively low doses could efficiently increase the element's uptake by the plant. This study answered this question because we showed that fertigation with Si at a concentration of 1.8 mM in both water conditions efficiently increased the element's content in the plant, that is, its uptake (Tables 2, 3). This finding should change the philosophy of supplying Si in the sugarcane crop for

fertigation because using soluble sources through well-diluted Si solutions can reduce the amount of the element applied and directly impact the best cost ratio/benefit of using Si in agriculture.

It is important to highlight that the soil's water condition also influenced the Si fertigation efficiency. It led to a higher content of the element in the leaves and stems of plants without water deficit. In other words, plants under water restriction presented a loss in Si uptake (Tables 2, 3). The lower soil water availability can decrease the Si content in the root (Shukla et al., 2018). Furthermore, the decrease in the soil's water content causes an effect on the Si concentration in the soil solution, which can reach a Si concentration above 3 mM, resulting in possible polymerization of part of this element, with a consequent decrease in the availability in the soil for plant absorption (Schaller et al., 2021). However, even under water deficit regarding the control plants, there was the absorption of Si in the plants, a fact also verified in other studies on young sugarcane plants (Teixeira et al., 2021), a necessary condition for the element to benefit the plant.

The Si supply in the soil can also positively affect the nutrients uptake, especially P in sugarcane in the stem production phase. However, these effects are almost unknown when the beneficial element is supplied via fertigation in different soil water regimes. The presence of Si in the soil can compete for binding sites in minerals, decreasing P uptake, consequently increasing this nutrient's availability for plants (Schaller et al., 2019). Phosphorus is highly adsorbed in tropical soils, resulting in its low availability for plants (Hanyabui et al., 2020). However, Si has increased this nutrient's mobility in soils.

An interesting Si effect was observed regarding P absorption in the plant. The nutrient content in the leaves and stems promoted by the Si supply increased in plants cultivated in both water regimes, especially in Dystrophic Red Latosol and Quartzarenic Neosol (Table 2). This result evidenced the synergistic effect of Si increasing P uptake, which was also observed in sugarcane (Teixeira et al., 2020) and quinoa (Lata-Tenesaca et al., 2021). It can be explained by the fact that Si can regulate the expression of P transporting genes associated with the increase in the exudation rate of organic acids by the plant responsible for improving the P uptake and availability in the soil (Kostic et al., 2017).

The initial underlying benefit of Si on plant life may be involved in modifying the C:N:P stoichiometry, as there was previous evidence in a short-term study in the tillering phase in the sugarcane crop (Teixeira et al., 2020). However, there was a lack of information regarding the crop production phase. This gap was filled because in this study, in the sugarcane stem formation phase, the Si supply, by increasing the content in the plant, also modified the C:N:P stoichiometry in both water regimes. It was evidenced by the fact that there was a decrease in C and N concentrations in the leaves, except for C in PWR in Eutrophic Red Latosol, and an increase in Si concentrations. These facts contributed to the decrease of the C:P, C:Si, and N:P stoichiometric ratios, and at the same time, there was an increase in the C:N stoichiometric ratio (Figure 2). These results reinforce the Si's ability to modify these nutrients' homeostatic balance (Viciado et al., 2019).

Thus, we found that the stoichiometric changes seen from the C:P, C:N, C:Si, and N:P ratios promoted by Si fertigation in the two water conditions, except for the C:P ratios in Eutrophic Red Latosol, which had higher Si content, and, in AWD condition, in Quartzarenic Neosol, were sufficient to increase the C, N, and P nutritional efficiency (Figures 4, 5). It increased the ability of sugarcane plants to use nutrients in their metabolism (Prado, 2021), as stoichiometric modifications alter ecological interactions due to the role of these nutrients in the plant's biological and biochemical functions (Prado and Silva, 2017).

The Si role in sugarcane production is an important topic verified by many authors (Camargo et al., 2017, 2019, 2021b; Marchiori et al., 2017; Bezerra et al., 2019). However, there was a lack of greater understanding of the underlying mechanisms that allow a better understanding of the stoichiometric and nutritional components in the plant's response, not just under stress but also without stress.

Our study showed for the first time that fertigation with Si in sugarcane without stress was responsible for gains in leaf biomass, which reflected in stems in sugarcane plants cultivated in Quartzarenic Neosol and Eutrophic Red Latosol, except in Dystrophic Red Latosol (Figure 5D). This result confirms that plant responses change depending on the cultivated soil. The absence of an increase in stem dry mass in Dystrophic Red Oxisol may be more related to lower Si absorption than the other evaluated tropical soils. There was lower Si content in the stems with a

28 and 23% reduction compared to the cultivated plants Quartzarenic Neosol and Eutrophic Red Latosol, respectively (Table 3). The lack of response in this soil may be associated with a high P concentration (Table 1), with high adsorption of this nutrient occurring in highly weathered tropical soils, such as the Eutroferic Red Latosol. In the soil, Si can compete with phosphate compounds for binding sites on minerals, thus reducing the concentration of the beneficial element in the soil solution (Schaller et al., 2021) and reducing plant uptake. This fact can be observed by the P content in the plants between the two Latosols, which have greater P fixing powers, and it is not recommended to compare to Quartzarenic Neosol due to their lower capacity to fix P (low amount of clay) (Table 3). On the other hand, our study clarifies the possible mechanisms through which Si acts on sugarcane cultivated even without water deficit, indicating the establishment of a new C:N:P homeostatic balance responsible for increasing the nutrient use efficiency and providing higher dry mass biosynthesis. Overall, this is confirmed by multivariate analysis (PCA and hierarchical clustering), indicating a high similarity of dry mass production with Si fertigation in plants without stress, and an association with increased C and N use efficiency, the C, N, and P contents, and the decrease of the C:P, C:Si, and N:P stoichiometric ratios (Figures 6, 7).

According to the multivariate analysis, under water deficit, there was something similar indicating a strong relationship between the C use efficiency and the dry mass production in leaves and stems in the three tropical soils studied associated with fertigation with Si. It revealed that Si increases C use efficiency to increase dry mass biosynthesis in plants. This effect is probably due to the plant's metabolic economy strategy since C needs 10 to 20 times more energy than Si to be incorporated into the organic skeleton. A 1% increase in Si in the biomass composition promotes a C decrease from 1.3 to 5.9% (Xia et al., 2020).

It should be noted that, for the first time, using soluble sources via fertigation with Si is also proven efficient in mitigating the damage caused by the water deficit regime in different soils (Figure 5), which is similar to studies using high Si doses incorporated into the soil (Camargo et al., 2017, 2021b; Clemente et al., 2019). However, most studies with this element do not compare the differences in plant response between soils since they study only one soil.

Our studies indicated a difference in the response of plants to the Si supply in different soils. Such effects reinforce that using the fertigation strategy with Si in a water deficit regime is more beneficial in tropical soils with low Si availability in the soil solution, such as Quartzarenic Neosol. The cluster analysis also confirmed the soil type effect on sugarcane cultivation, indicating that in Quartzarenic Neosol and Eutrophic Red Latosol, there were similar responses for Si fertigation for the variables evaluated in the stem, as it reduced the biomass losses with water deficit. Meanwhile, plants cultivated in Dystrophic Red Latosol were different. Our results show that dry mass production in the stem under water deficit conditions was associated with an increase in the Si concentration and content and a decrease in the C:Si and C:P stoichiometric ratios, especially in sugarcane plants grown in Quartzarenic Neosol and Eutrophic Red Latosol (Figure 6). It indicates that the lower Si absorption, compared to plants grown in another soil (Table 3), was not enough to change these stoichiometric ratios and express the high level of benefits. This differential Si response in sugarcane in different soils indicates the importance of edaphic characteristics in Si management in agricultural systems, such as mineralogical composition, texture, Fe and Al oxide contents, and organic matter, which are factors that can alter the success of Si fertigation and the highest stem yield (Camargo and Keeping, 2021).

Considering the results, it was clear that the first hypothesis can be accepted since Si, after fertigation application and uptake, is sufficient to modify C, N, and P stoichiometric homeostasis in leaves and stems. However, the second hypothesis tested can be partially accepted. Although Si induced stoichiometric modification, it was sufficient to increase nutritional efficiency and alleviate the losses in dry mass production of leaves and stems of sugarcane cultivated under water deficit. It also increases dry mass production of leaves and stems in the irrigated crop without water deficit, but it did not occur in all soils. In Dystrophic Red Latosol, Si benefits were limited to increasing stem production, especially in crops without water deficit. Therefore, Si use is not indicated in this soil type in properly irrigated sugarcane areas.

Our discovery enables adequate Si use, via fertigation, to increase the productivity of the sugarcane crop under water stress and without stress, depending

on the cultivated soil, allowing a better understanding of the underlying Si mechanisms involved.

5 Conclusion

The biological losses caused by water deficit in sugarcane plants are related to the homeostatic imbalance of C:N:P, causing reductions in nutrient use efficiencies and directly impacting dry mass biosynthesis. Silicon becomes a viable agronomic alternative in sugarcane crops with water restrictions, reducing the biological losses of water deficit, modifying the homeostatic balance of C:N:P, improving the use efficiency of these nutrients, and improving plant performance. Using Si in sugarcane cultivation without water stress also proved to be efficient in improving plant performance, alternating homeostatic nutritional balance, increasing the C, N, and P use efficiencies, and increasing the dry mass production of leaves and stems.

The responses of sugarcane plants to Si application are limited depending on the type of cultivation soil, altering the intensity of responses to the benefits of the beneficial element. The strategic use of Si fertigation in a water deficit regime becomes more advantageous in tropical soils with low availability of Si in the soil solution, such as Quartzarenic Neosol. The research perspective is that Si can contribute to the sustainable cultivation of sugarcane in tropical soils in irrigated regions or under a water deficit regime.

6 References

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CHAPTER 3 - New approaches to the effects of silicon on sugarcane ratoon under irrigation in Quartzipsamments, Eutrophic Red Oxisol, and Dystrophic Red Oxisol³

ABSTRACT

Background: C:N:P homeostasis in plants guarantees optimal concentrations of these nutrients in plant metabolism, however, one of the causes to the effects of deficit irrigation is the loss of C:N:P homeostasis in leaves and stems, causing a reduction in the growth of sugarcane. Being able to measure the impact of water deficit on C:N:P homeostasis in plants from the stoichiometric ratios of the concentrations of these nutrients in leaves and stems. This loss causes a decrease in nutritional efficiency, but can be mitigated with the use of silicon. Silicon favors the homeostasis of these nutrients and crop productivity. The magnitude of this benefit depends on the absorption of Si by the plant and Si availability in the soil, which varies with the type of soil used. Thus, this study aims to evaluate whether the application of Si via fertigation is efficient in increasing the absorption of Si and whether it is capable of modifying the homeostatic balance of C:N:P of the plant, causing an increase in nutritional efficiency and consequently in the production of biomass in leaves and stems of sugarcane ratoon cultivated with deficient and adequate irrigations in different tropical soils.

Results: Water deficit caused biological losses in the concentrations and accumulations of C, N, and P, and reduced the nutrients use efficiency and biomass production of sugarcane plants cultivated in three tropical soils because of disturbances in the stoichiometric homeostasis of C:N:P. The application of Si increased the concentration and accumulation of Si, C, N, and P and their use efficiency and reduced the biological damage caused by water deficit due to the modification of homeostatic balance of C:N:P, thus ensuring sustainability of the production of sugarcane biomass in tropical soils. However, the intensity of attenuation of such deleterious effects stood out in plants cultivated in Eutrophic Red Oxisols. Si contributed biologically by improving the performance of sugarcane ratoon with an adequate irrigation due to the optimization of stoichiometric ratios of C:N:P; increased the accumulation and the use efficiency of C, N, and P, and promoted production gains in biomass of sugarcane in three tropical soils.

Conclusion: Our study shows that fertigation with Si can mitigate the deleterious effects of deficient irrigation or potentiate the beneficial effects using an adequate irrigation system due to the induction of a new stoichiometric homeostasis of C:N:P, which in turn improves the nutritional efficiency and production biomass of sugarcane cultivated in tropical soils.

Keywords: beneficial element, *Saccharum officinarum* L., homeostatic balance of C:N:P, tropical soils, fertigation with Si.

