UNIVERSIDADE ESTADUAL PAULISTA - UNESP
CÂMPUS DE JABOTICABAL

FERTIRRIGAÇÃO COM SILÍCIO EM CAPIM ZURI CULTIVADO SOB ESTRESSES DE FÓSFORO E DE NITROGÊNIO EM DOIS SOLOS TROPICAIS

Cintia Carmen de Faria Melo
Engenheira Agrônoma

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Orientador: Prof. Dr. Renato de Mello Prado

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Tese apresentada à Faculdade de Ciências Agrárias e Veterinárias – Unesp, Câmpus de Jaboticabal, como parte das exigências para a obtenção do título de Doutora em Agronomia (Ciência do Solo).

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Impacto potencial desta pesquisa

Impulsionar a produção de alimentos de origem animal como carne e leite por contribuir para a melhoria nutricional em silício, nitrogênio e fósforo das pastagens, para uma maior conservação do solo e da água e uso racional de fertilizantes em conformidade com o objetivo de desenvolvimento sustentável 2 (ODS 2 – Fome zero e agricultura sustentável).

Potential impacto of this research

Boost the production of foods of animal origin such as meat and milk by contributing to the nutritional improvement in silicon, nitrogen and phosphorus of pastures, for greater soil and water conservation and rational use of fertilizers in accordance with the sustainable development objective 2 (SDG 2 – Zero hunger and sustainable agriculture).

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DADOS CURRICULARES DA AUTORA

CINTIA CARMEN DE FARIA MELO, nascida em Xinguara – PA, em 23 de julho de 1993, filha de Maria Cármen de Melo e José Olímpio de Melo. Possui título de Engenheira Agrônoma (2017) pela Universidade Federal de Viçosa – *Campus* Rio Paranaíba, MG. Durante a graduação desenvolveu pesquisas na área de fertirrigação de pastagens sob orientação do Prof. Dr. Luís César Dias Drumond, foi bolsista de iniciação científica entre 2015 e 2016 estudando a microbiologia do solo de pastagem sob aplicação de efluentes. Participou de programas de iniciação à docência como monitora de Organografia e Sistemática Vegetal. Em junho de 2019, obteve o título de Mestra em Agronomia pelo programa de Pós-Graduação em Agronomia (Produção Vegetal), na Universidade Federal de Viçosa (UFV), *Campus* Rio Paranaíba, sob orientação do Prof. Dr. Alberto Carvalho Filho, como bolsista Capes. Após a conclusão do mestrado, atuou como pesquisadora na iniciativa privada em projeto de reuso de efluentes na fertirrigação de pastagens (Casanare, Colômbia). Em agosto de 2021, iniciou o curso de Doutorado em Agronomia pelo programa de Pós-graduação em Agronomia (Ciência do Solo) na Universidade Estadual Paulista "Júlio de Mesquita Filho" (UNESP), *Campus* de Jaboticabal, sob orientação do Prof. Dr. Renato de Mello Prado, desenvolvendo pesquisas sobre a fertirrigação com silício na mitigação de desordens nutricionais em gramíneas forrageiras cultivadas em solos tropicais. Durante o doutorado, como membra do Grupo de Estudos em Nutrição de Plantas da Unesp (Genplant) colaborou em outras pesquisas desenvolvidas na Unesp, realizou estágio em docência na área de Fertilidade do Solo, participou de eventos, e publicou artigos.

“A terra boa semeada é quem ouve a palavra e a compreende, e produz frutos” (Mt 13, 23).

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FERTIRRIGAÇÃO COM SILÍCIO EM CAPIM ZURI CULTIVADO SOB ESTRESSES DE FÓSFORO E DE NITROGÊNIO EM DOIS SOLOS TROPICAIS

RESUMO - Os desequilíbrios por deficiência ou excesso de nitrogênio (N) e de fósforo (P) nos solos limitam a produção de gramíneas forrageiras tropicais e os efeitos subjacentes na planta são pouco relatados. O uso do silício (Si) pode ser uma estratégia sustentável para mitigar esses estresses, mas não estão claros os mecanismos biológicos envolvidos. Os objetivos deste estudo foram elucidar os danos causados pela deficiência e pelo excesso de N e de P em capim Zuri (*Megathyrsus maximus*) em dois solos tropicais, e avaliar se a fertirrigação com nanosílica durante o cultivo da forrageira é eficiente em atenuar os danos biológicos dos estresses nutricionais e os principais mecanismos envolvidos. Quatro experimentos foram desenvolvidos em ambiente controlado, e diferentes aspectos foram discutidos nos três estudos que compõe esse trabalho. Em dois experimentos foram analisados desequilíbrios de N, sendo um em Latossolo Vermelho distroférrico típico e outro em Neossolo Quartzarênico distrófico típico e outros dois experimentos com desequilíbrios de P, nos mesmos dois solos citados. Os tratamentos foram arranjados em esquema fatorial 3x2, com três estados nutricionais de N ou de P da planta (deficiente, adequado e excessivo) combinados com ausência (-Si) ou presença de Si (+Si) aplicado diariamente via fertirrigação (1,5 mmol L^{-1}), com quatro repetições, em delineamento inteiramente casualizado. Tanto a deficiência quanto o excesso de N ou de P alteraram o equilíbrio nutricional entre C, N e P na parte área da planta, diminuindo a eficiência de uso de C, prejudicando o crescimento e a produção de matéria seca (MS). Os danos por excesso de N e de P ocorreram em ambos solos, mas diminuíram a produção de MS apenas no capim cultivado em solo arenoso, indicando a necessidade de manejo mais cauteloso das fertilizações nesses solos. A fertirrigação com nanosílica incrementou os teores de Si na parte aérea de *M. maximus* em todos os estados nutricionais de N ou de P. Dentre os principais mecanismos benéficos do Si observados na atenuação dos estresses nutricionais estão a melhoria da homeostase elementar entre C, N e P, a maior eficiência de uso desses nutrientes pelas plantas, e a melhor assimilação de C nas plantas sob excesso de N ou de P. Assim, houve aumento no perfilhamento do capim Zuri sob excesso de N ou de P, melhorando a produção de MS. Nas deficiências o uso do Si atenuou as alterações na homeostase C:N:P e na morfogênese, mas não o suficiente para melhorar a produção de MS. Sob excesso de P a fertirrigação com Si diminuiu a mortalidade de perfilhos e o teor de lignina das plantas, e em ambos desequilíbrios de N ou P, o Si promoveu diminuição da senescência foliar e melhorou aspectos nutricionais da biomassa como o teor de proteína, sem diminuir a digestibilidade da MS. A fertirrigação com nanosílica pode mitigar os danos causados por excesso de N ou de P em *M. maximus* em solos tropicais de textura arenosa, e melhorar aspectos bromatológicos da forragem em plantas submetidas a desequilíbrios de N ou de P, e sob suficiência nutricional. Espera-se que a fertirrigação com Si contribua com a melhoria da produção de forragem em pastos tropicais, corroborando para suprir a necessidade global de proteína animal com maior sustentabilidade dos sistemas de produção.

Palavras-chave: elemento benéfico, estequiometria elementar, estresse nutricional, gramínea forrageira, *Megathyrsus maximus*

FERTIRRIGATION WITH SILICON IN ZURI GUINEAGRASS CULTIVATED UNDER PHOSPHORUS AND NITROGEN STRESS IN TWO TROPICAL SOILS

ABSTRACT - Imbalances due to deficiency or excess of nitrogen (N) and phosphorus (P) in soils impair the production of tropical forage grasses and the underlying effects on the plant are little reported. The use of silicon (Si) may be a sustainable strategy to mitigate these stresses, but the biological mechanisms involved are unclear. The objectives of this research were to elucidate the damage caused by deficiency and excess of N and P in Zuri guineagrass (*Megathyrsus maximus*) in two tropical soils, and to evaluate whether fertigation with nanosilica during forage plants cultivation is efficient in mitigating biological damage of nutritional stress and the main mechanisms are involved. Four experiments were carried out in a controlled condition, two to analyze N imbalances, one in a Oxisol and the other in a Entisol (Quartzipsamment), and two other experiments for P imbalances, for the same two soils mentioned. The treatments were arranged in a 3x2 factorial scheme, with three nutritional states of N or P of the plant (deficient, adequate and excessive) combined with the absence (-Si) or presence of Si (+Si) applied daily via fertigation (1.5 mmol L^{-1}), with four replications, in a completely randomized design. Both deficiency and excess of N or P altered the nutritional balance between C, N and P in tissues, reducing the efficiency of C use, impairing growth and dry matter (DM) production. Both deficiency and excess of N or P altered the nutritional balance between C, N and P, reducing the C use efficiency, harming growth and dry matter (DM) production. Damage due to excess N and P occurred in both soils, but reduced DM production only in grass grown in sandy soil, indicating the need for more cautious management of fertilization in these soils. Fertigation with nanosilica increased Si content in the leaves of *M. maximus* in all nutritional states of N or P. Among the main beneficial mechanisms of Si observed in the mitigation of nutritional stress are the improvement of elemental homeostasis between C, N and P, the greater efficiency of use of these nutrients by plants, and the better C assimilation in plants under excess N or P. Thus, there was an increase in the tillering of Zuri guineagrass under excess N or P, improving DM production. In deficiencies, the use of Si attenuated changes in C:N:P homeostasis and morphogenesis, but not enough to improve DM production. Under excess P, fertigation with Si reduced tiller mortality and plant lignin content, and in both N and P imbalances, Si promoted a decrease in leaf senescence and improved nutritional aspects of biomass such as protein content, without decrease DM digestibility. Fertigation with nanosilica can mitigate the damage caused by excess N or P in M. maximus in tropical soils with sandy texture, and improve bromatological aspects of forage in plants subjected to N or P imbalances, and under nutritional sufficiency. Fertigation with Si is expected to contribute to the improvement of forage production in tropical pastures, helping to meet the global need for animal protein with greater sustainability of production systems.

Keywords: beneficial element, elemental stoichiometry, nutritional stress, forage grass, *Megathyrsus maximus*

CAPÍTULO 1 - Considerações gerais

1 Introdução

Os pastos são fonte de alimento para a criação de animais que convertem a forragem em proteína de alta qualidade para a alimentação humana, e quando bem manejadas contribuem para a conservação do solo e da água (Pereira et al., 2022). As regiões tropicais e subtropicais contribuem com aproximadamente 47% da carne e do leite produzidos por ruminantes no mundo, tendo os pastos como base alimentar (Gurgel et al., 2019). No Brasil, as áreas de pastagem somam 163 milhões de hectares (ABIEC, 2022), cultivadas principalmente com gramíneas forrageiras tropicais de alto potencial produtivo como as do gênero *Megathyrsus* (sin. *Panicum*) e *Uroclhoa* (sin. *Brachiaria*) (Pezzopane et al., 2016).

As plantas forrageiras são cultivadas em uma diversidade de ambientes e condições edafoclimáticas (Phelps e Kaplan, 2017), a exemplo dos solos tropicais com elevado grau de intemperismo e pobres em nutrientes (Oliveira et al., 2023), sendo cultivadas em sistema extensivo com baixo investimento na fertilidade do solo (Dias-Filho et al., 2014; Santos et al., 2024). Esses fatores causam desequilíbrios nutricionais importantes nas plantas forrageiras como a deficiência de nitrogênio (N) e a de fósforo (P), que afetam diretamente a produção de matéria seca de forragem (Ramos et al., 2009; Delevatti et al., 2019).

Buscando maior produtividade e rentabilidade na pecuária a pasto, tem havido a conversão de sistemas extensivos para manejos mais intensivos com uso da irrigação por sistemas de aspersão e gotejamento, contribuindo para atender a demanda mundialmente crescente por carne bovina e otimizando o uso das terras já desmatadas (McAllister et al., 2020; Bento et al., 2021). No entanto, a falta de um manejo assertivo trouxe novos desafios como as fertilizações excessivas, que podem elevar os teores disponíveis de N e de P no solo (Damian et al., 2020; Pereira et al., 2022), aumentando o risco de toxicidade às plantas (Barhoumi, 2017; Malhotra et al., 2018) e problemas ambientais (Turner et al., 2000), podendo diminuir o retorno econômicos da pecuária.

A severidade dos danos causados por desequilíbrios de N e de P nas plantas podem ser influenciados pela dinâmica desses nutrientes no solo. Os solos de textura

arenosa apresentam baixa capacidade de adsorção de fosfato em relação aos solos argilosos ricos em óxidos de ferro (Fe) e de alumínio (Al) (Alovisi et al., 2020), e assim, a deficiência pode ser agravada em solos argilosos. Por outro lado, sob fertilizações excessivas de P, os solos arenosos podem manter maior concentração de fosfato em solução, o que aumenta os riscos de toxicidade nas plantas (Pavinato et al., 2020). Em solos ricos em argilas oxídicas, esse risco pode estar restrito a um curto período de tempo após a fertilização, pois quanto maior o tempo de contato do fosfato com os sítios de adsorção, menor a disponibilidade de P em solução (Rajput et al., 2014).

A textura do solo também influencia na dinâmica do N, principalmente em relação à sua perda por lixiviação, que é facilitada em solos arenosos devido à sua alta condutividade hidráulica (Azad et al., 2020), o que contribui para a ocorrência de deficiência de N. A toxicidade de N por sua vez, está associada geralmente à sua forma amoniacal (NH_4^+), e os solos argilosos podem ser menos susceptíveis que os arenosos, pois, apresentam maior capacidade de troca de cátions (CTC), retendo mais os íons NH_4^+ (Beusch et al., 2019).

Em condições normais de cultivo, não é comum uma concentração elevada de NH_4^+ na solução do solo devido a ação de bactérias nitrificantes, que o convertem em nitrito (NO_2^-) e logo em nitrato (NO_3^-). Porém, a ureia contém um contaminante, o biureto ($NH_2CONHCONH_2$), substância que pode prejudicar a nitrificação quando aplicada junto a doses altas de ureia (Xue et al., 2022), possibilitando o acúmulo de NH_4^+ na solução do solo, e a elevação de seu teor na parte área das plantas.

A deficiência ou o excesso de N ou de P causam distúrbios metabólicos nas plantas, afetando a eficiência fotossintética e a assimilação de carbono © (Goyal e Huffaker, 1984; Takagi et al., 2020; Araújo et al., 2022). As plantas necessitam de concentrações adequadas de nutrientes em seus tecidos, e também um equilíbrio estequiométrico entre os nutrientes para utilizá-los com maior eficiência biológica convertendo-os em biomassa, com destaque para as relações entre C, N e P que tem funções estruturais nas plantas (Elser et al., 2010; Costa et al., 2024). No entanto, essa homeostase elementar é alterada sob desordens nutricionais impostos às plantas em seu meio de cultivo, causando prejuízos ao seus metabolismo e desenvolvimento (Sousa Júnior et al., 2022).

Em gramíneas forrageiras os danos causados pelo excesso de N ou P ao seu metabolismo e desenvolvimento ainda não são conhecidos, pois os estudos são raros e limitados (Barhoumi, 2017; Cocozza et al., 2020), sendo focados nos danos biológicos relativos às deficiências de N ou P, embora majoritariamente estudados com cultivos em substrato inerte (Nanamori et al., 2004; Buchelt et al., 2020; Araújo et al., 2022). Além disso, falta esclarecer como o estado nutricional de N e de P pode influenciar a dinâmica de crescimento, a estrutura e morfologia da planta, bem como a composição química e valor nutritivo da matéria seca (Zanine et al., 2020; Paiva et al., 2023).

Além de analisar o risco e os prejuízos da deficiência ou excesso de N e de P em gramíneas forrageiras e compreender como essas plantas lidam com essas desordens, é necessário também buscar possíveis alternativas para mitigar esses danos. A aplicação de elementos benéficos como o silício (Si) tem sido eficiente na atenuação desses prejuízos. O Si pode ser absorvido na forma de ácido monosilísico, que se polimeriza como sílica gel na epiderme de folhas e caules (Ma et al., 2001), mas também é absorvido na forma de óxido de Si se estiver na forma de nanopartículas (SiO_2 nano) e deposita na parte área das plantas (Souza Júnior et al., 2022). No entanto, a ação do Si não está apenas na estrutura da planta, mas também otimizando sua defesa antioxidante quando submetida a condições estressantes (Bhardwaj, et al., 2023).

O Si interage com a absorção e a utilização de nutrientes pelas plantas (Hu et al., 2018; Pavlovic et al., 2021), o que favorece a homeostase elementar e pode aumentar a eficiência de uso de nutrientes e a eficiência fotossintética em gramíneas (Oliveira et al., 2019; Carvalho et al., 2022). Porém, o teor de Si disponível nos solos mais intemperizados é baixo, sendo necessário sua aplicação nos cultivos (Sommer et al., 2006).

Fontes sólidas de Si como as escórias de siderurgia são utilizadas há certo tempo (Prado e Fernandes, 2001) mas, as fontes solúveis como os silicatos de sódio e silicato de potássio potencializam a absorção de Si pelas plantas sem necessidade de doses elevadas (Oliveira et al., 2019), e permite a aplicação por meio de fertirrigação (Teixeira et al., 2021; Silva et al., 2023), embora exija cuidados para não ocorrer a polimerização. Recentemente tem se popularizado o SiO_2 nanoparticulado,

que pode otimizar a absorção e os benefícios do Si devido ao tamanho diminuto das partículas e sua alta estabilidade, por ser um composto que não apresenta cargas e suas partículas ficam dispersas na solução (Raza et al., 2023; Flores e Xavier, 2023; Alves et al., 2024). No entanto, ainda não se conhece o potencial de uso da nanosílica na atenuação de estresses nutricionais em gramíneas forrageiras cultivadas em diferentes solos.

Diante do exposto, nota-se que há necessidade de avançar o conhecimento sobre a nutrição nitrogenada e fosfatada em gramíneas forrageiras, bem como sua possível sinergia com o Si, para fortalecer o cultivo sustentável dessas plantas em diferentes solos. Para isso, este estudo investigou as seguintes hipótese (i) a deficiência e o excesso de fertilização fosfatada ou nitrogenada prejudicam o equilíbrio nutricional e a homeostase C:N:P em gramínea forrageira cultivada em solos tropicais ii) esses desequilíbrios nutricionais modificam a dinâmica de crescimento, diminuindo a produção e alterando a composição química da forragem iii) a aplicação de SiO_2 nanoparticulado pode atenuar os prejuízos causados pelos desequilíbrios de P e de N em gramínea forrageira em solos tropicais.

Se as hipóteses forem aceitas, serão elucidados os danos biológicos da deficiência e do excesso de dois elementos chave na produção de matéria seca em gramínea forrageira cultivada em solos tropicais, e como essa espécie lida com esses danos. Simultaneamente, poderá surgir uma estratégia sustentável a partir do uso do Si para aumentar a tolerância da planta a esses estresses.

Portanto, os objetivos deste trabalho foram avaliar os danos causados pela deficiência e pelo excesso de P e de N no cultivo de gramínea forrageira *Megathyrsys maximus* cv Zuri em solos tropicais de diferentes texturas, analisar os efeitos da aplicação de Si na estequiometria CNP e eficiência de uso e nutrientes, e elucidar os mecanismos biológicos envolvidos.

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2 Revisão de literatura

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2.1 Impact of nutritional disorders of nitrogen and phosphorus in Poaceae and future prospects: a review

Impacto de desordens nutricionais de nitrogênio e de fósforo em poáceas e perspectivas futuras: uma revisão

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Abstract

Nitrogen (N) and phosphorus (P) deficiencies limit the productivity of crops the most, including of Poaceae, which have a C4 photosynthetic system and a high capacity for biomass accumulation in tropical regions, with a high requirement for these nutrients. The excess P and N (especially in the ammoniacal form) can cause nutritional disorders predominantly in very intensive cultivation systems. However, studies on the subject are scarce. The aim of this review is to address the occurrence and effects of deficiency of and excess N and P in Poaceae and its relationship with soil acidity. The main impacts of these nutritional disorders on the physiology and production of these plants were discussed. Possible alternatives to attenuate the nutritional imbalances of N and P in grasses are presented.

Additional keywords: soil acidity; nutritional stress; silicon in grasses; Poaceae.

Resumo

As deficiências de nitrogênio (N) e de fósforo (P) são as que mais limitam a produtividade dos cultivos incluindo as poáceas, que apresentam sistema fotossintético C4, alta capacidade de acúmulo de biomassa em regiões tropicais e alta exigência destes nutrientes. No entanto, o excesso de P e de N (especialmente na forma amoniacal) pode provocar desordens nutricionais, principalmente em sistemas de cultivo muito intensivos, mas os estudos sobre o tema são limitados. O objetivo dessa revisão é abordar a ocorrência e os efeitos da deficiência e do excesso de N e de P em poáceas, e sua relação com a acidez do solo. Foram discutidos os principais impactos dessas desordens nutricionais na fisiologia e na produção dessas plantas, e apresentadas possíveis alternativas para atenuar os desequilíbrios nutricionais de N e de P em poáceas, como a fertilização com silício.

Palavras-chave: acidez do solo; estresse nutricional; silício em gramíneas; Poaceae.

Introduction

Adequate mineral nutrition promotes the growth and production of cultivated plants (Marschner, 1995). However, if there is a deficiency of or excess nutrients in the plant, the metabolic functions become compromised, resulting in lower growth and visual symptoms characteristic of each nutrient (Malavolta et al., 1997; Prado, 2021). Symptoms may vary according to species. The nutritional deficiency that predominates in tropical regions occurs when nutritional requirements are not met.

The Poaceae family comprises species known as grasses. They are among the main species cultivated in tropical regions, such as corn (Mattos & Silveira, 2018), sugarcane (Soltangheisi et al., 2019) and forage plants (Rojas-Downing et al., 2017; Martins, 2021). However, low levels of N and P available in the soil limit biomass production (Touhami et al., 2022). Limiting levels of N are related to a low content of soil organic matter (SOM) and a high rate of N loss from nitrogen fertilizers by leaching or volatilization (Minato et al., 2020; Pereira et al., 2022).

Available P contents are low in tropical soils because of a parent material with a low P content. Also, this nutrient can have a high specific adsorption to the surface of colloids in the clay fraction (Lemos & Prado, 2017). However, aiming a high productivity in intensive production areas, often without adequate monitoring through soil and leaf analysis, high doses of conventional and organic fertilizers are used continuously, generating excessive accumulation of N and P in the soil (Lu & Tian, 2017; Omara et al., 2019). Such excess N and P causes a decrease in productivity and the environmental contamination of the water table or rivers, lowering the sustainability level of crops (Walton et al., 2020).