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Novas abordagens para os efeitos do silicógeno na soqueira de cana-de-açúcar sob irrigação em Neossolo Quartzarênico, Latossolo Vermelho Eutrófico e Latossolo Vermelho Distrófico

RESUMO

Antecedentes: A homeostase C:N:P nas plantas garante concentrações ótimas desses nutrientes no metabolismo vegetal, porém, uma das causas para os efeitos da irrigação deficitária é a perda da homeostase C:N:P nas folhas e caules, causando uma redução no crescimento da cana-de-açúcar. Sendo capaz de medir o impacto do déficit hídrico na homeostase C:N:P em plantas a partir das razões estequiométricas das concentrações desses nutrientes nas folhas e caules. Essa perda causa diminuição da eficiência nutricional, mas pode ser amenizada com o uso do silício. O silício favorece a homeostase desses nutrientes e a produtividade das culturas. A magnitude desse benefício depende da absorção de Si pela planta e da disponibilidade de Si no solo, que varia com o tipo de solo utilizado. Assim, este estudo tem como objetivo avaliar se a aplicação de Si via fertirrigação é eficiente em aumentar a absorção de Si e se é capaz de modificar o balanço homeostático de C:N:P da planta, ocasionando um aumento na eficiência nutricional e consequentemente na produção de biomassa em folhas e caules de soca de cana-de-açúcar cultivada com irrigações deficientes e adequadas em diferentes solos tropicais.

Resultados: A deficiência hídrica causou perdas biológicas nas concentrações e acúmulos de C, N e P e reduziu a eficiência de uso de nutrientes e a produção de biomassa de plantas de cana-de-açúcar cultivadas em três solos tropicais devido a distúrbios na homeostase estequiométrica de C:N:P. A aplicação de Si aumentou a concentração e acúmulo de Si, C, N e P e sua eficiência de uso e reduziu os danos biológicos causados pelo déficit hídrico devido à modificação do equilíbrio homeostático de C:N:P, garantindo assim a sustentabilidade da produção de biomassa de cana-de-açúcar em solos tropicais. No entanto, a intensidade de atenuação desses efeitos deletérios se destacou em plantas cultivadas em Latossolos Vermelhos Eutróficos. O Si contribuiu biologicamente melhorando o desempenho da soqueira de cana-de-açúcar com irrigação adequada devido à otimização das relações estequiométricas de C:N:P; aumentou o acúmulo e a eficiência de uso de C, N e P e promoveu ganhos de produção em biomassa de cana-de-açúcar em três solos tropicais.

Conclusão: Nosso estudo mostra que a fertirrigação com Si pode atenuar os efeitos deletérios da irrigação deficitária ou potencializar os efeitos benéficos com um sistema de irrigação adequado devido à indução de uma nova homeostase estequiométrica de C:N:P, que por sua vez melhora a eficiência nutricional da cana-de-açúcar cultivada em solos tropicais.

Palavras-chave: elemento benéfico, *Saccharum officinarum* L., equilíbrio homeostático de C:N:P, solos tropicais, fertirrigação com Si.

1 Introduction

The use of irrigation systems has expanded in recent years aiming the cultivation of sugarcane. The main objective is to increase sugarcane productive potential, as irrigation systems increase the nutritional efficiency of fertilization, favoring physiological and biochemical processes and consequently the growth and development of the crop (Verma et al. 2021). Thus, the scientific area of irrigated agriculture has gained significant momentum since the beginning of the 21st century (Wrachien et al. 2021). This includes studies on sugarcane (Duden et al. 2021) because of the lengthening of water deficit periods during the crop growth cycle resulting from the after effects of climate change (Gunarathna et al. 2018).

In parallel, the availability of “fresh” water suitable for irrigated systems has suffered a considerable decrease in recent years. However, the water demand for irrigation is expected to increase by 11% by 2050, which results in a greater challenge for many regions that live under water restrictions (Wrachien et al. 2021). In addition, the fact that many irrigated systems depend on electricity and their high costs in energy have led to increases in expenditure in recent years (Raza et al. 2022b).

This scenario indicates an urgent need for new approaches that can enhance the viability of irrigated sugarcane systems by increasing the production of stalks in crop areas with adequate irrigation or areas with deficient irrigation due to water scarcity. In the countryside, marginal regions with water deficit problems may reach 35% of the soil's water retention capacity (Wrachien et al. 2021) and cause a significant decrease in crop productivity. And these effects can be aggravated in soils with low water retention capacity, such as Quartzipsamments. For this reason, understanding the water deficit in different soils becomes important, especially to understand tropical soils, such as latosol and Quartzipsamments.

Thus, water deficit is the main abiotic stress factor limiting sugarcane production worldwide, as it forms a strong relationship between growth rate and optimal soil moisture regimes (Carneiro et al. 2020; Surendran et al. 2016). This indicates that sugarcane crops are responsive to irrigation and at the same time tolerant to lack of water (Dias and Sentelhas 2019). The biological damages of water

deficit to sugarcane are known, especially in the physiological processes of plants (Bezerra et al. 2019; Camargo et al. 2017; Teixeira et al. 2021b, a). However, other biological damages have recently been reported due to changes in the homeostatic balance of C:N:P (Oliveira Filho et al. 2021b; Teixeira et al. 2020).

A known and sustainable alternative to attenuate stress in crops is the beneficial element Si. It may also affect plants without stress (Carvalho et al. 2022; Cooke and Leishman 2016b; Souza Júnior et al. 2022). An advantage of this element is its relatively low cost compared to nutrients present in conventional fertilizers (Feng 2000). It also poses no risk to the environment (Bokor et al. 2021). Studies carried out on Si in sugarcane crops attest to its benefits to plants grown under water deficit; these studies reported mainly the effect of Si on the water losses reduction, that is, transpiration (Bezerra et al. 2019; Camargo et al. 2019). However, there is recent evidence that Si may affect nutritional components that are vital to the growth and development of sugarcane crops (Prado 2021).

The first studies evaluating the relationships of Si in plant nutrition specifically considering the stoichiometry of C:N:P in sugarcane were carried out by our research group (Genplant) at Universidade Estadual Paulista (São Paulo, Brazil). The starting point was studies evaluating the beneficial effects of Si on elemental stoichiometry at the initial growth phase of pre-sprouted seedlings in sugarcane cultivated up to 30 days (Teixeira et al. 2020) and up to 80 days (Oliveira Filho et al. 2021b) in water deficit and in plants grown without stress for 90 days (Frazão et al. 2020) and 125 days (Souza Júnior et al. 2022). However, these studies were carried out using soilless cultivation in sand and nutrient solution, or in only one type of soil (Quartzipsamments). Thus, it is clear that this line of investigation is just beginning, and that there is a need for further works that aim to consolidate yet another benefit of Si which is still little explored. Therefore, considering that the Si absorption process is governed by several factors, such as genetics (cultivars) and availability of Si in the soil (Prado 2021), it is possible that the effects of this beneficial element on plant elemental stoichiometry may be affected by soil types.

Tropical soils, despite having a high total Si content due to desilication process, have a relatively low available Si content in them (0.5 mol L^{-1} acetic acid extractor), reaching 5.4 mg dm^{-3} in Red Yellow Oxisol, 6.7 mg dm^{-3} in Dark Red

Oxisol, and 2.7 mg dm^{-3} in Quartzipsamments (Korndörfer et al. 1999). Thus, strong crop responses to Si application are expected, especially in soils with a Si content below the critical level, that is, 15 mg dm^{-3} of Si (0.5 mol L^{-1} acetic acid extractor) (Haynes 2014) or $6\text{--}8 \text{ mg kg}^{-1}$ (extractor in CaCl_2 0.01 mol L^{-1}) (Korndörfer et al. 1999). However, soil types differ in mineralogical composition, texture, Fe and Al oxide contents, and organic matter (Camargo and Keeping 2021). These elements govern the availability of Si in the soil, which justifies the importance of studies considering different soils. These studies could be carried out with sugarcane ratoon, that is, the sprouting of the plant after the first cut or growth cycle. Information about Si at this crop stage is even scarcer.

Considering the above and given the need for a better understanding of the harmful underlying effects of water deficit especially in sugarcane ratoon, the ability of Si to reverse this stress and even improve the plant's stress-free response may be a new approach to study the benefits of Si in this species at the ratoon stage. For this, it is pertinent to test the following hypotheses: (i) initially verify whether sugarcane ratoon, without Si application, is sensitive to irrigation deficit due to disturbances in the stoichiometric homeostasis of C:N:P, leading to losses in the use efficiency of these nutrients and consequently contributing to the productivity of ratoon cultivated in three tropical soils; if this is confirmed, (ii) whether the use of Si can modify this element's stoichiometry and mitigate the damage caused by water deficit by improving the nutritional efficiency of these nutrients, affecting the productivity of ratoon cultivated under deficient irrigation, and also (iii) consider adequate irrigation in three tropical soils.

This research evaluates these hypotheses with the objective of assessing whether the application of Si via fertigation is efficient in increasing the absorption of Si and whether it is capable of modifying the homeostatic balance of C:N:P of the plant, causing an increase in nutritional efficiency and consequently in the production of biomass in leaves and stalks of sugarcane ratoon cultivated with inadequate and adequate irrigation in different tropical soils.

2 Results

2.1 C, N, P and Si concentrations

Fertigation with Si increased the concentration of Si in sugarcane leaves and stems in the absence (AWD) and in the presence of water deficit (PWD) in Quartzipsamments, Eutrophic Red Oxisols, and Dystrophic Red Oxisols (Table 1). Water deficit, in turn, reduced the efficiency of Si fertigation compared to the condition of absence of water deficit, however, the absorbed Si was sufficient to increase the beneficial element concentration in leaves and stems of sugarcane plants cultivated in three tropical soils. In addition, plants that did not receive Si via fertigation, water deficit decreased the ability of plants to absorb Si from the soil, leading to a decrease in the concentration of Si in leaves of sugarcane plants cultivated in Eutrophic Red Oxisols and Dystrophic Red Oxisols, while stems were only affected in plants grown in Eutrophic Red Oxisols (Table 1).

Carbon concentration in leaves and stems decreased in plants grown in Eutrophic Red Oxisols and in stems of plants grown in Dystrophic Red Oxisols in PWD and in the absence of Si fertigation (Table 1). Also, there was a decrease in C concentrations in leaves under the two water conditions studied in Quartzipsamments fertigated with Si; in Dystrophic Red Oxisols, there was a decrease only in the absence of water deficit (AWD); and in Eutrophic Red Oxisols, the treatments did not affect C concentration in leaves (Table 1). In stems, fertigation with Si decreased the concentration of C under both water conditions studied here in sugarcane cultivated in Dystrophic Red Oxisols; in Quartzipsamments, there was a decrease in C concentration only in AWD; and in Eutrophic Red Oxisols, the C concentration in stems decreased in the presence of water deficit (PWD) (Table 1).

Water deficit increased the N concentration in stems of sugarcane plants cultivated in the three tropical soils studied here in the absence of Si application. There was a similar response in leaves of plants cultivated in Eutrophic Red Oxisols. However, there was also a decrease in N concentration in leaves of plants grown in Dystrophic Red Oxisols in the absence of Si application (Table 1). Fertigation with Si also decreased the concentration of N in leaves and stems of plants under AWD and

PWD in sugarcane cultivated in the three tropical soils. However, there was a decrease only in AWD in Dystrophic Red Oxisols (Table 1).

Water deficit decreased P concentration in leaves and stems of plants without Si fertigation in all three tropical soils (Table 1). On the other hand, P concentration in leaves and stems increased in the two water conditions (AWD and PWD) in plants with Si fertigation in crops in the three tropical soils (Table 1).

Table 01. C, N, P, and Si concentrations in leaves and stems of sugarcane plants in two water deficit conditions (presence: 35%, and absence: 70% of water retention) combined with absence (0.0 mmol L⁻¹) and presence of fertigated Si (1.8 mmol L⁻¹) in three tropical soils (Quartzarenic Neosol; Eutroferic Red Latosol; and Dystrophic Red Latosol)

Water deficit	Si	Quartzipsamments		Eutrophic Red Oxisols		Dystrophic Red Oxisols	
		leaf	Stem	leaf	stem	leaf	stem
C (g kg ⁻¹)							
Presence	without	437.27 Aa	413.52 Aa	437.35 Aa	425.81 Aa	428.55 Aa	422.71 Aa
	with	422.63 Ab	408.22 Aa	433.72 Aa	413.88 Ab	426.70 Aa	416.62 Ab
Absence	without	430.78 Aa	416.71 Aa	417.14 Ba	413.31 Ba	432.04 Aa	416.20 Ba
	with	417.98 Ab	406.6 Ab	416.77 Ba	414.39 Aa	419.92 Bb	411.59 Bb
N (g kg ⁻¹)							
Presence	without	4.37 Aa	3.67 Aa	8.89 Aa	5.17 Aa	6.25 Ba	4.22 Aa
	with	3.53 Bb	3.15 Ab	7.76 Ab	4.47 Ab	6.01 Aa	3.84 Aa
Absence	without	4.50 Aa	2.87 Ba	4.80 Ba	3.06 Ba	6.93 Aa	3.10 Ba
	with	4.05 Ab	2.48 Bb	4.26 Bb	2.53 Bb	5.33 Bb	2.52 Bb
P (g kg ⁻¹)							
Presence	Without	0.55 Bb	0.58 Bb	0.23 Bb	0.41 Bb	0.68 Bb	0.99 Bb
	With	0.63 Aa	0.62 Ba	0.27 Ba	0.48 Ba	0.71 Ba	1.12 Ba
Absence	Without	0.61 Aa	0.68 Ab	0.33 Ab	0.48 Ab	0.75 Ab	1.15 Ab
	with	0.64 Aa	0.71 Aa	0.38 Aa	0.54 Aa	0.85 Aa	1.42 Aa
Si (g kg ⁻¹)							
Presence	Without	2.81 Ab	1.97 Ab	3.64 Bb	3.13 Bb	3.44 Bb	2.36 Ab
	With	10.00 Ba	4.19 Ba	9.18 Ba	4.77 Ba	8.06 Ba	5.64 Ba
Absence	Without	3.41 Ab	2.41 Ab	5.55 Ab	5.66 Ab	4.85 Ab	3.41 Ab
	With	17.91 Aa	7.53 Aa	19.42 Aa	13.63 Aa	12.67 Aa	8.39 Aa

Different uppercase letters indicate differences in water deficit and different lowercase letters indicate differences in Si fertigation by Tukey test ($p < 0.05$).