This review aims to explain the importance and the effects of nutritional disorders arising from deficiency and the relationship with soil acidity. It also aims to discuss the importance of excess nitrogen and phosphorus in the cultivation of some species of grasses such as rice, sugarcane, fodder, sorghum, and wheat. In addition, some perspectives regarding future research are addressed seeking to understand and mitigate these nutritional disorders.

Soil acidity and nutrient availability

In the cultivation of crops, liming is fundamental to increase the availability of nutrients and consequently the absorption of these nutrients by plants. Liming is necessary when there is a high acidity in the soil together with a low availability of nutrients, which compromises the productivity of crops. Soil acidification is a natural process resulting from a base poverty of the parent material and/or weathering processes that lead to a loss of soil cations such as calcium, magnesium, and potassium. However, this acidification may accelerate while cultivating the soil, as soil bases are removed by the harvested product as well. Furthermore, the decomposition of SOM and the addition of nitrogen fertilizers also contribute to soil acidification (Natale et al., 2012).

The main direct effects of soil acidity are low base saturation and aluminum (Al^{3+}) toxicity. Base saturation is a percentage of soil surface charges at the solid phase that are occupied by basic cations (Ca^{2+}, Mg^{2+}, and K^{+}), which are plant nutrients. In acid soils, most charges are occupied by acid cations (H+ and Al^{3+}). Therefore, nutrients may be lost by leaching (Brady & Weil, 2013). Thus, before carrying out fertilizations, it is necessary to release the soil charges so that the added nutrients are retained and can be absorbed by the crop according to its demand.

Aluminum toxicity restricts the growth of plant roots, making them thick and short and impairing the absorption of water and nutrients. This leads to water stress and nutritional deficiencies such as phosphorus, nitrogen, potassium, calcium, and magnesium deficiency (Singh et al., 2017; Sousa Junior et al., 2022). In sugarcane, for example, aluminum toxicity reduces nutrient use efficiency (Borges et al., 2020). In oxidic soils, acidity increases phosphate adsorption to the solid fraction (Vinha et al., 2021) due to the protonation of OH groups into iron and aluminum hydroxides, generating positive charges that adsorb phosphate (Farias et al., 2009).

Fortunately, soil acidity can be corrected by applying correctives, commonly limestone. Lime solubilization in the soil releases calcium and magnesium carbonates and hydroxyls, which react with free H^{+} in the soil solution. Thus, liming consumes soil acidity by raising the pH, favors the neutralization of Al^{3+} that precipitates in the form of hydroxide, provides calcium and magnesium, and increases the availability of phosphorus in the soil (Raij, 2011). In a corrected soil, there is better root development, favoring an efficient use

of water and nutrients by plants. The efficiency of liming depends on an early application at sowing, uniform distribution, and incorporation of limestone into the soil (Carneiro et al., 2018).

In addition to limestone, a sustainable option that may be used to correct soil acidity is steel slag. Steel slags are byproducts generated in the process of obtaining raw iron from iron ores and from other products, such as steel and its derivatives. Such materials have been used in many crops with positive results, such as raising pH and decreasing potential soil acidity, increasing base saturation and P availability, and increasing the production of stalks in sugarcane (Prado & Fernandes 2000; 2001; Prado et al., 2002a; Brassioli et al., 2009; Fonseca et al., 2009; Silva & Prado, 2019).

Steel slag consists of calcium and magnesium silicates, which are strong bases similar to calcium carbonate, that is, limestone. However, it may contain micronutrients in its composition (Prado et al., 2002b), requiring attention to the levels of potentially toxic heavy metals that may exist in its composition (O'Connor et al., 2021). The similarity of limestone and steel slag is well known, and both provide increases in pH and in the availability of P, Ca and Mg, resulting in a lower potential acidity and a higher base saturation (Vidal and Prado, 2011; Guimarães et al., 2019). Because it favors the availability of nutrients such as Ca, root growth in plants is better (Prado & Natale, 2004a).

Silicates are also sources of silicon (Si), a beneficial element for crops (Pereira et al., 2007a). It can increase the availability of phosphate in the soil as silicate competes with phosphate for adsorption sites (Prado & Fernandes, 2001). In marandu grass (*Urochloa brizantha*), nitrogen fertilization associated with slag increases Si absorption and forage dry matter production (Fonseca et al., 2009). It is important to remember that correctives must be applied based on soil chemical analysis and on the characteristics of the corrective material regarding granulometry and ability to neutralize acidity. The excessive use of correctives may compromise the aggregation of soil particles (Prado, 2003) and reduce the availability of micronutrients (Pereira et al., 2007b) and of P itself, as it can induce the formation of insoluble calcium phosphate, especially if applied on the soil surface (Penn & Camberato, 2019).

The need to adequately correct soil acidity for an optimal crop development has been studied for many years in tropical regions (Cruz et al., 1994; Santos et al., 1996; Caires & Rosolem, 1998; Kaminski et al. al., 2000; Prado et al., 2002a) and other regions of the world (Alley & Zelazny, 1987; Sumner et al., 1991; Noble et al., 1995; Scott et al., 2000). Due to its indispensable character, liming continues to be studied by soil scientists aiming to establish liming recommendations according to crop, source, and innovative technologies for applying corrective materials, respecting different production environments (Prado & Natale, 2004b; Bambolim et al., 2015; Galindo et al., 2017; Fontoura et al., 2019; Silva & Prado, 2019). Therefore, correcting soil acidity is a basic premise for a sustainable agricultural production as it ensures availability of nutrients and efficiency of fertilization, including of nitrogen and phosphate. Consequently, liming is the best economic return practice in agriculture.

3. Impacts of N and P deficiency in Poaceae

Nitrogen (N) and phosphorus (P) are essential elements for various forms of life on Earth. In most soils in tropical regions, these nutrients limit crop production, requiring fertilizer applications to reach high levels of productivity and thus meet the growing demand for food in the world. N and P deficiency occur in 18 and 43% of soils in cultivated areas in the world, respectively (Du et al., 2020).

Nitrogen is required in large amounts by crops. It is absorbed mainly in the forms of nitrate (NO_3^-) and ammonium (NH_4^+). It acts in vital plant processes, such as the synthesis of chlorophyll, nucleic acids and proteins. It is a component of all enzymes, including PEPC and RuBisCO, essential for the fixation of CO_2 in photosynthesis (Prado, 2021). Equally important is phosphorus, an essential component of molecules of ATP, NADPH, nucleic acids, sugar phosphates, and phospholipids, all of which play roles in photosynthesis (Hammond et al., 2004; Prado, 2021).

In addition to the natural scarcity of N and P in tropical soils, phosphate and nitrate anions may have a low availability as a result of some processes. Nitrate is poorly retained by the soil solid phase, making it prone to leaching losses (Bowles et al., 2018), while phosphate can be strongly adsorbed into soil solid particles (Santos et al., 2008), especially in clayey and highly weathered soils (Penn & Camberato, 2019; Pavinato et al., 2020). Also, the method of P application affects the productivity of sugarcane, as it is a demanding crop responsive to phosphate fertilization (Sousa Júnior et al., 2017); in corn crops, with more localized methods of application, it decreases the adsorption of P into the soil and increases absorption and crop production (Lemos et al., 2022).

P and N deficiency limits the production of Poaceous crops, such as forage (Primavesi et al., 2004; Hou et al., 2020), sugarcane (Caione et al., 2015a), corn (González et al., 2016), and rice (Deus et al., 2020). Thus,

plants grown in environments deficient in N or P have a low absorption efficiency of these and other nutrients, such as Ca, Mg, and S (Gondim et al., 2010). In trials with sorghum cultivation in nutrient solution, the individual omission of N and P reduced the production of dry matter of shoots and roots, and the deficiency of P impaired the absorption of N, K, Ca, S, Mg, and Mn in sorghum plants (Prado et al., 2007). In sugarcane, N and P deficiencies reduced plant growth by 91 and 57%, respectively, with a lower nutrient uptake, progressing to visual symptoms such as slow development (Vale et al., 2011). N and P have structural functions and transfer and storage of energy in the plant. Therefore, their deficiencies compromise the synthesis of proteins and nucleic acids (Carstensen et al, 2018), resulting in lower plant growth.

Forage grasses have a high demand and a high ability to remove nutrients from the soil (Werner et al., 1996). Therefore, N and P deficiencies reduce growth and tillering. Conversely, adequate fertilization with these nutrients improves the morphogenetic and structural characteristics of forages (Farias et al., 2019; Ramos et al., 2009), as well as the production of forage mass in pre- and post-grazing (Zanine et al., 2020). In addition to the amount of forage, deficiencies of N and P affect forage quality. Animals that consume forage poor in N or P may present abnormalities such as poor formation of bones and teeth and low fertility (Malavolta et al., 1986). This occurs because the deficiency in nitrogenous compounds in the forage implies ruminal conditions that limit microbial activity, forage intake, digestibility, and animal performance (Lazzarini et al., 2009; Mwangi et al., 2019). Phosphorus is also essential for metabolism, transfer of energy and genetic information, and it is required by the rumen microbiota of animals (Karn, 2001).

In plants, there is a strong synergy between N and P in plants (Rietra et al., 2017). The lack of P slows down the process of energy transfer and storage in the plant (Malavolta, 1989) and impairs cell division, reducing the length and renewal of roots (Silva & Delatorre, 2009). The low supply of N reduces mass production and has a negative effect on the absorption of other macronutrients by forage plants (Fernandes et al., 2008; Fonseca et al., 2011). It also decreases tillering, thus explaining the low biomass production of leaves and low pasture height (Martuscello et al., 2019). In maize (*Zea mays* L.), nitrogen limitation reduced shoot growth and photosynthetic capacity (Khamis et al., 1990) due to a decrease in chlorophyll content (Malavolta et al., 1997).

Plants respond to deficiencies using some survival strategies. Under N limitation, they can activate the expression of high-affinity NO_3^- transporters, with absorption at low concentrations and high efficiency in N remobilization (Lezhneva et al., 2014). Plants cultivated in a low-P environment undergo changes in root architecture, carbon metabolism, and membrane structure (Vance et al., 2003). In addition, they dissipate excess energy, protecting the photosynthetic apparatus (Stirbet & Govindjee, 2011), and activate the expression of genes that improve the efficiency of P use (Hammond et al., 2004).

Organic matter is the main N reservoir in the soil. It also provides P and other nutrients (Brady & Weil, 2013). There is also a significant contribution of N to the soil by atmospheric N_2 fixation carried out by free-living fixing bacteria associated with Poaceae (Keymer & Kent, 2014; Roley et al., 2018). However, even with these inputs, it is still necessary to complement the supply of N and P to sustain high yield cultivated systems; this may be done either with chemical or organic fertilizers (Omara et al., 2019). This occurs because the extraction of nutrients from the soil does not occur constantly during the crop production cycle; on the contrary, the absorption curve has a sigmoid shape characterized by an initial phase of low growth and nutrient absorption by plants.