2.2 Stoichiometric ratios of C:N, C:P, C:Si, and N:P

Water deficit reduced the stoichiometric C:N ratio in leaves of sugarcane plants cultivated in Eutrophic Red Oxisols in the absence of Si application, and there was a similar decrease response in the C:N ratio in stems in all three soils of tropical

regions (Fig. 1a and 1b). On the other hand, the application of Si via fertigation promoted an increase in the stoichiometric ratio C:N of leaves in PWD in Quartzipsamments and Eutrophic Red Oxisols, while it did not differ in Dystrophic Red Oxisols (Fig. 1a). For the stoichiometric ratio C:N in stems, there was also an increase promoted by Si fertigation in AWD (Fig. 1b).

The C:P ratio in leaves and stems increased in the presence of water deficit in sugarcane plants grown in the absence of Si fertigation in all three tropical soils (Fig. 1c and 1d). Furthermore, there was a decrease in the C:P ratio of leaves and stems of plants with Si fertigation in the two water conditions studied in all three tropical soils (Fig. 1c and 1d).

Water deficit also caused an increase in the C:Si ratio in leaves and stems in plants in the absence of fertigation with Si in Eutrophic Red Oxisols and Dystrophic Red Oxisols (Fig. 2a and 2b). On the other hand, there was a decrease in the C:Si stoichiometric ratio in leaves and stems of sugarcane fertigated with Si in the two water conditions studied here in the three tropical soils (Fig. 2a and 2b).

The stoichiometric ratio of N:P in leaves and stems also increased in the presence of water deficit in the absence of Si application in all three tropical soils (Fig. 2c and 2d). Meanwhile, there was a decrease in the stoichiometric ratio of N:P in leaves and stems in the presence of fertigation with Si in sugarcane plants in the two water conditions studied here in all three tropical soils (Fig. 2c and 2d).

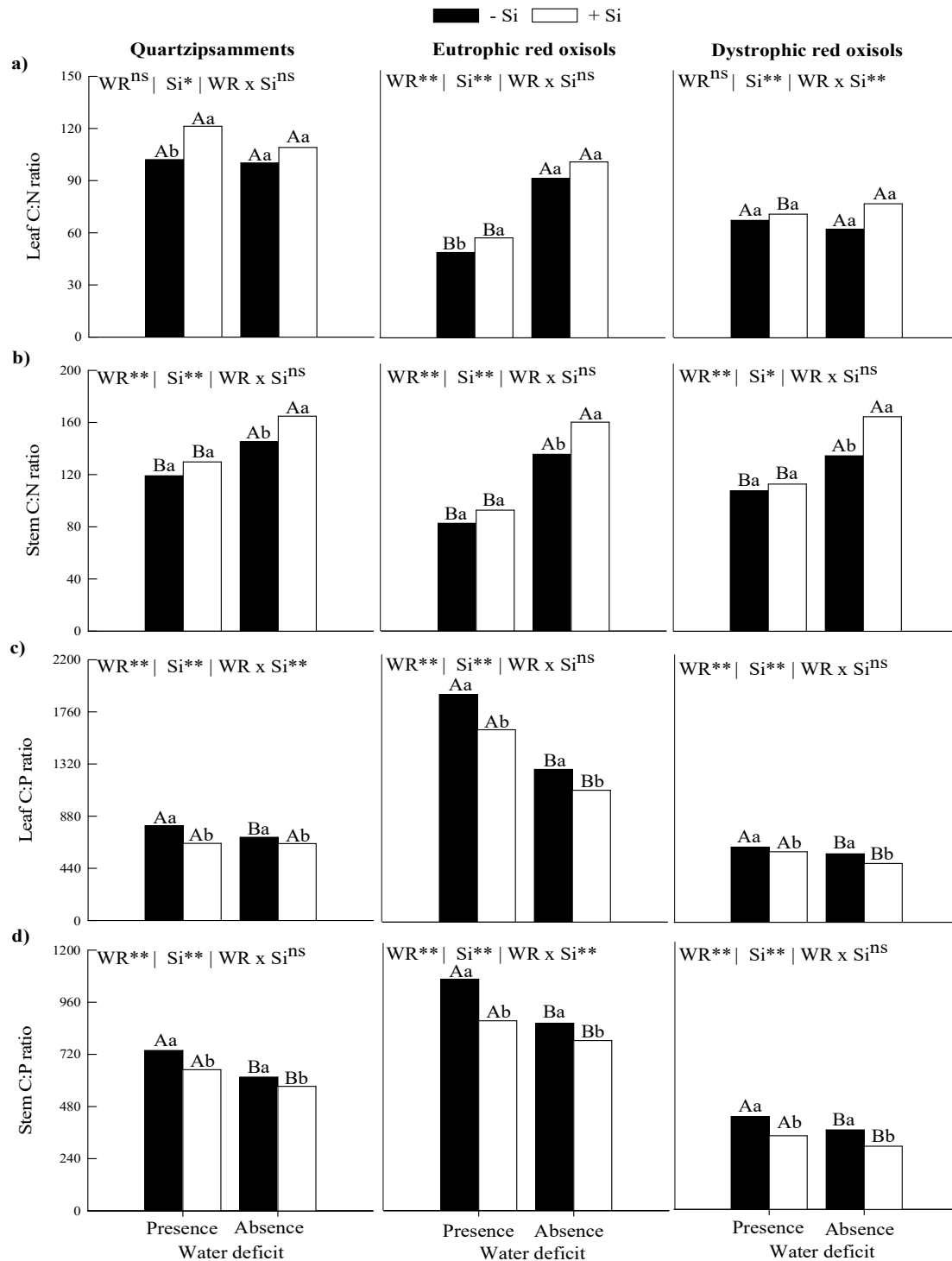


Figure 1. Stoichiometric ratios of C:N (a, b) and C:P (c, d) in leaves and stems of sugarcane plants in two water deficit conditions (presence: 35%, and absence: 70% of water retention) combined with absence (0.0 mmol L⁻¹) and presence of fertigated Si (1.8 mmol L⁻¹) in three tropical soils (Quartzarenic Neosol; Eutroferic Red Latosol; and Dystrophic Red Latosol). WR: water retention capacity; ** and *: significant at 1% and 5% probability, respectively; NS = not significant at 5% probability. Different uppercase letters indicate differences in water deficit and different lowercase letters indicate differences in Si fertilization by Tukey test ($p < 0.05$).

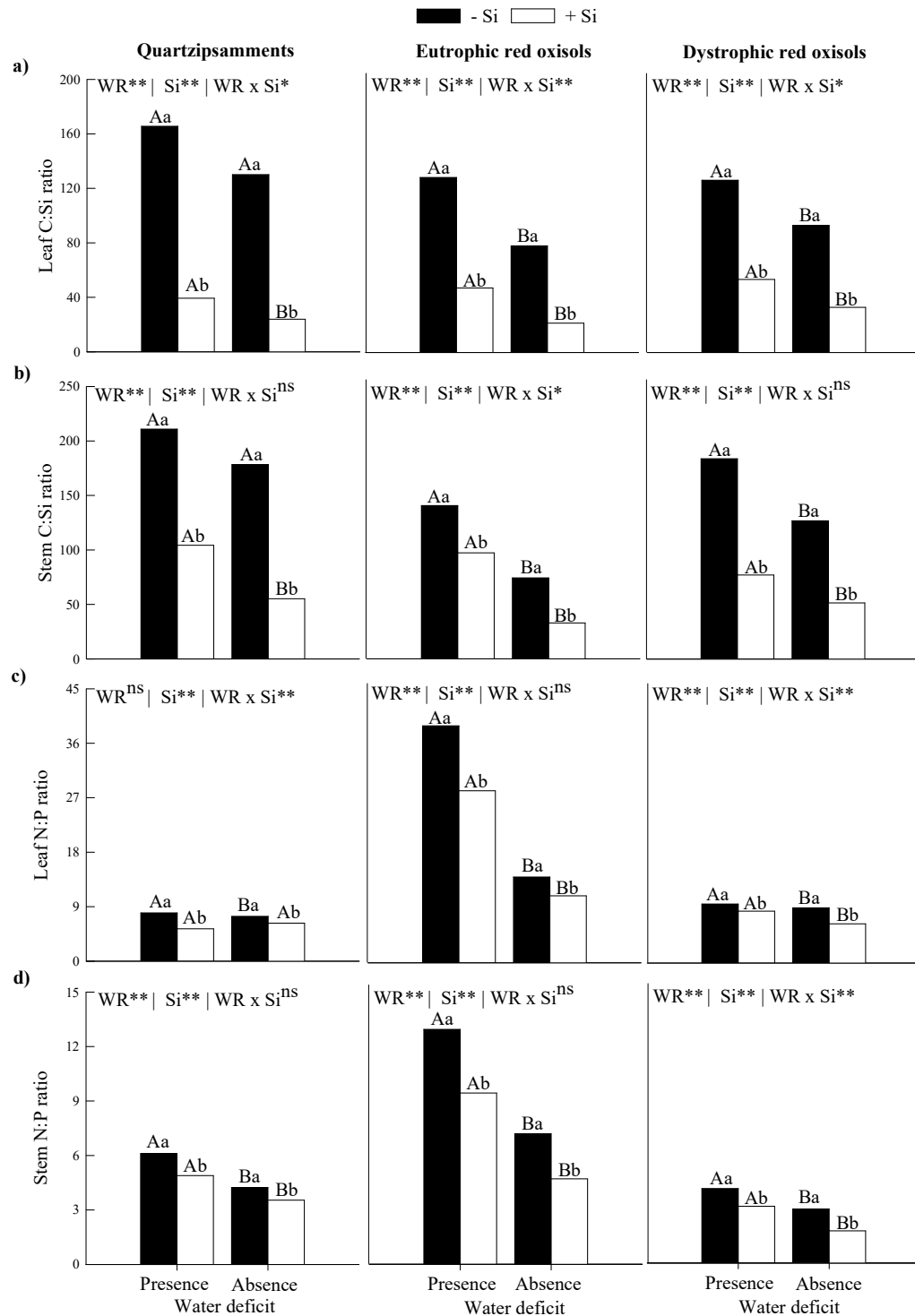


Figure 2. Stoichiometric ratios of C:Si (a, b) and N:P (c, d) in leaves and stems of sugarcane plants under two water deficit conditions (presence: 35%, and absence: 70% of water retention) combined with absence (0.0 mmol L⁻¹) and presence of fertigated Si (1.8 mmol L⁻¹) in three tropical soils (Quartzarenic Neosol; Eutroferic Red Latosol; and Dystrophic Red Latosol). ** and *: significant at 1% and 5% probability, respectively; NS = not significant at 5% probability. Different uppercase letters indicate differences in water deficit and different lowercase letters indicate differences in Si fertilization by Tukey test ($p < 0.05$).

2.3 Si, C, N, and P contents

Water deficit reduced the Si content in leaves and stems in plants without Si application in the three tropical soils (Table 2). Meanwhile, fertigation with Si increased the Si content in leaves and stems of sugarcane in the two water conditions studied here in the three tropical soils (Table 2).

C content decreased in leaves and stems in plants under PWD, irrespective of Si supply, in different tropical soils (Table 2). On the other hand, fertigation with Si increased the C content in leaves and stems of plants in the two water conditions in all three tropical soils. However, plants grown in Quartzipsamments and Dystrophic Red Oxisols showed an increase in C content in leaves only under PWD and in stems only under PWD in Quartzipsamments and Eutrophic Red Oxisols (Table 2).

The water deficit caused a reduction in N contents in leaves and stems, in the absence of Si supply, in sugarcane cultivated in Quartzipsamments and in Dystrophic Red Oxisols, while in Eutrophic Red Oxisols a reduction in N content was observed only in the stem (Table 2). On the other hand, the N content in leaves of sugarcane fertigated with Si increased in PWD in Quartzipsamments and in AWD in Dystrophic Red Oxisols, but, it did not differ in Eutrophic Red Oxisols (Table 2). For stems, there was an increase in N content in sugarcane fertigated with Si under PWD in Quartzipsamments and Eutrophic Red Oxisols, however, there was no response in Dystrophic Red Oxisols (Table 2).

Water deficit caused a reduction of P content in leaves and stems in sugarcane plants with and without Si application in all three tropical soils (Table 2). The supply of Si increased P content in sugarcane leaves in the two water conditions (AWD and PWD) in the three tropical soils (Table 2). On the other hand, the P content in stems increased with Si fertigation in both water conditions (AWD and PWD); however, in Quartzipsamments there was an increase only in PWD (Table 2).

Table 02. C, N, P, and Si content in leaves and stem of sugarcane plants in two water deficit conditions (presence: 35%, and absence: 70% of water retention) combined with absence (0.0 mmol L⁻¹) and presence of fertigated Si (1.8 mmol L⁻¹) in three tropical soils (Quartzarenic Neosol; Eutroferic Red Latosol; and Dystrophic Red Latosol)

Water deficit	Si	Quartzipsamments		Eutrophic Red Oxisols		Dystrophic Red Oxisols	
		Leaf	Stem	leaf	Stem	leaf	stem
C (mg per plant)							
Presence	without	7013.7 Bb	1772.8 Bb	3783.3 Bb	514.4 Bb	8339.7 Bb	1850.2 Bb
	with	9722.6 Ba	2669.5 Ba	4431.1 Ba	1129.2 Ba	8909.7 Ba	2125.1 Ba
Absence	without	12234.0 Aa	4577.5 Aa	5522.8 Ab	1571.7 Aa	11377.0 Aa	3520.7 Ab
	with	12443.0 Aa	5099.8 Aa	6644.0 Aa	1906.2 Aa	11642.0 Aa	3865.6 Aa
N (mg per plant)							
Presence	without	69.87 Bb	15.72 Bb	77.14 Aa	6.24 Bb	122.66 Ba	17.72 Ba
	with	87.96 Ba	20.56 Ba	77.25 Aa	12.19 Aa	126.36 Ba	19.61 Ba
Absence	without	122.52 Aa	31.56 Aa	55.44 Ba	11.29 Aa	171.65 Aa	29.05 Aa
	with	119.00 Aa	30.31 Aa	63.82 Ba	11.70 Aa	161.20 Ab	23.89 Aa
P (mg per plant)							
Presence	without	8.78 Bb	2.59 Bb	2.00 Bb	0.49 Bb	13.17 Bb	4.33 Bb
	with	15.05 Ba	4.07 Ba	2.59 Ba	1.31 Ba	14.79 Ba	6.27 Ba
Absence	without	17.44 Ab	7.49 Aa	4.19 Ab	1.68 Ab	19.37 Ab	10.01 Ab
	with	19.28 Aa	8.91 Aa	6.07 Aa	2.51 Aa	23.34 Aa	13.26 Aa
Si (mg per plant)							
Presence	without	50.81 Bb	8.76 Bb	31.44 Bb	4.67 Bb	67.20 Bb	10.37 Bb
	with	242.51 Ba	24.87 Ba	95.53 Ba	12.43 Ba	168.06 Ba	28.58 Ba
Absence	without	96.79 Ab	28.60 Ab	66.94 Ab	21.55 Ab	144.02 Ab	26.93 Ab
	with	534.00 Aa	94.40 Aa	299.06 Aa	63.01 Aa	346.45 Aa	79.48 Aa

Different uppercase letters indicate differences in water deficit and different lowercase letters indicate differences in Si fertigation by Tukey test ($p < 0.05$).

2.4 C, N, and P use efficiency and biomass partition

The reduction in C use efficiency in leaves and stems of plants occurred in the absence of Si fertigation in all three tropical soils (Fig. 3a and 3b). The application of Si via fertigation increased the efficiency of C use in leaves and stems of plants in the two water conditions studied here in the three soils (Fig. 3a and 3b).

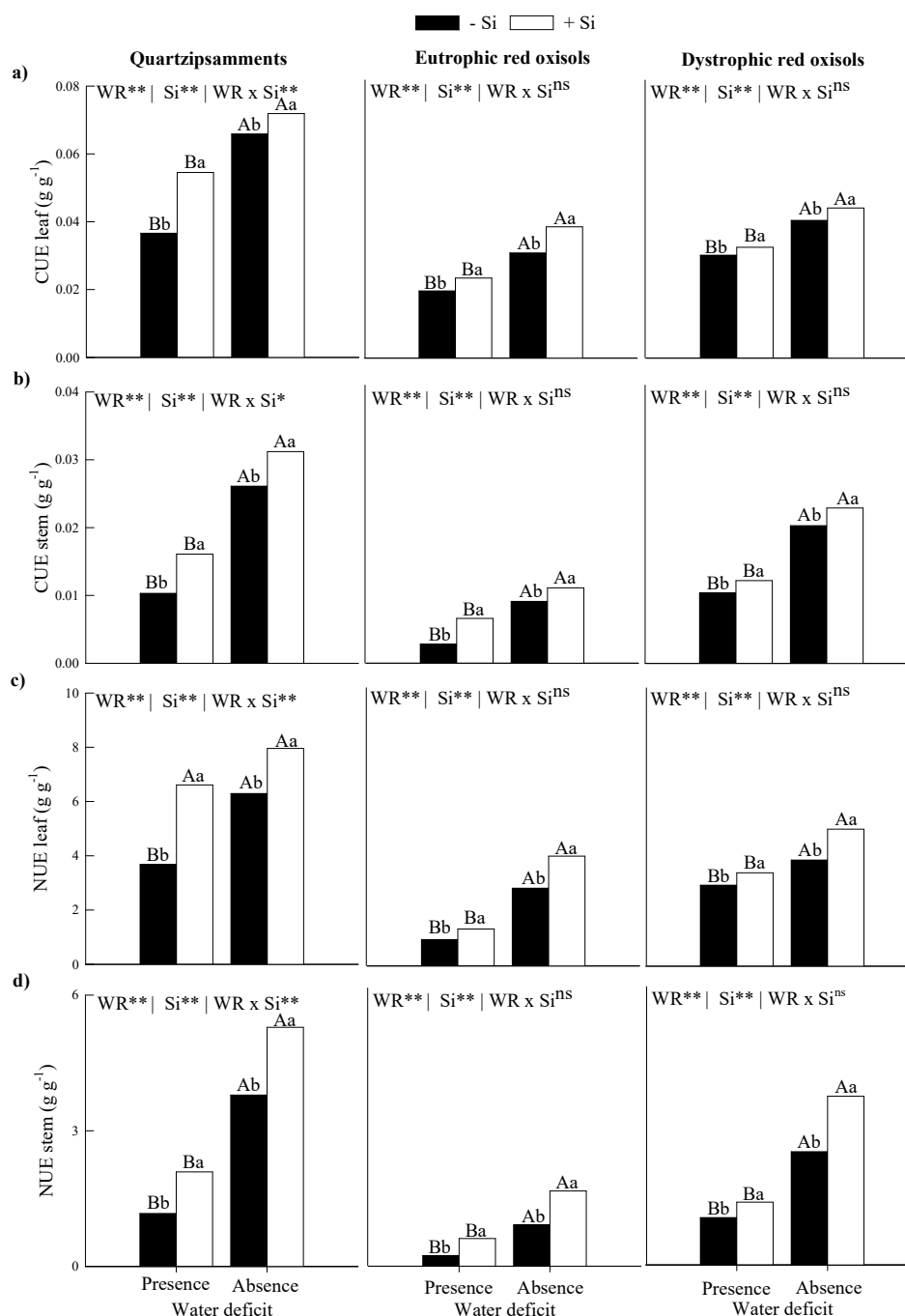


Figure 3. Efficiency use of carbon (a, b) and nitrogen (c, d) in leaves and stems of sugarcane plants in two water deficit conditions (presence: 35%, and absence: 70% of water retention) combined with absence (0.0 mmol L⁻¹) and presence of fertigated Si (1.8 mmol L⁻¹) in three tropical soils (Quartzarenic Neosol; Eutroferic Red Latosol; and Dystrophic Red Latosol). ** and *: significant at 1% and 5% probability, respectively; NS = not significant at 5% probability. Different uppercase letters indicate differences in water deficit and different lowercase letters indicate differences in Si fertilization by Tukey test ($p < 0.05$).

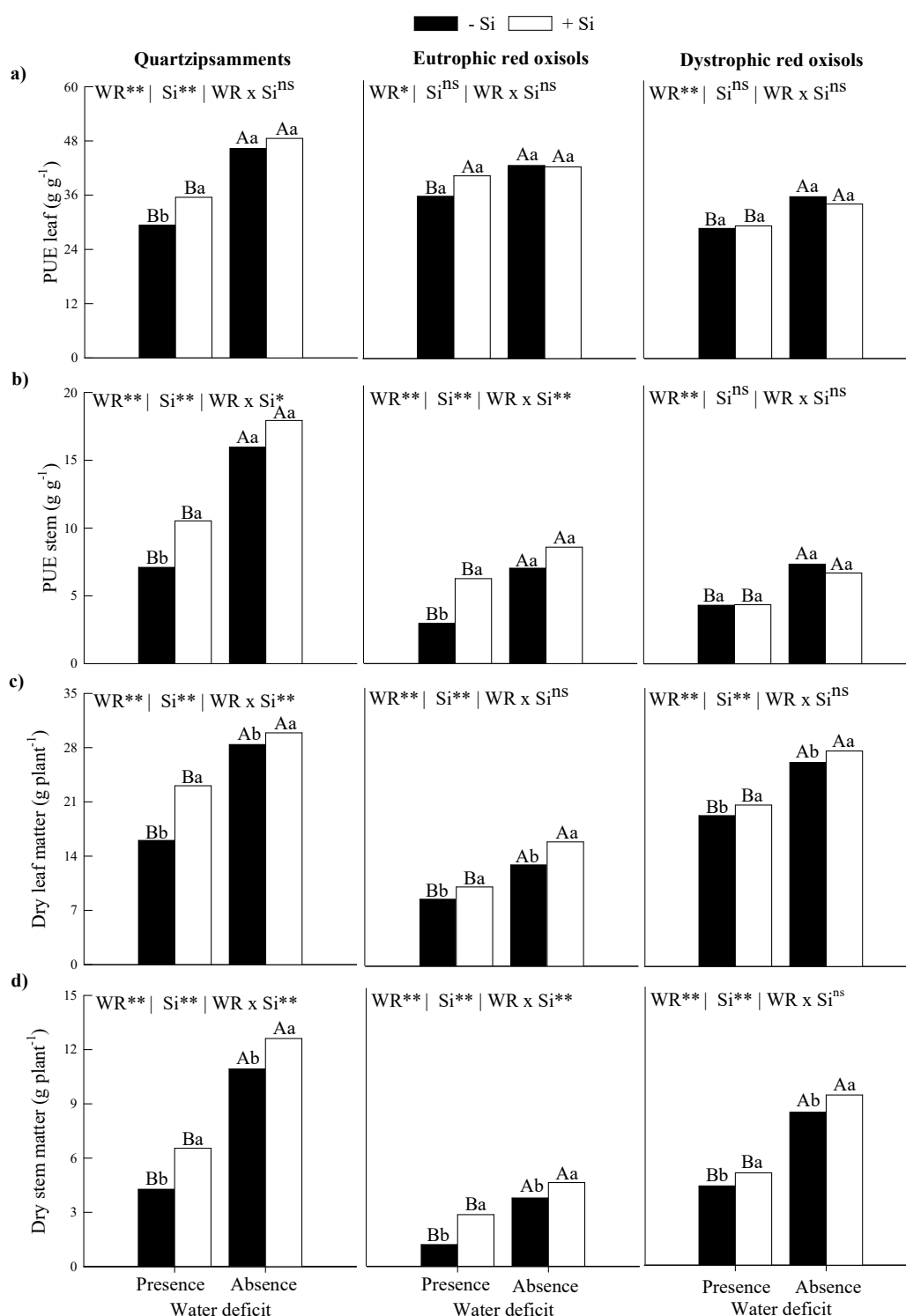


Figure 4. Phosphorus use efficiencies (a, b) and dry mass partition (c, d) in leaves and stems of sugarcane plants in two water deficit conditions (presence: 35%, and absence: 70% of water retention) combined with absence (0.0 mmol L^{-1}) and presence of fertigated Si (1.8 mmol L^{-1}) in three tropical soils (Quartzarenic Neosol; Eutroferic Red Latosol; and Dystrophic Red Latosol). ** and *: significant at 1% and 5% probability, respectively; NS = not significant at 5% probability. Different uppercase letters indicate differences in water deficit and different lowercase letters indicate differences in Si fertilization by Tukey test ($p < 0.05$).