In order to allow an optimal productivity of crops in view of the high cost of chemical fertilizers, their use has been associated with organic residues in the cultivation of Poaceae, such as filter cake in sugarcane (Caione et al., 2015a; Caione et al., 2015b; Castillo et al., 2015) if enriched with microorganisms, it favors even the availability of P in the soil (González et al., 2016). Organic sources supply N and P to the soil and make soil P more available as organic acids compete with phosphate for the adsorption sites of soil colloids (Pavinato & Rosolem, 2008), allowing a greater P absorption and sugarcane productivity (Moda et al., 2015; Vasconcelos et al., 2017). Animal residues such as bovine manure or liquid pig manure are also used in the cultivation of grasses as a source of N and P, reducing production costs (Soares-Filho et al., 2018), especially in pasture fertilization (Drumond et al., 2006; Zanine & Ferreira, 2015).

A recent strategy to mitigate nutritional deficiency in plants could be the use of Si. It is a sustainable alternative without posing risks to the environment (Teixeira et al., 2020). Many studies have indicated that Si provides resilience to plants under stressful conditions (Ma, 2004; Verma et al., 2020; Souri et al., 2021), including those under nutritional imbalance (Ali et al., 2020; Silva and Prado, 2021). The application of Si improves the production of the forages *Megathyrsus maximus* and *Urochloa brizantha* grown in a medium deficient in K, Ca, or Mg by improving the use efficiency of these nutrients (Buchelt et al., 2020). This also occurs for N, P, and Ca in these species (Araújo et al., 2022). Si can be beneficial even in non-stressed plants.

In other grasses such as rice, the use of Si improved the production of N-deficient plants by modifying the C:Si stoichiometry (Deus et al., 2020). This change is certainly because of the lower energy cost of Si incorporation in relation to the synthesis of carbon compounds (Klotzbücher et al., 2017; Hao et al., 2020). Si also improved N uptake in deficient maize plants (Silva et al., 2021) and increased P accumulation and use efficiency in sorghum grown in P-deficient medium (Silva & Prado, 2021), improving the production of dry matter of plants.

Occurrence and effects of excess N and P on Poaceae

Fertilization with N and P has allowed transforming low fertility soils into highly productive areas (Singh, 2018; Pavinato et al., 2020). On the other hand, such a need placed Brazil among the five countries in the world that consume fertilizers the most. Brazil accounts for 3 and 11% of the global consumption of nitrogen and phosphate fertilizers, respectively (Lu & Tian, 2017). Part of this demand is because, in tropical soils, it is necessary to apply fertilizer doses that can exceed the amount of P fixation (Gichangi et al., 2009; Brenner et al., 2018) and the high requirement of N to provide a high yield of Poaceae (Galindo et al., 2018; Ronsani et al., 2018).

Global analyses indicate that the rate of fertilizer application to supply N and P to the soil has been increasing since the 1960s. In Brazil, fertilizers are found in regions of intensive production, in soils cultivated with agricultural crops or pasture (MacDonald et al., 2011; Lu & Tian, 2017; Li et al., 2019). In corn crops, for example, the applied amount of P increased by 105% in the last 20 years in Brazil in search of a higher productivity (Pavinato et al., 2020). Similarly, in intensive pastures, high doses of fertilizers are also required (Primavesi et al., 2005), especially those that provide N, which is a nutrient that determines productivity (Omara et al., 2019). However, nutrient input often exceeds crop demand (Reid et al., 2019).

The continuous application of high doses of nitrogen and phosphate fertilizers leads to accumulation of N and P in the soil and excessive absorption by plants. The excessive absorption of a nutrient increases its leaf content, causing a decrease in the production of dry matter either due to the toxicity of the element or by competitive inhibition of absorption, transport or assimilation of other nutrients (Malavolta et al., 1986). The level at which N becomes excessively depends on the species and even the variety (Goyal & Huffaker, 1984). Among its effects are a lower synthesis of phenolic compounds (Elhanafi et al., 2019), reduction of transpiration and photosynthesis (Sperling et al., 2019), and the carbon:nitrogen ratio of plants (C:N) (Santi et al., 2019). al., 2003). Excess absorption of P increases its content in plant shoots, causing toxicity (Malhotra et al., 2018) and metabolic imbalances that affect biomass production (Malavolta et al., 1997).

The excessive application of N decreases the physiological and internal N use efficiency, reduces grain yield (Wang et al., 2011), and increases cadmium (Cd) content in wheat grains (Li et al., 2011) and in Tanzania grass (Leite & Monteiro, 2019). In sugarcane, high doses of N increased tillering but reduced stem diameter, with a consequent decrease in production (Vale et al., 2013). The excess N predisposes the plants to a greater attack by pests (Scriber, 1984), such as fall armyworms in corn due to the high concentration of easily assimilable free amino acids in leaf tissues (Sampaio et al., 2007); it even reduces alkaloid production (Rasmussen et al., 2007).

The increased uptake by the root and translocation of P to shoots leads to excess P accumulating in older leaves, causing P toxicity (Aung et al., 2006), which compromises photosynthetic performance, as observed for the grass Arundo donax (Cocozza et al., 2020). Excess P uptake leads to increased N uptake (Rietra et al., 2017), which stimulates plant senescence (Chiou et al., 2006) and compromises their C:N and C:P homeostasis (Elser & Hamilton, 2007). In rice, excess P increased susceptibility to diseases (Campos-Soriano et al., 2020).

Studies on excess N have focused on ammonia toxicity (NH_4^+). They indicate that the use of Si may attenuate its toxic effects in several cultivated species (Silva Junior 2019; Campos et al., 2020; Leal et al., 2021; Viciedo et al., 2020). Si seems to promote mechanisms to attenuate the excess of P, such as the modulation of P uptake, by regulating the gene expression of transporters (Hu et al., 2021). However, the effects of excess P and N in grasses are not yet clear. Further tests are necessary on the use of Si attenuating the damage caused in these plants, especially when cultivated in soils. In this sense, an unprecedented study began indicating that Si can attenuate toxicity in a forage cultivated in Typic Quartzipsamment (Entisol), a fact observed visually. However, it is important to advance in research to understand the physiological and nutritional aspects involved in this process (Melo et al., 2023).

Final considerations and future perspectives

The direct and indirect effects of deficiency of and toxicity by N and P in Poaceae highlights the need to carry out fertilizations adapting the doses of nutrients to the demand of crops and promote a greater use efficiency of nutrients by plants. For this, some actions are necessary.

It is necessary to update fertilization recommendation tables and the appropriate levels of nutrients for crops by carrying out comprehensive research on different cultivation systems and technological levels that are currently used so that fertilization efficiency can increase. In these studies, it is essential that the updated nutritional standards be accurate, that is, it is necessary to verify whether the resulting diagnoses are really true before publication in technical bulletins recommending nitrogen and phosphate fertilization for crops. For example, if the diagnosis of N or P deficiency is true, the application of these nutrient in the soil causes an increase in production; thus, the diagnosis was assertive. It is also necessary to investigate the synergy of N and P in plants of the Poaceae group because it would allow using optimized doses and avoiding surpluses. Thus, the scientific basis for N and P fertilization can be updated, ensuring an economic return for this activity with a rational fertilization and less occurrence of nutritional imbalances.

It is also advisable to use more sustainable sources such as organomineral fertilizers and recommend non-symbiotic N fixation, especially in pastures. In addition, it is necessary to improve the area of microbiology to optimize and explore the benefits of the symbiosis of microorganisms with plants, which may contribute to a lower dependence on nitrogenous and phosphate fertilizers. Advances in genetic improvement are also important, with a focus on selecting new cultivars of grasses that present high efficiency in absorbing and using N and P so that production can be achieved more efficiently.

Recent research has indicated that the use of beneficial elements such as silicon can improve nutritional efficiency in forage grasses, rice, corn, and sorghum grown in nutrient solution (Buchelt et al., 2020; Deus et al., 2020; Silva et al., 2021; Silva & Prado, 2021). However, there is a lack of studies on Poaceae crops planted in soil, especially in field conditions, using fluid sources of Si in irrigated systems. This could be important to evaluate its potential as a mitigator of N and P deficiency and verify whether it is possible to reduce the doses of these nutrients without loss of productivity.

Excess N and P has been scarcely investigated (Silva Junior et al., 2019; Sharma et al., 2007). Studies on the mitigation of N toxicity by Si are restricted to non-poaceous species such as passion fruit (Silva Junior et al., 2019), cotton (Leal et al., 2021), among others. Therefore, information on Poaceae is incipient (Hu et al., 2018; Cocozza et al., 2020). The results of Hu et al. (2018) for rice crops indicate that Si can also attenuate excess P, regulating its uptake by the plant. Therefore, it is possible that the use of Si in irrigated or dryland systems be a viable alternative to increase production in soils with very high levels of P. However, studies are lacking to prove this hypothesis.

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2.2 Silício na mitigação de estresses causados por desequilíbrios de nitrogênio ou fósforo em gramíneas

2.2.1 Silício: benefícios às plantas em condições estressantes

Diversos elementos inorgânicos são absorvidos do meio de cultivo pelas plantas, mas apenas 14 são considerados nutrientes, e compõem maiores ou menores percentuais da matéria seca (MS) das plantas, a saber nitrogênio (N), fósforo (P), potássio (K), cálcio (Ca), magnésio (Mg) e enxofre (S) (macronutrientes), e cobre (Cu), manganês (Mn), ferro (Fe), zinco (Zn), cobalto (Co), molibdênio (Mo) e níquel (Ni) (micronutrientes) (Prado, 2021). Porém, muitos outros elementos são absorvidos do solo, sendo alguns benéficos como é o caso do silício (Si), um elemento que favorece o crescimento da maioria das plantas em diversas circunstâncias, conhecido por otimizar a defesa das culturas contra estresses bióticos e abióticos (Kirkby, 2023), embora não haja evidências suficientes para classificar o Si como nutriente (Marschner, 2012).

As espécies vegetais foram classificadas em três grupos conforme sua capacidade de absorção e acúmulo de Si: acumuladoras (teor de Si > 1% da MS), excludentes ou não acumuladoras (teor de Si < 0,5% da MS), e intermediárias (teor de Si entre 0,5 e 1% da MS) (Ma e Takahashi, 2002). Basicamente foram descritas três formas de absorção de Si. A absorção ativa ocorre quando a concentração de Si na seiva xilemática torna-se maior que na solução externa comum em espécies acumuladoras, absorção passiva que ocorre na mesma taxa de absorção de água (intermediárias), e absorção mais lenta que a da água, com via de rejeição do Si (não acumuladoras) (Marschner, 2012; Costa et al., 2024). Ressalta-se que mesmo um alto acúmulo de Si não causa danos às plantas, pois, embora o ácido monosilício possa interagir com polifenóis e pectina na parede celular, ele se polimeriza (sílica gel) e não altera a pressão osmótica das plantas (Ma et al., 2001), e fontes como a nanosílica (SiO_2 nano) não interagem com componentes celulares, pois, não apresentam carga (Souza Júnior et al., 2022).

Um dos principais estresses abióticos presentes nos cultivos são aqueles causados por desequilíbrios nutricionais, por deficiência ou excesso de um nutriente no solo. Pastos cultivados nos trópicos úmidos por exemplo, estão sujeitos a deficiências graves de nutrientes como N ou P especialmente em sistemas extensivos (Delevatti et al., 2019; Touhami et al., 2022), enquanto sob manejo intensivo podem ocorrer fertilizações excessivas que também prejudicam a produção de biomassa (Lu e Tian, 2017; Phohlo et al., 2022).