Water deficit also induced a reduction in N use efficiency in leaves and stems in plants without Si fertigation in the three tropical soils (Fig. 3c and 3d). This increase in efficiency also occurred for N use efficiency in leaves and stems in sugarcane fertigated with Si in the two water conditions studied in the three tropical soils (Fig. 3c and 3d).

The efficiency of P use in leaves and stems also decreased in the PWD in sugarcane without Si fertigation in different tropical soils (Fig. 4a and 4b). In PWD, there was an increase in the efficiency of P use in leaves in sugarcane fertigated with Si in Quartzipsamments. However, there was no difference in Eutrophic Red Oxisols and Dystrophic Red Oxisols (Fig. 4a). For stems, there was also an increase in the efficiency of P use in sugarcane fertigated with Si in PWD in Quartzipsamments and Eutrophic Red Oxisols; however, there were no responses in plants grown in Dystrophic Red Oxisols (Fig. 4b).

Water deficit caused a reduction in the production of dry mass in leaves and stems in plants without Si application in all three tropical soils. On the other hand, the production of dry mass by leaves and stems increased with Si fertigation in the two water conditions studied here in the three tropical soils (Fig. 4c and 4d).

2.5 Multivariate analyses

2.5.1 Hierarchical cluster analysis

The hierarchical cluster analysis of leaves indicated that under PWD conditions without Si fertigation there was a greater dissimilarity from the other conditions evaluated in Quartzipsamments, while in Dystrophic Red Oxisols there was a greater dissimilarity in AWD with Si fertigation and in Eutrophic Red Oxisols. Two groups were formed related to the two water conditions (Fig. 5). For response variables, there were similar responses for the three soils as for leaves and stems, indicating the formation of two groups, the first group formed by concentrations of C and N and the stoichiometric ratios C:P, C:Si, and N:P, and the second group formed by the concentrations of P and Si, stoichiometric ratio C:N, contents of C, N, P, and Si, efficiency of use of C, N, and P and dry mass. However, the efficiency of P use in leaves was found for the first group rather than for the second group in Eutrophic Red Oxisols (Fig. 5).

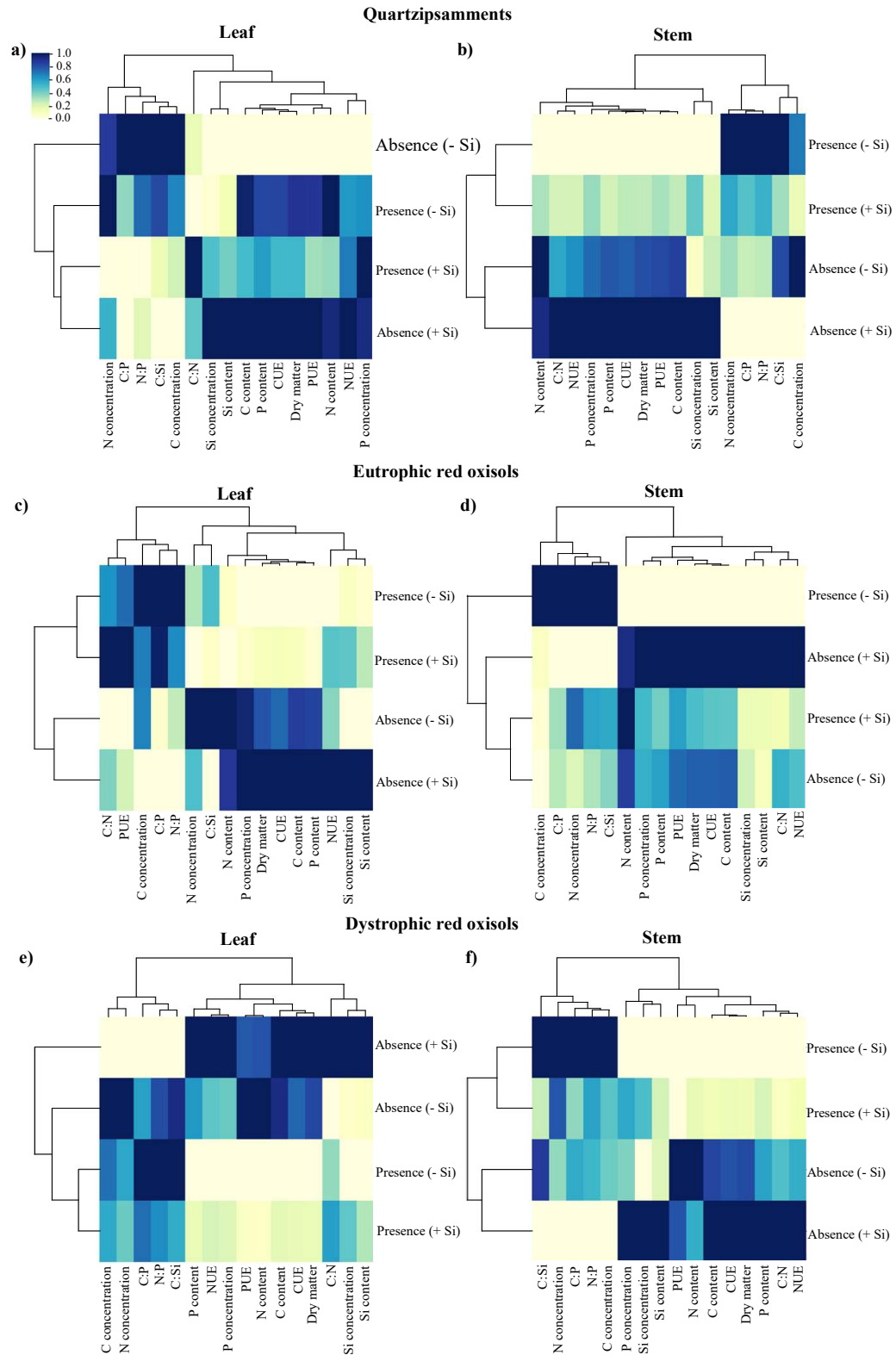


Figure 5. Heat map of hierarchical clustering of variables of concentrations and accumulations of C, N, P, and Si, stoichiometric ratios of C:N:P:Si, use efficiency of C, N, and P and dry mass partition in leaves (a, c, e) and stems (b, d, f) of sugarcane plants in two water deficit conditions (presence: 35%, and absence: 70% of water

retention) combined with absence (0.0 mmol L^{-1}) and presence of fertigated Si (1.8 mmol L^{-1}) in three tropical soils (Quartzarenic Neosol; Eutroferric Red Latosol; and Dystrophic Red Latosol). CUE: C use efficiency; NUE: N use efficiency; PUE: P use efficiency.

In Quartzipsamments, cluster analysis indicated an association of similarity of Si and P concentrations, C, P, and Si contents, C, N, and P use efficiencies, and dry mass in AWD fertigated with Si in leaves and stems, while the stoichiometric ratios of N:P, C:P, and C:Si and the concentration of C were associated with PWD without Si fertigation in leaves and stems (Fig. 5a and 5b). Furthermore, N concentration and content were associated with AWD without Si fertigation in leaves and stems (Fig. 5a and 5b).

For Eutrophic Red Oxisols, the cluster analysis indicated a greater similarity of P and Si concentrations, C, P, and Si contents, C and N efficiencies, and dry mass to AWD fertigated with Si in leaves (Fig. 5c), while in stems there was a greater association of P and Si concentrations, C, P, and Si contents, C, N, and P use efficiencies, C:N stoichiometric ratio, and dry mass to AWD fertigated with Si (Fig. 5d). For PWD without Si fertigation, there was a greater association of C concentration and C:P and N:P stoichiometric ratios in leaves and C and N concentrations, C:P stoichiometric ratios, and C:Si and N:P in stems (Fig. 5c and 5d). Furthermore, the P use efficiency and the C:N ratio were associated with PWD fertigated with Si and the concentration, and the content of N and C:Si ratio were associated with AWD without Si fertigation in leaves (Fig. 5c).

In AWD fertigated with Si in Dystrophic Red Oxisols, there was an association with P and Si concentrations, C, P, and Si contents, C and N use efficiencies, C:N stoichiometric ratio, and dry mass in leaves and stems (Fig. 5e and 5f). For AWD without Si fertigation, there was an association between N and C concentrations, N content, and P use efficiency in leaves, while in stems there was an association between P use efficiency and N content (Fig. 5e and 5f). Finally, for PWD without Si fertigation, the stoichiometric ratios C:P, C:Si, and C:Si in leaves and the concentrations of C and N and the stoichiometric ratios C:P, C:Si, and C were associated with Si in stems (Fig. 5e and 5f).

2.5.2 Principal component analysis

Principal component analyses (PCA) of leaves explained 95.4, 97.0, and 99.3% of the variable responses of sugarcane cultivated in Quartzipsamments, Eutrophic Red Oxisols, and Dystrophic Red Oxisols, respectively (Fig. 6). For stems, the PCA explained 98.6, 98.0, and 97.6% in cultivation on Quartzipsamments, Eutrophic Red Oxisols, and Dystrophic Red Oxisols (Fig. 6).

In Quartzipsamments, the PCA of leaves indicated an association of C and N concentrations and stoichiometric ratios C:P, C:Si, and N:P to AWD and PWD without Si fertigation and C and N contents to AWD with absence and presence of Si fertigation, while P content, C and N use efficiency, and dry mass production associated with Si fertigation in AWD (Fig. 6a). Also, P and Si concentrations, Si content, and dry C:N ratio associated with Si fertigation in both water conditions (Fig. 6a). For stem, the PCA indicated an association of C and N concentrations to AWD and PWD without Si fertigation and the stoichiometric ratios C:P, C:Si, and N:P to PWD without Si fertigation. The stoichiometric ratios C:P, C:Si, and N:P, Si concentration and content, and C:N ratio associated with AWD and PWD with Si fertigation (Fig. 6b). Furthermore, C, N, and P contents, C, N and P use efficiencies, P concentration, C:N ratio, and dry mass associated with AWD with the absence and presence of fertigation with Si (Fig. 6b).

For Eutrophic Red Oxisols, regarding the response variables in leaves, C and N concentrations and the N:P ratio associated with PWD with the absence and presence of fertigation with Si, and the N content associated with PWD fertigated with Si, while the stoichiometric ratio C:Si associated with the two water conditions with the absence of fertigation with Si (Fig. 6c). It also showed that the highest concentration and content of Si associated with AWD fertigated with Si, and that the C:P ratio associated with PWD without Si fertigation (Fig. 6c). Additionally, P concentration, C and P contents, C, N, and P use efficiency, C:N ratio, and dry mass production associated with AWD with the absence and presence of Si fertigation (Fig. 6c). In stems, the PCA showed association of C:P, N:P, and C:P ratios and N concentration to PWD with the absence and presence of fertigation with Si, and the concentration of Si, P and Si contents, and the C:N ratio associated in AWD with Si

fertigation (Fig. 6d). Also, the PCA showed that the highest C concentration associated with PWD without fertigation with Si, and the highest N content associated with AWD fertigated with Si (Fig. 6d). Furthermore, P concentration, C content, C, N, and P use efficiency, and dry mass associated with AWD with the absence and presence of fertigation with Si (Fig. 6d).

For the PCA of response variables in leaves of sugarcane cultivated in Dystrophic Red Oxisols, there was an association between the concentrations of N and C and the stoichiometric ratios of C:P, C:Si, and N:P to PWD and AWD in the absence of Si fertigation. Also, the concentration and content of Si and the C:N ratio also associated with the two water conditions, however with the presence of Si fertigation (Fig. 6e). It also showed that C, N, and P use efficiencies, C, N, and P contents, P concentration, and dry mass production associated with AWD in the absence and presence of Si fertigation (Fig. 6e). The PCA of stem response variables indicated an association of the stoichiometric ratios N:P, C:P, C:Si and the concentration of C to PWD in the absence of fertigation with Si; it also indicated an association of the concentration of N to PWD in the absence and presence of Si fertigation (Fig. 6f). The PCA of stem response variables also evidenced an association of P and Si concentrations and Si content to AWD in the presence of Si fertigation, and the association of N content and P use efficiency associated to AWD in the absence of Si fertigation (Fig. 6f). Moreover, C and N use efficiency, C and P contents, and other above dry mass also associated with AWD in the absence and presence of Si fertigation (Fig. 6f).

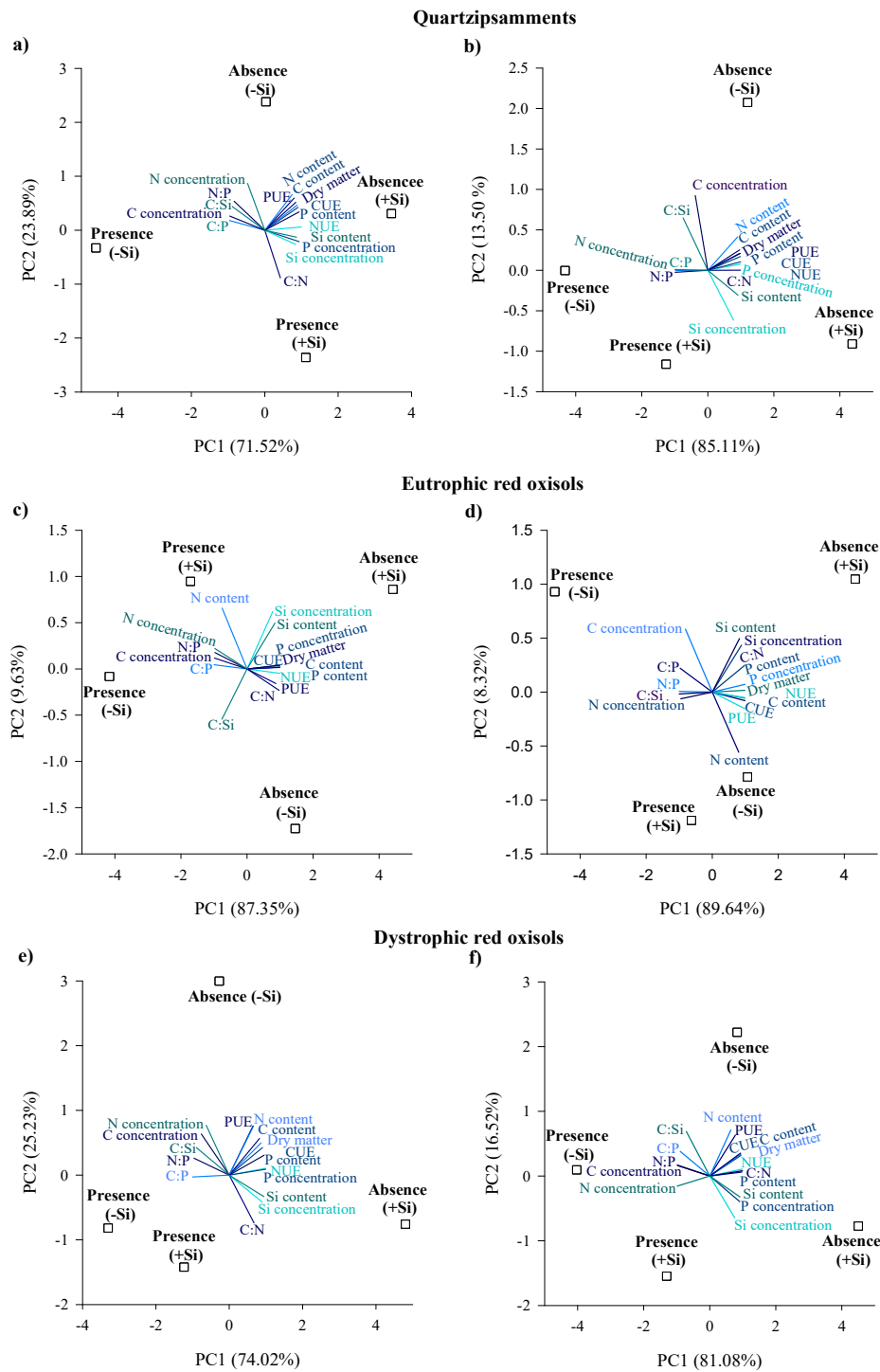


Figure 6. Principal component analysis of variables related to concentrations and accumulations of C, N, P, and Si, stoichiometric ratios of C:N:P:Si, use efficiency of C, N, and P and dry mass partition in leaves (a, c, e) and stems (b, d, f) of sugarcane plants in two water deficit conditions (presence: 35%, and deficit: 70% of water retention) combined with absence (0.0 mmol L⁻¹) and presence of fertigated Si (1.8 mmol L⁻¹) in three tropical soils (Quartzarenic Neosol; Eutroferic Red Latosol; and Dystrophic Red Latosol). CUE: C use efficiency; NUE: N use efficiency; PUE: P use efficiency.

3 Discussion

3.1 Biological damages of water deficit to sugarcane ratoon without Si supply

Losses by water deficit in sugarcane crops have already been related to the increase in water loss in tissues, which induces oxidative stress and decreases photosynthetic rates (Bezerra et al. 2019). However, recent studies have shown nutritional damage especially in the homeostasis of nutrients with a vital structural function for plant growth (Oliveira Filho et al. 2021b; Teixeira et al. 2020).

In this research, we showed that water deficit changes the homeostatic balance of C:N:P, which occurs due to the decrease in the C:N ratio in stems and the increase in the stoichiometric ratios C:P and N:P in leaves and in stems in three tropical soils (Fig. 1 and 2). Additionally, water deficit reduced the stoichiometric ratio C:N in leaves of sugarcane plants cultivated in Eutrophic Red Oxisols and decreased the stoichiometric ratio C:Si in sugarcane plants cultivated in Eutrophic Red Oxisols and Dystrophic Red Oxisols. In regrowth of *Panicum maximum*, there was also a loss in the stoichiometric ratio C:N, reducing the concentration of C and causing instability in the metabolism of the culture (Rocha et al. 2022a). However, it was verified in plants of the first cycle of *Panicum maximum*, that the impact of the water deficit may not alter the C:N stoichiometry ratio, as observed for the cultivar Masai, while for the BRS Zuri cultivar, the C:N ratio was change (Rocha et al. 2022b). These facts show that the impacts of the water deficit can change depending on the cultivar in the first cycle, however, in the second cycle (stubs or regrowth), this tolerance is lost. The results of our research reinforce that the deficit impacts are more severe in stumps, directly impacting C:N:P homeostasis.

These alterations in the homeostatic balance of C:N:P caused by water deficit result in direct implications to the concentrations of these elements, causing a clear decrease in the C, N, and P contents of the plant (Tables 1 and 2). This decrease in N and P absorption in most of the studied soils (Table 2) and a deficient water regime possibly happens due to the mobility of nutrients in the soil, which reduces their diffusion until reaching the surface of roots and their entry into the plant (Ahanger et al. 2016). Water deficit also induces a reduction in the transport of nutrients from plant roots to shoots due to a decrease in the transpiration rate, which changes the

efficiency of transporters (Silva et al. 2011). In addition, water deficit, by decreasing the redistribution of nutrients in plants, impairs the internal cycling of nutrients (Gerloff and Gabelman 1983), aggravating the homeostatic balance C:N:P, and causes direct effects on the reduction in the use efficiency of C, N, and P (Fig. 3 and 4). This results in losses of dry mass in leaves and in stems in all three tropical soils studied (Fig. 4c and 4d).

Therefore, our results prove that the disturbances caused by water deficit in relation to the plant that receives an adequate irrigation have a strong nutritional component that causes an imbalance of C:N:P, impairing nutritional efficiency and consequently contributing to productive loss of sugarcane crops. It is quite clear that the loss of elementary stoichiometric homeostasis of sugarcane caused by water deficit paves the way for future specific studies on proteomics involving the cycling of the nutrients C, N, and P seeking to better understand the underlying effects of water stress on this species.

3.2 Biological contribution of Si in sugarcane ratoon with deficient irrigation

Studies with application of Si via fertigation in sugarcane crops with deficient irrigation are restricted (Costa et al. 2022; Oliveira Filho et al. 2021a, b; Teixeira et al. 2020, 2022). This raises concerns, as it may decrease the absorption of Si depending on the soil and restrict its biological benefits in the plant.

This problem did not occur in this study, as we showed that fertigation with Si in sugarcane plants, in relation to its absence, is efficient in increasing the concentration and content of Si in leaves and stems in all three tropical soils even with irrigation deficit (Tables 1 and 2). This is because sugarcane plants have efficient Si transporters (Wang et al. 2021).

Such increases in Si content in sugarcane plants due to fertigation with Si in relation to the absence of Si application are sufficient to reduce the nutritional imbalance water deficit causes. This occurs because the use of Si increases the C:N stoichiometric ratio in leaves of plants grown in Quartzipsamments and Eutrophic Red Oxisols and decreases the C:P, C:Si, and N:P ratio in leaves and stems in all three tropical soils (Fig. 1 and 2). These changes in C:P:N stoichiometry induce a

new homeostatic equilibrium, tending to reestablish stoichiometric relationships similar as those of sugarcane plants grown in an adequate water regime.

The induction of a new homeostatic balance of C:N:P caused by Si under water deficit conditions also occurs in 30-day pre-sprouted seedlings (Teixeira et al. 2020), and 90-days (Oliveira Filho et al. 2021a), 150-days (Costa et al. 2022) and 160-days (Teixeira et al. 2022) sugarcane plants. The induction of a new C:N:P homeostasis is not only restricted in sugarcane plants, but has also been observed in forage (Rocha et al. 2022b, a), quinoa (Lata-Tenesaca et al. 2021), wheat (Neu et al. 2017), sorghum and sunflower (Carvalho et al. 2022; Hurtado et al. 2020). This helps to consolidate another benefit of Si in the cultivation of sugarcane that also occurs in sugarcane ratoons, but it is not restricted only to this crop. At this crop stage, little is known about the effects of homeostatic changes in C:N:P in sugarcane and mainly its implications to the production of biomass in stalks in different tropical soils. In this scenario, stoichiometric modifications change ecological interactions due to stress, but the supply of Si is effective to contribute to reverse this stress, maintaining optimized biological and biochemical functions of nutrients in agroecosystems (Prado and Silva 2017).

This stoichiometric homeostasis caused by Si generated another benefit to the supply of Si in sugarcane crops with water deficit, as it increased the contents of C, N, and P in sugarcane plants cultivated in all three tropical soils (Table 2). Si positively affects N and P nutrition, increasing the efficiency of NH_4^+ transporters (OsAMT), stimulating NO_3^- expression (BnaNTR2.1), increasing gene expression related to inorganic phosphorus (Pi) uptake and upregulating the gene coding of Pi transporters (TaPHT1;1 and TaPHT1;2) (Pavlovic et al. 2021). Furthermore, there are several reports that under conditions of low N availability, there was an increase in the concentrations of this nutrient in the presence of Si, indicating the synergistic effect of the two elements (Cuong et al. 2017; Deus et al. 2020; Mabagala et al. 2020; Mali and Aery 2008; Pati et al. 2016). In quinoa, it was shown that Si's role in controlling the C flux modified N and P concentrations, increasing the concentrations of these nutrients (Lata-Tenesaca et al. 2021). Moreover, this homeostasis promoted by Si also increased the use efficiency of these nutrients in leaves and stems in the three soils studied, except for P in Dystrophic Red Oxisols (Fig. 3). Thus, it is

possible that the stoichiometric change, such as the decrease in the C/Si ratio, as mentioned above, due to the absorption of Si by the crop under deficient irrigation, may contribute to explain the increase in the use efficiency of C. This is because, according to Kim et al. (2007)(Kim et al. 2007), plants can employ strategies of using Si to replace C in the cell wall, providing lignin-like structural strength.

The biological role of Si in replacing C in cell walls also contributes to changing the metabolism of N and P, as there is an improvement in the photosynthetic apparatus, consequently increasing the photosynthetic rate of plants, reducing the concentration of C and increasing the concentrations of N and P (Frazão et al. 2020). Possibly, there is a multiple effect of Si on N metabolism, but not yet fully elucidated. New studies understanding the mechanisms of Si in the modification of N metabolism are still necessary, mainly of the implication of Si in the homeostasis of nutrients, not knowing until now, the proportions of modification of this beneficial element in the metabolism of nutrients and its implications in the sustainability of agricultural systems.

The beneficial interaction of P and Si is possible to occur in two ways of acting resulting in the improvement of the metabolism of P, being the improvement of the efficiency of absorption and the increase of the efficiency of use by the tissues (Pavlovic et al. 2021). In fact, several reports are found in the literature on stressed plants the beneficial effect of Si in increasing the P concentration (Costa et al. 2022; Hu et al. 2020a). Evidence indicated that Si improves the absorption of P by increasing the biosynthesis of exudates, such as malate and citrate, which have the role of competing with P for adsorption sites or, even, forming complexes of Al and Fe, increasing the availability of P in the soil solution (Hu et al. 2020a; Kostic et al. 2017).