Os efeitos benéficos do Si na atenuação de estresses nutricionais em diversas culturas minimizam o prejuízo na produção de biomassa, devido à manutenção da maquinaria fotossintética, regulação da absorção e transporte de nutrientes da raiz para a parte aérea e diminuição do estresse oxidativo e de danos celulares (Ali et al., 2020; Araújo et al., 2022). A interação do Si com a aquisição de nutrientes pelas plantas parece ser um importante mecanismo na atenuação do estresse nutricional (Pavlovic et al., 2021), principalmente em espécies acumuladoras de Si como as gramíneas (Poaceae). Em plantas de arroz cultivadas sob excesso de P, a absorção de P foi diminuída devido a regulação negativa do transportador de P nas plantas que receberam Si (Hu et al., 2018), enquanto no sorgo deficiente em P, as plantas aumentaram a absorção de P quando o Si foi fornecido (Silva e Prado, 2021).

Além de interagir com os nutrientes inorgânicos nas plantas, a absorção de Si também pode modificar as relações estequiométricas entre carbono (C), N e P em gramíneas sob condições estressantes (Teixeira et al., 2022). De fato, o teor de C das plantas pode diminuir à medida que o Si é incorporado nas paredes celulares, processo de menor custo energético em relação à síntese de compostos estruturais de C, a exemplo da lignina (Hao et al., 2020). Isso é importante pois, à medida que o Si melhora o equilíbrio estequiométrico C:N:P nos tecidos vegetais, a planta consegue utilizar com mais eficiência os nutrientes na produção de biomassa (Elser et al., 2010).

Muitos estudos em sistema hidropônico têm indicado que os mecanismos acima descritos estão envolvidos na ação do Si como atenuador de deficiências nutricionais em gramíneas, a exemplo da deficiência ou excesso de N ou P (Deus et al., 2020; Campos et al., 2020; Silva e Prado, 2021; Minden et al., 2021; Araújo et al., 2022). No entanto, faltam pesquisas sobre o potencial do Si em atenuar os estresses de N ou P quando impostos por meio dos solos, considerando as interações que

ocorrem entre a matriz sólida do solo, os nutrientes e as plantas no ambiente de cultivo.

2.2.2 Fertilização com Si em gramíneas sob estresses nutricionais

O Si é abundante nos solos, mas sua disponibilidade às plantas na forma de ácido monosilícico é baixa, principalmente em solos mais intemperizados, que já passaram pelo processo de dessilicação, e apresentam minerais residuais resistentes ao intemperismo como caulinita, óxidos de ferro e alumínio, e quartzo (Linden e Delvaux, 2019). As plantas também podem absorver o Si a partir da dissolução de fitólitos (sílica fitogênica) que se depositam no solo por meio da serrapilheira e restos de cultivos (Haynes, 2014), mas a exportação com as colheitas torna esse aporte cada vez menor, justificando a fertilização com Si para obter seus benefícios nos cultivos.

A fertilização de cultivos como cana-de-açúcar e pastagens com Si iniciou-se com a reutilização de resíduos de siderurgia compostos por silicatos de cálcio. O silicato tem ação corretiva do pH e compete com o fosfato pelos sítios de adsorção, aumentando a disponibilidade de P no solo (Prado e Fernandes, 2001; Luz et al., 2011; Moda et al., 2015; Aguiar et al., 2021). No entanto, a baixa solubilidade desse material confere liberação lenta do Si, o que não é interessante em cultivos intensivos, embora sua aplicação em capim irrigado tenha promovido absorção de Si pelas plantas de *U. brizantha* cv. Marandu (Melo et al., 2010).

Com a crescente demanda por fontes solúveis, o uso de silicato de sódio e silicato de potássio foi impulsionado, pois permitiram a aplicação por meio de fertirrigação (Buchelt et al., 2021; Silva et al., 2023). Porém, essas fontes são passíveis de polimerização do Si com a variação de pH, o que pode tornar o elemento indisponível às plantas (Haynes, 2019; Souza Júnior et al., 2021). O uso dessa fonte tem sido eficiente em promover seus efeitos benéficos na atenuação de deficiências de macronutrientes como K, Ca ou Mg em forrageiras *Urochloa brizantha* cv. Marandu e *Megathyrsus maximus* cv. Massai (Araújo et al., 2022), deficiência de ferro em sorgo (Teixeira et al., 2020), deficiência de manganês em cana-de-açúcar (Oliveira et al., 2021), e diminuiu os prejuízos da toxicidade de sódio em sorgo (Hurtado et al., 2019), e de alumínio em cana-de-açúcar (Sousa Júnior et al., 2022), além de mitigar a toxicidade de P ou N em culturas como o tomate (Barreto et al., 2016) e maracujá

(Silva Júnior et al., 2019). Além disso, o Si pode melhorar a produção de plantas forrageiras sem afetar o valor nutritivo da biomassa (Buchelt et al., 2023), ou mesmo incrementar o teor de proteína e diminuir a fibra insolúvel em detergente ácido (Borawska-Jarmułowicz et al., 2022).

O advento da nanotecnologia trouxe novas fontes de Si como o SiO_2 nanoparticulado tem levantado interesse da comunidade científica, pois o tamanho diminuto de suas partículas e sua alta estabilidade em solução sem risco de polimerização podem favorecer a absorção do Si (Wang et al., 2022; Alves et al., 2023). Isso facilita o preparo da solução para fertirrigação dos pastos, pois, não necessita de estabilização com sorbitol, o que é necessário para os silicatos solúveis. Embora não promova os benefícios do silicato na correção de acidez e disponibilidade de fosfato no solo, a nanosílica apresenta vantagem de não interagir com cátions no solo, evitando interação com a disponibilidade de micronutrientes. Por isso, destaca-se a necessidade de investigar o potencial dessa fonte em promover os benefícios do Si em gramíneas forrageiras cultivadas sob estresses nutricionais.

Diante do exposto, evidencia-se que o uso do Si é benéfico na mitigação de desequilíbrios nutricionais nas culturas, com grande potencial em gramíneas. Porém, esses estudos não abordam a interação entre planta e solo que influenciam a absorção de nutrientes, pois são realizados majoritariamente em substrato inerte. Logo, é razoável questionar se os benefícios do Si na atenuação de desequilíbrios nutricionais nas plantas podem variar conforme a severidade dos danos causados às plantas em função do tipo de solo em que é cultivada.

As interações entre os nutrientes e a matriz sólida do solo podem influenciar na ocorrência de desequilíbrios nutricionais, a exemplo da deficiência de P, pois, solos com maior grau de intemperismo, ricos em óxidos de Fe e de Al, e com textura mais argilosa apresentam elevada capacidade de adsorção de fosfato, em relação a solos arenosos (Brady e Weill, 2013; Alovisi et al., 2020).

Em relação ao N, solos argilosos armazenam mais N associado a matéria orgânica (Almeida et al., 2021), enquanto solos de textura mais arenosa podem permitir maior disponibilidade do N aplicado via fertilizantes embora facilite a lixiviação (Soione et al., 2020). Portanto, o tipo de solo pode influenciar a severidade dos danos causados por deficiência ou excesso de P ou N nas plantas, bem como o potencial de

mitigação desses estresses pelo uso do Si, o que requer investigação para as gramíneas forrageiras, que são cultivadas em uma diversidade de solos e manejos (Oliveira et al., 2017; Farhan et al., 2024), suscetíveis a desequilíbrios nutricionais.

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CAPÍTULO 2 - Nanosilica modulates C:N:P stoichiometry attenuating phosphorus toxicity more than deficiency in *Megathyrsus maximus* cultivated in an Oxisol and Entisol[1]

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Nanosilica modulates C:N:P stoichiometry attenuating phosphorus toxicity more than deficiency in *Megathyrsus maximus* cultivated in an Oxisol and Entisol

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ABSTRACT - Silicon (Si) nanoparticles can attenuate nutritional disorders caused by phosphorus in forages through nutritional homeostasis. This paper aims to evaluate the effects of P deficiency and toxicity in *Megathyrsus maximus* cultivated in two types of soils and to verify whether Si application via fertigation can mitigate these imbalances. The following two experiments were carried out: cultivation of forage plants in pots with Entisol and Oxisol, in a 3 × 2 factorial design, with three nutritional levels of phosphorus (deficient, adequate, and excessive) and two Si concentrations in the irrigation water (0 and 1.5 mmol L^{-1}). Height, number of tillers, rate of leaf senescence, dry matter production, C:N, C:Si, C:P, and N:P ratios; and C, P, and N use efficiencies were evaluated in two growth cycles. P imbalances hampered carbon assimilation, C:N:P homeostasis, and dry matter production. Nanosilica fertigation promoted silicon uptake, improving C:N:P homeostasis and nutritional efficiency in plants under P deficiency and toxicity. Leaf senescence was reduced with addition of Si in plants grown in Oxisol in the three nutritional states of P. Silicon attenuated the stress caused by P toxicity in Entisol and Oxisol, improving production in plants without nutritional stress in Oxisol. The supply of Si nanoparticles in the cultivation of *M. maximus* can contribute to a more efficient and sustainable use of phosphorus in pastures.

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1 Introduction

Forage plants (Poaceae) are found in different countries[1], constituting the main feed source in cattle raised worldwide[2]. Forage cultivated in tropical soils are subjected to nutritional stress due to the limitation of nutrients in the soil (especially P), which is a fact of worldwide occurrence in pasture production[3,4]. Phosphate has low availability in soils due to strong weathering and/or sorption of the element in the soil matrix[5,6], reducing tillering and the production of forage grasses[7]. In another scenario, intensive cultivation based on the empirical and frequent use of mineral fertilizers[8], as well as on the frequent use of organic compounds rich in P in pastures[9] may contribute to induce excess P in plants[10–12].

P toxicity in forage plants cultivated in soils is still little discussed, especially in soils with a sandy texture (Entisol), which have a low P adsorption capacity compared to clayey soils, such as an Oxisol, resulting in a high concentration of the element in solution, increasing the risk of toxicity in plants[13,14]. Among the metabolic disorders caused by P toxicity, there are the reduction of enzymatic reactions[15], chlorophyll content[16], and photosynthetic rate[17]. This nutritional disorder is aggravated by increased N uptake[18], which unbalances C:N and C:P homeostasis[19] and can accelerate leaf senescence, causing leaf chlorosis and/or necrosis[20,21].

A sustainable strategy to minimize the effects of P imbalance in forage would be the use of silicon (Si), as forage are plants that accumulate this element[22] and this is a practice that does not pose a risk to the environment. Extensive reviews indicate that Si provides plant resilience under stressful conditions[23–26], but studies involving Si mitigating P stress in forages are limited. The absorption of Si by plants occurs in the form of monosilicic acid (H_4SiO_4)[27,28], which is transported by the apoplast and symplast to the root xylem. When it reaches the leaves, it is mainly deposited on the cell walls, being polymerized, forming phytoliths and silica bodies[29].