The results indicate the importance of C, N, and P homeostasis in reaching a stabilization to optimize the metabolism of these nutrients and, consequently, increase the capacity of plants to convert nutrients into biomass (Prado 2021). This fact was confirmed here since the using Si in plants under water deficit promoted an increase in the biomass content of leaves and stems in all three soils studied.

Thus, it is evident that Si can attenuate the water deficit in sugarcane in the studied soils. However, as multivariate analysis showed, it was possible to detect

additional information showing that the level of such mitigation was more intense in one type of soil than in the others (Fig. 5). The response in terms of stem production of the crop grown under water deficit that received Si was similar as that of plants with an adequate irrigation (in the absence of Si), but this only occurred in Eutrophic Red Oxisols. In other words, in the other soils, Si did not induce such a high performance in plants. This result highlights the agronomic importance of using Si in sugarcane cultivation in Eutrophic Red Oxisols, indicating that it is possible to completely reverse the decreases in productivity by cultivating with irrigation deficit by equaling an adequate irrigation. This indicates that the efficiency of silicate fertilization is influenced by soil type, showing the importance of considering the mineralogical composition, texture, contents of Fe and Al oxides, and soil organic matter (Camargo and Keeping 2021), in addition to the levels of available Si in the soil. The intensity of the beneficial effects of Si under water deficit changes according to edaphic characteristics. Consequently, the intensity of modification of the homeostatic balance C:N:P increased, especially the C:N ratio of 9, 18, and 4% for Quartzipsamments, Eutrophic Red Oxisols, and Dystrophic Red Oxisols, respectively (Fig. 1 and 2). This greater intensity of modification of this stoichiometric ratio in Eutrophic Red Oxisols may have contributed to the greater benefit of Si in attenuating the deleterious effects of water deficit.

It was clear that our results are sufficient to confirm the second hypothesis, i.e., the results indicate that the using Si can modify the stoichiometry of C:N:P and mitigate the damage caused by water deficit by improving the nutritional efficiency of these nutrients, which in turn affects the productivity of sugarcane ratoon cultivated with deficient irrigation in the three soils studied. It is possible that the impact of Si on nutritional stoichiometry is driven by two paths, the first being the increase in the efficiency of nutrient use and, the second, the activation of physiological mechanisms that increase the efficiency of nutrient absorption, however, this needs to be proven.

Therefore, this research shows concrete indications that contribute to the sustainability of sugarcane cultivation in irrigated systems with water deficit by using Si, exerting an environmental implication due to the decrease in water use. This is important, as the water demand for irrigated systems is expected to increase in the

coming years (Wrachien et al. 2021), in addition to the costs, especially of electric energy (Raza et al. 2022b).

3.3 Biological contribution of Si in improving the performance of sugarcane ratoon with adequate irrigation

Fertigation with Si in an adequate water regime, in relation to its absence, improved Si absorption and increased the concentration and contents of Si in leaves and stems of sugarcane plants cultivated in the three tropical soils (Tables 1 and 2). The greater absorption of Si by sugarcane plants occurs because of a greater transpiration. Consequently, the mass flow of nutrients increased due to a greater availability of water in the soil (Cramer et al. 2009). The higher water supply to plants that received Si in relation to its absence allowed increasing the Si content in leaves by 5.5, 4.5, and 3.0 times in plants grown in Quartzipsamments, Eutrophic Red Oxisols, and Dystrophic Red Oxisols, respectively (Table 2). This indicates a greater recovery of Si applied to plants grown in Quartzipsamments in relation to the other soils possibly due to the lower adsorption of anionic Si in this soil, although Si may be more mobile in this soil, especially in water regimes more voluminous than the one studied, that is, 70% of the water retention capacity.

The greater efficiency of Si fertigation resulted in the alteration of the homeostatic balance C:N:P, which was evidenced with the increase in the C:N ratio only in stems, which in turn indicates a lower demand of C per unit of N, i.e., a preliminarily better use of N in the metabolism of stress-free plants. In addition, the use of Si caused a decrease in C:P, C:Si, and N:P ratios in leaves and stems of sugarcane plants cultivated with adequate irrigation in the three tropical soils. This may indicate a greater demand of metabolism of P and Si (Fig. 1 and 2).

Therefore, the results prove these beneficial effects of Si in sugarcane plants with adequate irrigation because causing a homeostasis of C:N:P directly promotes an increase in the use efficiency of these nutrients. The effects of a greater efficiency in the use of N and P contribute to increase the performance of their metabolic functions that are involved with the composition of vital organic compounds for physiological processes (Prado 2021), thus contributing to increase the use efficiency

of C. Changes in the primary metabolism of plants caused by Si may induce a greater redistribution of amino acids to the draining tissues and increase the use efficiency of N (Detmann et al. 2012a, b) and the use efficiency of P (Teixeira et al. 2020).

In addition, noteworthy was an increase in the use efficiency of C also associated with a decrease in the stoichiometric ratio C:Si. This may occur because there are reports that Si can replace C in organic compounds with low metabolic costs if compared to that of C, generating ten to 20 times less metabolic energy for incorporation into organic molecules (Xia et al. 2020). In plants grown under stress, this can also occur, as indicated above, but in plants without stress there is a tendency for this energy balance to be directed towards the synthesis of biomass and consequently in crop productivity. This is due to the optimization of C metabolism, which increases the production of organic compounds, including C skeletons and structural nutrients such as N and P (Viciedo et al. 2019b). Therefore, the findings prove the importance of Si in the nutrition of stress-free sugarcane plants grown in different tropical soils. This reinforces the finding that Si is important not only to plants under stress, but also to plants under no stress (Cooke and Leishman 2016b; Frazão et al. 2020). Our research contributes to the thesis that this occurs due to Si role in C, N, and P homeostasis, which is little reported in the literature.

The better performance of plants induced by fertigation with Si and by favoring nutritional efficiency of C, N, and P directly reflects on the synthesis of biomass of leaves and stems, as observed in the three tropical soils studied here (Fig. 4c and 4d). The PCA analysis reinforces that dry mass biosynthesis is completely related to increased C use efficiency in the three tropical soils cultivated with adequate irrigation (Fig. 6).

The benefit of Si in improving nutrient uptake and use efficiency was also evidenced in sorghum and sunflower plants, resulting in improved nutritional efficiency (Hurtado et al. 2019). In wheat plants, it evidenced the role of Si in promoting the improvement of P nutrition, proposing a possible allocation of P to the reproductive organs to the detriment of the vegetative organs, consequently, increasing grain production (Neu et al. 2017), consequently increasing the efficiency

of P use. This is due to Si replacing parts of the C compounds (Schaller et al. 2012a), allowing allocation of energy resources.

The results of this research allow us to accept the third hypothesis, since the use of Si in sugarcane plants cultivated using adequate irrigation by increasing the element content in the plant is enough to modify the stoichiometric ratio C:N:P, thus increasing the efficiency of metabolism in increasing the use efficiency of C, N, and P and consequently the production of sugarcane biomass.

In general, deficient irrigation with no Si supply causes biological damage to sugarcane ratoons because Si can induce the loss of stoichiometric C:N:P homeostasis, which is responsible for reducing the use efficiency of these nutrients in sugarcane ratoon cultivated in all three tropical soils. However, it is possible to cultivate sugarcane under deficient irrigation because the use of fertigation with Si can mitigate losses, as it stabilizes the stoichiometric ratio C:N:P in a way that increases the efficiency of nutrient use and sustains the production of dry mass of sugarcane ratoon. However, the type of cultivation soil affects the intensity of Si benefits. In addition, these Si benefits repeated in plants with adequate irrigation, indicating that the effects of Si also happen in non-stressed plants.

Our finding, i.e., identifying that Si modulates the stoichiometric homeostasis of C:N:P, which directly interferes with the nutritional efficiency of these nutrients in sugarcane ratoon cultivated in different tropical soils, opens new paths for a sustainable cultivation of sugarcane under different water regimes. Therefore, this finding should greatly increase the use of Si in sugarcane crops, producing global implications, as it will be useful in many regions with a regular precipitation or irrigated areas and in regions with irregular precipitation or irrigated areas with low water availability.

4 Methods

4.1 Experimental area and weather conditions

Three experiments were carried out in a greenhouse at São Paulo State University Júlio Mesquita Filho (UNESP), Jaboticabal (Brazil), using the variety RB 962860 of sugarcane in three tropical soils: Quartzipsamments (NQ), Eutrophic Red Oxisol (LVe), and Dystrophic Red Oxisol (LVd). During the conduction of the study,

meteorological data, maximum temperature (48.4 ± 5.1 °C), minimum temperature (27.4 ± 3.4 °C), and relative air humidity (55.7 ± 9.2 %) at the site of the experiments were monitored daily using a thermo-hygrometer (Figure 7).

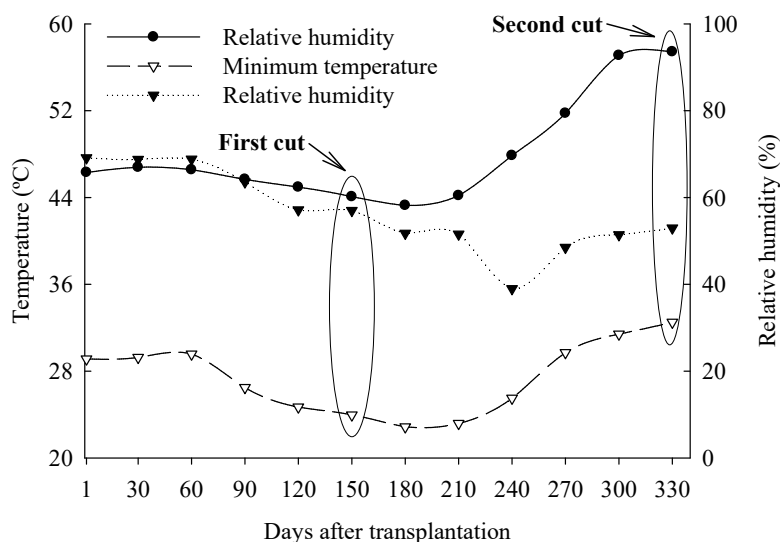


Figure 7. Air temperature and relative humidity during the experimental period.

4.2 Experimental design and installation

The treatments were arranged in a 2×2 factorial design in randomized blocks. There were three experiments with two water conditions, with deficient and adequate irrigation corresponding to 35 and 70% of the soil water retention capacity, combined with the absence (0.0 mmol L^{-1}) and the presence of Si (1.8 mmol L^{-1}) applied via fertigation in five replications. The experimental plot was characterized by pre-sprouted sugarcane seedlings at 60 days of age, after sprout emergence, in polypyrène pots with a volume of 20 L, filled with 18 L of soil sample. Sugarcane seedlings of the RB 962869 variety were purchased from a certified commercial plant nursery. The pre-sprouted seedlings, during production and throughout their growth, did not receive Si application. After transplanting, plants were pruned at 0.3 ± 0.02 m from the soil surface. The experiment was carried out in two cultivation cycles (plant cane and ratoon cane), of 150 days each. At the end of the first cultivation cycle, the plants were cut at 0.1 m from the soil surface; later, in the second cycle of cultivation, they were cut again after the new sprouting of plants (15 days after the cut).

Soil chemical analysis was performed before transplantation to characterize the chemical attributes (Raij et al. 2001), particle size (Donagema et al. 2011), and determination of the Si concentration (Korndorfer et al. 2004) (Table 3). Soil texture was characterized as sandy, loamy, and sandy loamy in Quartzipsamments, Eutrophic Red Oxisol, and Dystrophic Red Oxisol, respectively. Subsequently, liming was performed 45 days before transplantation using the base saturation method (V%), seeking to correct the saturation to 60% (PRNT = 125%, CaO: 48%; MgO: 16%) (Raij et al. 2001). After 30 days of soil incubation, phosphate fertilization was carried out; during transplantation, nitrogen, potassium, and micronutrient fertilization were applied through fertigation, with N (urea – 45% N), K (potassium chloride – 60% K₂O), and micronutrient fertilization (boric acid – 17% B - and zinc sulfate – 56% de Zn) in the second cycle after cutting the stems of the first crop cycle. Cover N and K fertilization were also performed 76 days after transplantation in the first cycle and 76 days after cutting the stems in the second cultivation cycle.