Tropical soils extensively cultivated with pastures present a high total Si content, but in unavailable forms[30]. The Si concentration available in the soil solution is relatively low, ranging from 0.1 to 0.6 mM L^{-1} of Si, which is caused by the intense weathering in these soils, added to the successive extraction of Si from crops without carrying out replacement, causing desilication[31,32], and the successive extraction of Si from crops without fertilization for tis replacement. Given the above context, it is important to supply Si for crops with low solubility sources, such as steel slags in the form of solid calcium silicate, which are incorporated into the soil[33,34]. However, the application of Si in forages (through sodium and potassium silicate) has been shown to be more efficient through fertigation[35–38], and recently, with the advancement of nanotechnology, Si nanoparticles have emerged[39,40]. Nanosilica has a nanoporous structure, with particle diameters of up to 100 nm and high specific surface area[41], which can favor absorption and enhance the accumulation of Si in the plant shoot. The use of nanosilica should be studied especially in Si-accumulating crops, such as forages plants.

A new approach discusses the benefits of Si for nutrient uptake in plants under limiting conditions[42] and for the modification of C:N:P stoichiometry in grasses, attenuating the water deficit[38,43] and nutritional deficiency in forage plants under hydroponic cultivation[44]. This change in C stoichiometry must be related to the incorporation of Si into the cell wall, being metabolized at a low energy cost compared to the synthesis of structural carbon compounds such as lignin[45,46], and these factors may favor plant growth under stress. Silicon can increase P uptake in P-deficient sorghum plants[47], and also interact with the soil, occupying phosphate adsorption sites, increasing the availability of P in the soil[42]. In rice plants under excess P, the beneficial element decreases P uptake by downregulating the P transporter gene[48], which may be a plant strategy for the homeostasis of this macronutrient in plant tissues.

Nutritional disorders related to P can cause disturbances in C and N homeostasis, aggravating its efficient nutritional use by forage plants, but there is a lack of research to prove this. The same applies to the potential of Si to reverse these stresses. Thus, in order to advance in the present topic, some hypotheses need to be tested: (i) whether the damage to the growth of forage plants under P deficiency and to plants under P excess is related to the modification of C:N:P stoichiometry, consequently causing the loss of nutritional homeostasis and decreasing the efficiency of use of C, N and P by the plant; (ii) whether the risk of P toxicity in forage plants is greater in soils with a sandy texture compared to clayey textures; (iii) and whether the application of Si in the form of a nanosilica-based fluid to the soil promotes the optimal absorption of the element for the plant, being sufficient to attenuate the deficiency of P or excess P through the C:N:P stoichiometric homeostasis, and the increase in efficiency of use of these nutrients in the plant depending on the cultivated soil.

If these hypotheses are confirmed, the underlying mode of action of Si on the stoichiometric homeostasis of forage plants cultivated in different soils under nutritional stress due to P deficiency or excess P will be verified. Therefore, the potential of nanosilica will be verified for the first time as a strategy to maximize the growth of forages in different cropping systems, whether in low-tech cultivation systems with sub-doses of P or in intensive cultivation, with the use of high doses of P and problems of excess in plants. It will still be known if the beneficial effect of Si in the attenuation of P imbalances may or may not vary according to the soil class. Thus, the optimized management of Si should boost the production of sustainable forage without risks to the environment.

In this context, this study was carried out with the objective of evaluating whether P imbalances alter the C:N:P stoichiometry in the *Megathyrsus maximus*, whether Si applied to the soil as nanoparticles attenuates the effects of P deficiency and toxicity, and improves C:N:P homeostasis by optimizing plant growth under P phosphorus levels (deficient, adequate and excessive) in Oxisol and Entisol.

2 Material and methods

Location and experimental design. Two independent experiments were carried out at the São Paulo State University (UNESP), municipality of Jaboticabal, Brazil, in 2021, under greenhouse conditions (one experiment was conducted in an Entisol (Quartzipsamment), and another experiment was conducted in

an Oxisol)[49], with the forage plant *M. maximus* cv. Zuri. We declare that the experiments were carried out in accordance with relevant guidelines and regulations. Treatments were arranged in a 3 × 2 factorial design, with three P nutritional levels of: deficient (zero application of P), adequate or sufficient (200 mg dm^{-3} of P), and excessive (600 mg dm^{-3} of P)[58], combined with the absence of Si (zero Si) and the presence of Si (1.5 mM), with four replicates, in a completely randomized design. The experimental unit consisted of two forage plants in a plastic pot (height: 32 cm; lower and upper base: 15 cm) filled with 6 kg of Oxisol sample and 8 kg of Entisol sample. The plants were cultivated during two growth cycles, that is, two cuts were performed in a total experimental period of approximately 90 days from sowing.

Installation of the experiments. For both experiments, soils were collected from the surface layer of the uncultivated area, in the 0–20 cm layer. The samples were air-dried and passed through a 6-mm mesh sieve, being subsequently subjected to chemical analysis (for soil fertility)[50] and Si content analysis[51]. The results of the chemical analysis for the Oxisol and Entisol were, respectively: pH in CaCl2 = 3.8 and 4.3; OM (organic mat- ter) = 34 and 9.0 mg dm^{-3}; P in resin extractor = 12 and 2 mg dm^{-3}; K = 1.4 and 3.0 mmolc dm^{-3}; Ca = 6 and 3.0 mmolc dm^{-3}; Mg = 2 and 1.0 mmolc dm^{-3}; H + Al = 85 and 16; T (cation exchange capacity) = 94 and 20.3 mmolc dm^{-3}; V (base saturation): = 10 and 21%; and Si = 3.0 and 1.0 mg dm^{-3}. The granulometric analysis carried out according to[52] showed the following results for Oxisol and Entisol, respectively: 51 and 94% sand, 6 and 1% silt, and 43 and 5% clay.

Limestone (total neutralization power: 125%, CaO: 58.5%, MgO: 9%) was applied to the soils to correct acidity and to increase base saturation to 70%[50], corresponding to doses of 0.48 and 2.25 g dm^{-3} in the Entisol and Oxisol, respectively. The limestone was homogenized with the soil, and soils were maintained moist and incubated for 40 days before sowing.

Fertilization was carried out through soil application by supplying K, S, Zn, and B at doses of 150, 50, 5, and 0.5 mg dm^{-3}, respectively, besides supplying 5 mg dm^{-3} of Fe to the Entisol, using the following sources: potassium chloride, calcium sulfate, zinc sulfate, boric acid, and iron chelate. Phosphorus was applied at doses of 0, 200[53], and 600 mg dm^{-3} in the plots corresponding to the deficient, adequate, and excessive levels of P, respectively, in the form of triple superphosphate. Nitrogen fertilization was carried out by N topdressing with 300 mg dm^{-3} of N in installments during each regrowth period, being always incorporated with irrigation.

Sowing was carried out directly in the soil of each plot by manually depositing approximately 20 seeds of *M. maximus* cv. Zuri in a circular groove at a depth of 1 cm. After seedling emergence, thinning was performed, maintaining two plants per pot. At 30 days after sowing, a uniform cut was carried out at 17 cm from the ground level in all pots to stimulate tillering, initiating the splitting of nitrogen fertilization and Si application, as well as the period of data collection. On that occasion, 4 mg dm^{-3} of P were applied to the plants in the deficient treatment (Entisol) to enable the minimum growth of these plants.

Experimental conditions. The temperature and relative humidity inside the greenhouse were monitored daily using a thermo-hygrometer. The maximum average temperature recorded was equal to 46.3 ± 5 °C, with a minimum average temperature of 21.8 ± 3 °C and average relative humidity equal to 47.6 ± 10%.

The water-holding capacity or available water capacity (AWC) of the soils was determined. Two pots filled with each soil were subjected to saturation in a container with water for 24 h. After saturation, the pots were covered with plastic and removed from the saturated environment for free drainage. After draining, soil samples were dried in an oven and the AWC was determined by the difference between the masses of drained (wet) and dry soil. The management of water replacement was established by maintaining the soils at 70% of AWC, a condition indicated for Poaceae[54], under which water is available and gas exchanges are maintained in the root zone. The pots were weighed daily in the late afternoon, after which evapotranspirated water was replaced[55].

Silicon supply. Silicon was supplied daily from the moment of sowing until the last cut of the plants, using a solution of 1.5 mmol L^{-1} of Si[36]. The solution was prepared with colloidal nanosilica (particle size between 8.5 and 9.7 nm, specific surface area of 300 m^2 g^{-1}, and pH 10.5). The same volume of solution was applied in all treatments, with the volume being defined based on the treatment with the smallest daily water demand. Thus, in treatments with greater water demand, irrigation was supplemented with deionized water. The volume of solution applied was quantified at the end of the experimental period, totaling 26.2 and 22.3 L of solution applied per pot, providing 1.09 and 0.94 g per pot of Si in the Oxisol and Entisol, respectively. In plots that did not receive Si, irrigation was always performed with distilled and deionized water.

Analysis. *Height, tillering, and senescence of plants.* At the end of each of the two regrowth cycles, plant height (cm) was measured considering the length from the base to the inflection of the fully developed leaves, using a ruler. The number of tillers, as well as green and senescent leaves were counted to calculate the percent- age of senescent leaves per pot (%).

Biomass production. The plants were cut twice when reaching 70 cm in height in the treatment with adequate P content[56]. This height was reached at 25 and 31 days after the uniform cut in the Entisol and Oxisol, respectively, when the first cut was made. At 28 and 32 days of regrowth in the Entisol and Oxisol, respectively, the second cut was performed. The cut was performed using scissors, leaving 30 cm of residual material above the ground and collecting only the mass of the grazing strata of plants. Then, samples were washed in detergent solution (0.1% v:v) and deionized water, successively, being dried in an oven with forced air circulation (65 ± 5 ºC) until reaching constant mass. After reaching constant mass, shoot dry matter per plot was determined (DM, g per pot). The dried material was then passed through a Willey mill.

Contents of C, N, P, and Si. C content was determined through wet digestion of the dry matter with a $K_2Cr_2O_7$ solution and titration with $FeSO_4$ by the modified Walkley–Black method[57]. To evaluate N

content, the sample was submitted to digestion with sulfuric acid, distillation by the Kjeldahl method, and determination by titration[58]. P was determined from nitric-perchloric acid digestion and reading in a spectrophotometer at 420 nm[59]. Si was extracted with alkaline digestion in hydrogen peroxide at 120 °C[60] and determined by reading in a spectrophotometer at 410 nm after a colorimetric reaction with ammonium molybdate[51]. The contents of each element were expressed in g kg^{-1}.

Stoichiometric ratios and use efficiency. C:N, C:P, N:P, and C:Si stoichiometric ratios were calculated using the contents of the elements in the dry matter. The use efficiencies of C, N, and P were calculated using the expression: ((total dry matter produced)^2/(total accumulation of nutrient in the plant))[61].

Statistical analysis. The assumptions of the analysis of variance were verified by testing normality, homogeneity, independence of residuals[62,63], and the presence of outliers[64]. The data from each experiment were sub- mitted to analysis of variance using the F test ($p < 0.05$). Means were compared using the Student–Newman– Keuls (SNK) test at 5% probability, using the statistical software SPEED Stat, version 2.4[65].

3 Results

P, Si, C, and N contents. In most situations evaluated (cuts and soils) there was a significant P x Si inter- action ($p < 0.05$) in the P, Si, C and N contents, that is, Si influences these contents differently depending on the state of P. Similarly, the effect of P state can also be influenced by the absence or presence of Si. Plants cultivated in the condition of P deficiency and excess P in the absence of Si showed lower and higher levels of the element in the plant, respectively, in both soils and forage cuts (Fig. 1a–d). In the absence of Si, the nutritional status of P influenced the Si content in the plants, resulting in a higher Si content in plants under P deficiency and excess P in Entisol in the first cut and under excess P in the second cut, as well as in plants under P deficiency of P in Oxisol in the first cut (Fig. 1e–h). The C content in plants grown without Si application was lower under P deficiency in both cuts and under excess P in the second cut in Oxisol (Fig. 1i,k). In the cultivation in Entisol in the absence of Si, a lower C content was observed in treatments with excess P in both cuts, as well as under deficiency in the first cut (Fig. 1j,l). In the absence of Si, there was higher N content in the plant under excess P in both cuts and soils (Fig. 1m–p).

In the presence of Si in Oxisol, a reduction in P content was observed in the condition of excess P in the second cut (Fig. 1c), while in plants cultivated in Entisol there was a higher P content in P-deficient plants and a lower P content in P-excess plants, as well as a lower P content in plants with excess P in both cuts (Fig. 1b,d). The application of Si in relation to its absence promoted a higher Si content in the plant for all nutritional levels of P, soils, and forage cuts (Fig. 1e–h). The C content of plants was lower in the presence of Si for all nutritional levels of P in the first cut in Oxisol and in the second cut in Entisol, as well as under excess P in the first cut in Entisol and in the deficiency and sufficiency of P in the second cut in Oxisol (Fig. 1i–l). In the presence of Si, there was a lower N content in plants under P sufficiency in both cuts and under excess P in the second cut in Oxisol (Fig. 1m,o), as well as in plants under excess P grown in Entisol in both cuts (Fig. 1n,p).

C:Si, C:N, C:P and N:P stoichiometric ratios. The P *x* Si interaction was significant ($p < 0.05$) for the C:Si ratio in both soils and cuts, and in at least one cut in each soil type for the C:N, C:P and N:P ratios. Cultiva- tion with the absence of Si resulted in the lowest value of the C:N ratio in plants under P deficiency and excess P in both soils, with the exception of the deficiency in the second cut in Entisol, in which the C:N ratio was not affected (Fig. 2a–d). The absence of Si in forage plant cultivation also resulted in higher C:N and C:Si ratios in the adequate nutritional status of P in both soils, decreasing in plants with P imbalances, except for the second cut of plants under excess P in Oxisol and under P deficiency in Entisol (Fig. 2a–h). The highest C:P and N:P ratios occurred in plants under deficiency, while the lowest value of these ratios occurred in plants with excess P, respectively, in both cuts and soils (Fig. 2i–l; m–p).

Fertigation with Si provided a lower C:Si ratio for plants, regardless of soil type or cut (Fig. 2e–h). In plants grown in Entisol, the presence of Si resulted in the lowest C:P and N:P ratios under P deficiency in both cuts, while resulting in the highest value of these stoichiometric ratios in plants grown under excess P in the second cut (Fig. 2j,l,n,p). In plants cultivated in Oxisol, the presence of Si resulted in an increase in the N:P ratio under the adequate level of P in the second cut of the grass forage (Fig. 2i,k,m,o).

Use efficiency of P, C, and N. The P *x* Si interaction was significant ($p < 0.05$) for P use efficiency in the second cut in both soils. In the absence of Si fertigation, P use efficiency by the plants was higher under nutrient deficiency in both cuts and soils, except for the first cut in Oxisol (Fig. 3a–d). P deficiency and excess P in the forage grass resulted in lower C and N use efficiency by the plants in both soils and cuts, with the exception of P deficiency in Entisol in the second cut, in which N use efficiency was not affected (Fig. 3e–l).

When there was the addition of Si, a greater value for P use efficiency was observed in plants under the three nutritional levels of P in the first cut, as well as in plants under P deficiency in the second cut and cultivated in Entisol (Fig. 3b,d). In plants grown in Oxisol, the presence of Si resulted in a higher P use efficiency only under the adequate and excessive levels of P in both cuts (Fig. 3a,c), while higher C use efficiency was observed in plants under P deficiency in the second cut (Fig. 3g) and in the condition of excess P in both forage cuts (Fig. 3e,g). In plants grown in Entisol, fertigation with Si resulted in the highest C use efficiency in plants under both P imbalances, being restricted to the second cut (Fig. 3h). There was an increase in N use efficiency in plants grown with Si in adequate nutritional status and excess P grown in Oxisol (Fig. 3i,k), as well as in plants with excess P grown in Entisol in both cuts (Fig. 3j,l). There was no effect of Si on N use efficiency of P-deficient plants in any of the evaluated soils and cuts (Fig. 3i–l).

Height, tillering, senescence, and dry matter production. For the parameters plant height and percentage of senescent leaves, there was a significant P *x* Si interaction ($p < 0.05$) in the second cut in Oxisol, and also for the number of tillers in Entisol, while for the dry matter production the factors acted independently. In the absence of Si, plant height presented a lower value in the nutritional condition of

excess P in both soils and cuts, as well as in Entisol under P deficiency in both cuts in relation to plants with adequate P status (Fig. 4a–d). In the absence of Si, the lowest value for the number of tillers occurred in plants under P deficiency in both soils and cuts (Fig. 4e–h), while the highest value occurred in plants under excess P grown in Oxisol in the first cut (Fig. 4e). Excess P resulted in the highest rate of foliar senescence, except for the first cut in Oxisol (Fig. 4i–l).

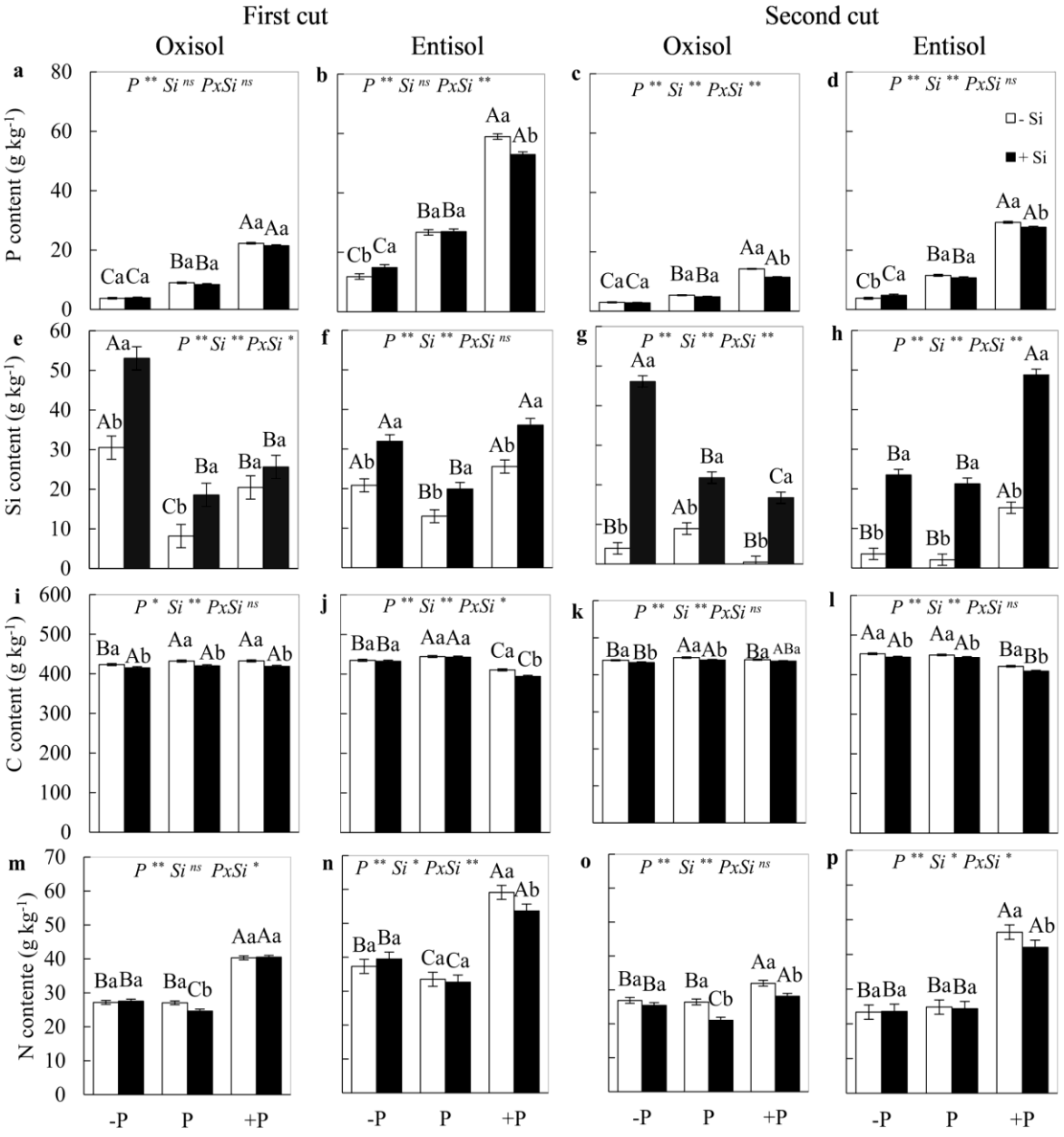


Figure 1. Phosphorous, silicon, carbon, and nitrogen content in the dry mass of the forage plant *M. maximus* cv. BRS Zuri, in the first (**a,b,e,f,i,j,m,n**) and second cuts (**c,d,g,h,k,l,o,p**), cultivated under phosphorus levels of deficiency (− P), adequacy (P), and excess (+ P) in Oxisol and Entisol, in the absence (− Si) and presence (+ Si, 1.5 mmol L^{-1}) of silicon. Ns, * and ** correspond to the non-significant F-test, significant at 5 and 1%, respectively. Lowercase letters indicate differences from Si within each phosphorus level, while uppercase letters indicate phosphorus levels according to the Si condition (SNK test, 5% probability). Bars represent the standard error of the mean, n = 4.

Shoot dry matter production in the absence of Si showed the lowest value in P-deficient plants grown in Oxisol in both cuts (Fig. 4m,o), as well as in plants grown in Entisol in the first cut (Fig. 4n). In plants under excess P and under the absence of Si, the lowest dry matter production occurred in Entisol and in both cuts (Fig. 4n,p). However, when plants were cultivated in Oxisol, this occurred only in the first cut (Fig. 4m).

Under excess P, plants fertigated with Si showed an increase in height in both soils and cuts, except for the first cut in Oxisol (Fig. 4a–d). In plants grown in Oxisol, there was a greater number of tillers in the adequate level of P in both cuts (Fig. 4e,g), as well as under excess P in the first cut in relation to the absence of Si (Fig. 4e). In plants grown in Entisol in the presence of Si, there was a greater number of tillers in plants under excess P in both cuts (Fig. 4f,h).