Table 3. Chemical characteristics of Quartzipsamments (NQ), Eutroferic Red Oxisols (Lve) and Dystrophic Red Oxisols (LVd)

Soil	pH	OM	P	S	K	Ca	Mg	Al	H+Al	CEC	V	m	Si	clay	silt	sand
	CaCl ₂	g dm ⁻³	mg dm ⁻³		-----		mmolc dm ⁻³	-----		-----	%		mg kg ⁻¹		g kg ⁻¹	
NQ	4.3	9	2	6	0.3	3	1	0	16	20.0	21	0	1	50	10	940
Lve	6.2	8	8	8	1.0	16	5	0	17	38.6	57	0	5	550	240	210
LVd	5.2	9	20	7	1.2	14	6	0	22	44.2	49	0	3	300	40	660

CEC: Cation exchange capacity; V: base saturation; m: aluminum saturation; pH: CaCl₂ by potentiometry; H+Al: SMP buffer by potentiometry; O.M.: organic matter by spectrophotometry; P: in resin by spectrophotometry; S: by turbidimetry; K, Ca and Mg: atomic absorption spectrometry; Si: 0.01 M calcium chloride.

4.3 Irrigation management

To determine the soil water retention capacity, lysimeters (20-L pots) were used with a soil sample (18 L) in three replications for each experiment and placed in a 250-L water tank filled with water up to 2/3 of the height of lysimeters for a period of 24 h. The surface of lysimeters were insulated with plastic film. After a period of 24 h, the lysimeters were freely drained, and their masses were evaluated at 0, 24, 36, 48, 60, and 72 h to determine water replacement capacity by the difference in wet and dry soil masses. Subsequently, the gravimetric and volumetric moistures were estimated, as well as soil density and gross irrigation depths of the treatments (Bernardo et al. 2019). Then, two lysimeters were installed in each experiment with

two levels of water retention (35 and 70% of the retention capacity). The mass was measured daily using load cells (model GL 50; Alfa Instrumentos Eletrônicos SA). Data were stored in a datalogger (CR10X Campbell Sci., Logan – USA). The datalogger data were extracted using the PC200W software, maintaining the soil moisture retention levels stable manually every two days for a period of 6 to 18 h.

The water retention level was kept at 70% of the water retention capacity in the two treatments after transplantation. Water deficit began at 30 days with a reduction of the retention capacity to 50% and, after seven days, to 35%. Subsequently, the measurement of masses of lysimeters was performed every two weeks using a digital scale and, whenever necessary, adjusted for possible variations in mass.

4.4 Fertirrigation with silicon

The application of Si was carried out via fertigation with an interval of two days using sodium and potassium silicate stabilized with sorbitol at a concentration of 0.0 and 1.8 mmol L⁻¹ (113.4 g L⁻¹ of Si, 18.9 g L⁻¹ of K₂O, 100 mL L⁻¹ of sorbitol, and pH = 11.8). The pH of the solution was adjusted to 6.0 ± 0.5 using a HCl solution (1 mmol L⁻¹) and a NaOH solution (1 mmol L⁻¹). Potassium balancing was performed in experimental plots without fertigation with Si (0.0 mmol L⁻¹), adding KCl in the fertigation solution (8.43 mg L⁻¹ of K). To determine the amount of solution with Si in the irrigation, the amount of water lost by evapotranspiration was measured in an interval of two days. To avoid a greater supply of Si in treatments with no water deficit, the amount of replacement of water loss through evapotranspiration in treatments with water deficit was used as a reference, adjusting this amount to a concentration of 1.8 mmol L⁻¹. Therefore, the replacement of water required by evapotranspiration in the water deficit treatments was carried out entirely by the solution with Si, while the treatments in the absence of water deficit were reconstituted by the solution with Si and deionized water.

4.5 Experimental evaluations

After 150 days of sugarcane plant sprouting, a cut was carried out 0.1 m from the soil surface of plant shoots, separating it into leaves and stems. The samples

were washed under running water, detergent solution (0.1% v/v), HCl solution (0.3% v/v), and deionized water. Then, they were dried in a forced air circulation oven (65 ± 5 °C) until constant mass. Then, the dry mass of leaves (MSF) and stems (MSC) were determined. Subsequently, the determination of C, N, P, and Si concentrations in MSF and MSC samples was carried out. The determination of C and N were calculated from the dry combustion (1000 °C) in an elemental analyzer (LECO truspec CHNS) calibrated with the standard LECO 502-278 (C = 45.00%). The determination of P was carried out from the nitric-perchloric digestion and the reading was performed by colorimetry (ammonium metavanadate method) (Carmo et al. 2000). Finally, Si was determined from alkaline digestion and the reading was conducted by colorimetry with ammonium molybdate (Korndorfer et al. 2004).

The stoichiometric ratios of leaves and stems were calculated from the quotient of the concentrations of C:N, C:P, N:P, and C:Si and the contents of C, N, P, and Si were estimated from the product of the element concentration and the dry mass. Finally, the use efficiency of C, N, and P were calculated by the ratio of the square of the dry mass and the nutrient content (Siddiqi and Glass 2008).

4.6 Data processing and statistical analysis

Data processing was performed using the Python programming language (v. 3.9.7; Python Software Foundation). Tixon outliers test was performed, when outliers were found, the value was eliminated, and the new value was estimated by the technique of partial derivatives. Subsequently, normality (Royston 1995) and homogeneity tests (Gastwirth et al. 2009) were performed. After preposition tests, an analysis of variance was performed ($p < 0.05$). When significant, results were submitted to Tukey test ($p < 0.05$). Multivariable analyses of hierarchical clusters were conducted and principal components analysis (PCA) was performed. The cluster analysis was based on the similarity coefficient of the Euclidean distance and the connection of the group by the single linkage method. The PCA was determined by the matrix of correlation.

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CHAPTER 4 – Final considerations

Understanding the silicon (Si) effects on sugarcane cultivation under different soil and water conditions can improve crop yield, thus enhancing food security in the face of climate change. The first chapter of this dissertation aimed to elucidate the mechanisms by which Si modifies plant responses to abiotic stress, highlighting the beneficial role of this element in modifying C, N, and P homeostasis, improving nutrient use efficiency, and reducing yield losses under adverse conditions. The second chapter focused on nutrient homeostasis of C, N, and P, as well as leaf and stem dry mass accumulation in tropical soils with different water regimes. This study revealed that Si addition improved nutrient homeostasis and leaf and stem dry mass accumulation, especially in soils with lower water availability. The third chapter focused on the stoichiometric modifications of C, N, and P and the yield of sugarcane regrowth in soils with different textures and fertilities under different water regimes. It was found that Si addition increased sugarcane regrowth biomass production in all soils studied, but the effects were more pronounced in soils with low fertility and sandy textures. Together, these studies suggest that Si addition can be beneficial for sugarcane production under adverse conditions, including soils with low fertility and limited water regimes. These results may have important implications for sustainable agriculture and food security in regions that depend on sugarcane production.

The study of Si use in sugarcane production reveals it as a multi-stress mitigator, reducing damages caused by water deficit in all three tropical soils and also capable of reducing damages caused by harvesting. The results of the third chapter of this dissertation show that sugarcane ratoon plants benefit from Si application in the absence of water deficit, modifying C, N, and P homeostasis, increasing nutrient use efficiency, and boosting leaf and stem biomass production in all three tropical soils. In this scenario, Si use may contribute to sugarcane regrowth, potentially increasing the longevity of sugarcane fields, but this needs to be confirmed.

The use of Si in consecutive sugarcane cycles can also modify plant tolerance over time, especially in regions with low water availability. Additionally, the continuous use of Si in crops contributes to increasing the amount of available Si in

tropical soils, making the benefits of Si more evident in subsequent cycles of this crop.

The use of Si can improve the yield and profitability of sugarcane production under different soil and water conditions. The results of our study can help producers identify the conditions in which Si application is most beneficial. Additionally, further studies are needed to investigate whether silicon application can improve the quality of sugarcane by increasing sucrose content and crop profitability, as well as whether it can enhance plant resistance to diseases and pests, promoting more sustainable cultivation practices.

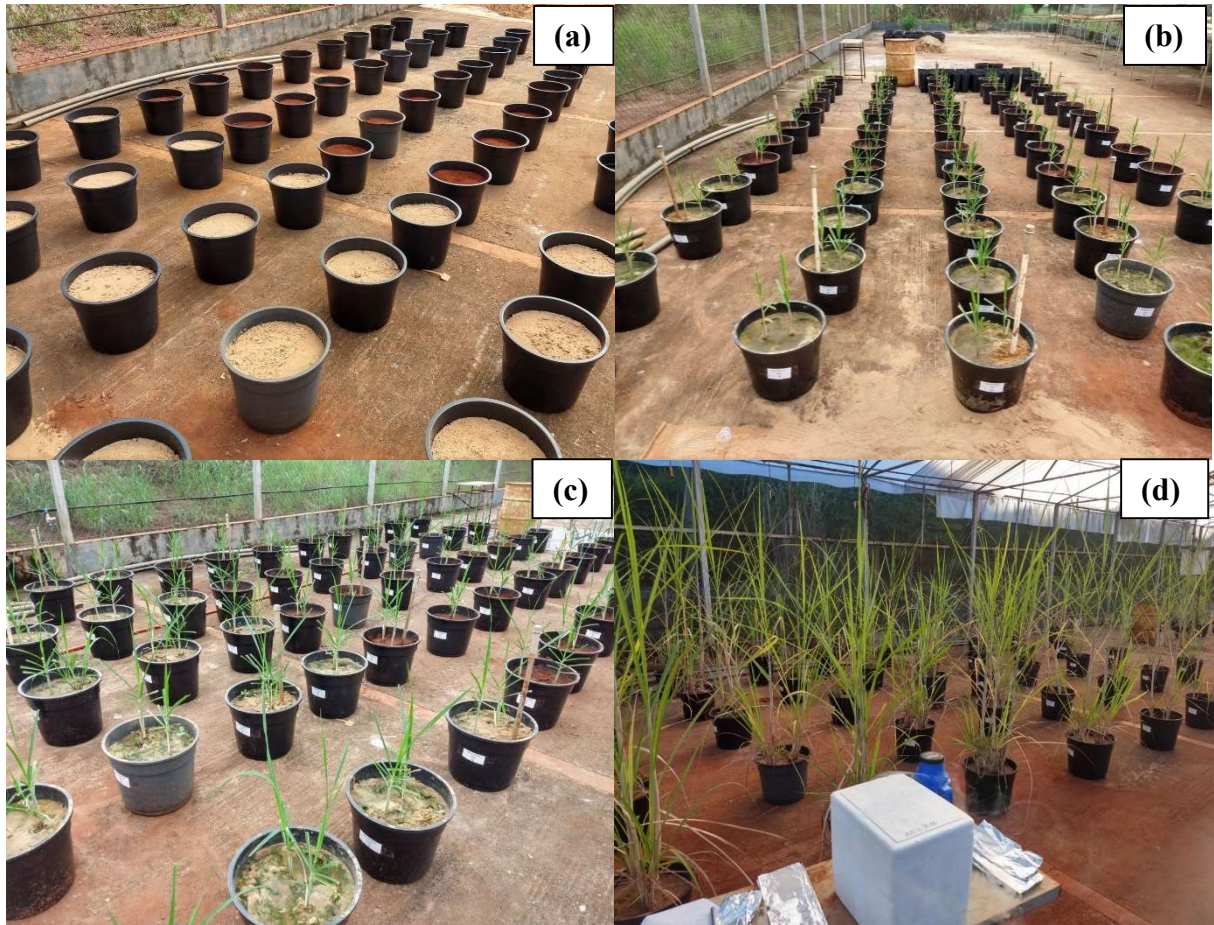
Studies on the effect of Si on sugarcane production under different soil and water conditions provide a solid foundation for future research. There are several future perspectives for the present studies, which include understanding the molecular mechanisms underlying the effect of silicon on sugarcane, including how silicon affects plant metabolism. Future studies can use advanced molecular biology techniques to identify the genes involved in the sugarcane response to silicon. Another important aspect to advance in understanding water stress is the identification of sugarcane varieties that are more resistant to this stress associated with the use of Si, which can significantly reduce the deleterious effects of water deficit and can be an important area for future research. Additionally, further studies are needed to test different cultivars and recommend the application of the element in more responsive cultivars.

The findings of these studies can be used to develop more effective management practices for sugarcane production, with the aim of improving crop yield and quality. The use of Si opens up a new path of research, allowing for increased water use efficiency in sugarcane production systems, highlighting the need for further studies to indicate the amount of water that can be saved with the use of Si. The innovative practice of Si use via fertigation will allow for a reduction in water use for sugarcane production, maximizing the efficient use of this resource and ensuring greater sustainability of production systems.

Future studies can evaluate the effectiveness of adding silicon to different soil types and climatic conditions to adopt the practice of silicate application in more promising situations.

Therefore, there are many future perspectives for studies on the effect of silicon on sugarcane production in a more sustainable way, which reduces environmental impact and promotes the production of healthy and high-quality food.

APPENDIX



Appendix 1. Experimental units arranged in the greenhouse prior to sugarcane seedling transplanting (a), sugarcane seedlings after sugarcane transplanting (b, c, d).