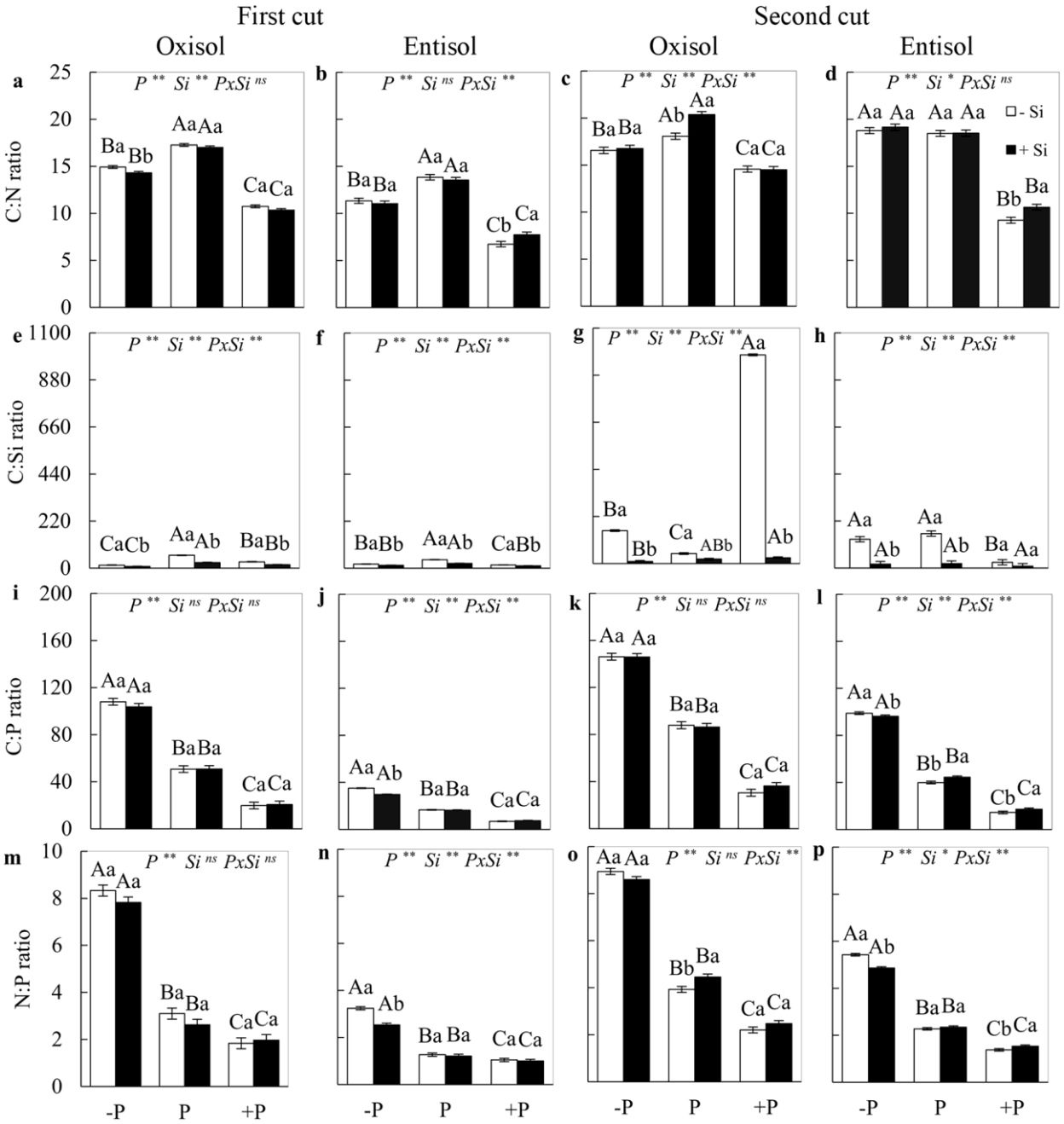


Figure 2. C:N, C:Si, C:P and N:P stoichiometric ratios in the forage plant *M. maximus* cv. Zuri, in the first (**a,b,e,f,i,j,m,n**) and second cuts (**c,d,g,h,k,l,o,p**), cultivated under phosphorus levels of deficiency (– P), adequacy (P), and excess (+P) in Oxisol and Entisol, in the absence (–Si) and presence (+Si 1.5 mmol L^{-1}) of silicon. Ns, * and ** correspond to the non-significant F-test, significant at 5 and 1%, respectively. Lowercase letters indicate differences from Si within each phosphorus level, while uppercase letters indicate phosphorus levels within each Si condition (SNK test, 5% probability). Bars represent the standard error of the mean, n = 4.

Under excess P, plants fertigated with Si showed an increase in height in both soils and cuts, except for the first cut in Oxisol (Fig. 4a–d). In plants grown in Oxisol, there was a higher number of tillers under the adequate level of P in both cuts (Fig. 4e,g), as well as under excess P in the first cut in relation to the absence of Si (Fig. 4e). In plants cultivated in Entisol and in the presence of Si, there was a greater number of tillers in plants under excess P in both cuts (Fig. 4f,h).

The rate of leaf senescence decreased with the addition of Si in relation to its absence in plants grown in Oxisol in the three nutritional levels of P and both cuts (Fig. 4i,k). In plants cultivated in Entisol, the rate of leaf senescence decreased with the addition of Si in plants under excess P in both cuts, as well as in the adequate level of P in the second forage cut (Fig. 4j,l). Si supply increased the dry matter production of plants under excess P grown in Entisol in both cuts (Fig. 4n,p), as well as in plants grown under adequate and excessive levels of P in Oxissol, in both cuts (Fig. 4m,o), with no effect on macronutrient deficiency in any of the soils or cuts.

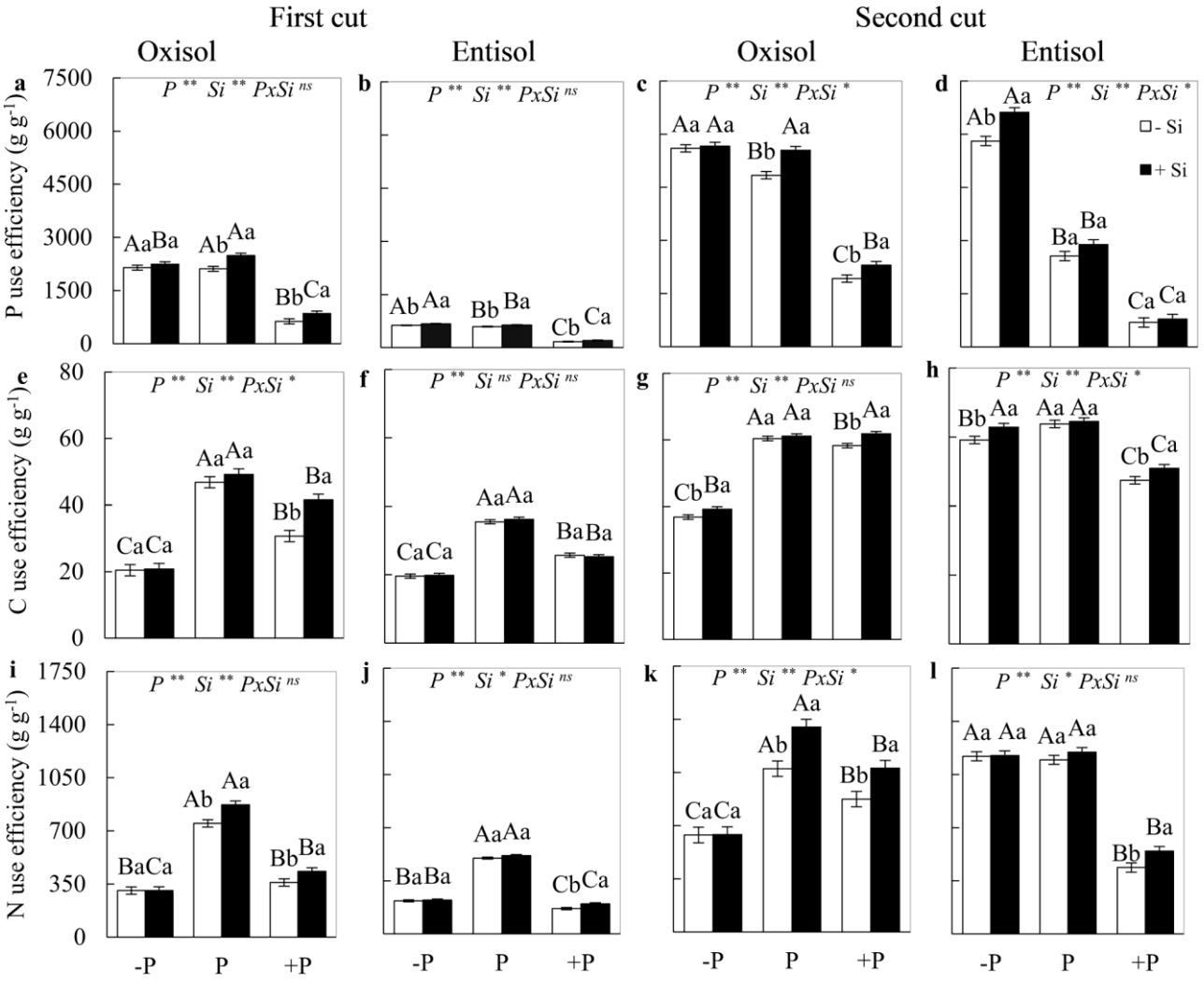


Figure 3. Use efficiencies of phosphorus, carbon, and nitrogen in the forage plant *M. maximus* cv. BRS Zuri, in the first (**a,b,e,f,i,j**) and second cuts (**c,d,g,h,k,l**), cultivated under phosphorus levels of deficiency (− P), adequacy (P), and excess (P) in Oxisol and Entisol, in the absence (− Si) and presence (+ Si, 1.5 mmol L^{-1}) of silicon. Ns, * and ** correspond to the non-significant F-test, significant at 5 and 1%, respectively. Lowercase letters indicate differences from Si within each phosphorus level, while uppercase letters indicate phosphorus levels within each Si condition (SNK test, 5% probability). Bars represent the standard error of the mean, n = 4.

4 Discussion

Biological damage caused by P imbalances in the plant without Si supply. The deficiency of P in the forage was clear, as plants cultivated without P application showed low P levels both in the plant cultivated in Oxisol (3.4 g kg^{-1}) and in Entisol (7.8 g kg^{-1}) in relation to the plant grown under the adequate P level in Oxisol (7.2 g $kg^{-1)}$ and Entisol (19.1 g kg^{-1}). P deficiency in the plant was expected, as the soils used in this experiment presented low levels of available P. This is common in weathered soils, especially in Oxisol, which has a high phosphate adsorption capacity[66,67].

Studies on the deficiency of P in forage plants are restricted to the evaluation of nutrient levels and symptoms[68–70], not analyzing whether this disorder causes stoichiometric changes. Thus, for the first time in a forage plant, it was verified that P deficiency decreased the C:Si ratio in plants, especially in the first cut, in plants grown in sandy or clayey soil. This is because plants deficient in P presented a higher Si content

compared to those under sufficiency due to greater Si absorption even without application of the element. This result confirms that the forage plant develops the ability to absorb natural Si from the soil when subjected to nutritional stress[24]. It is possible that the increase in Si absorption may have been favored by the liming of the soil, as phytoliths (a material rich in Si previously deposited in the soil) can be dissolved through an increase in the pH of the solution[71], favoring the availability of the element in the soil. However, in the second cycle there was a decrease in Si content in these P-deficient plants compared to the first forage cycle, confirming that although phytoliths are a source of Si[72,73], they do not sustain Si uptake over successive cuts.

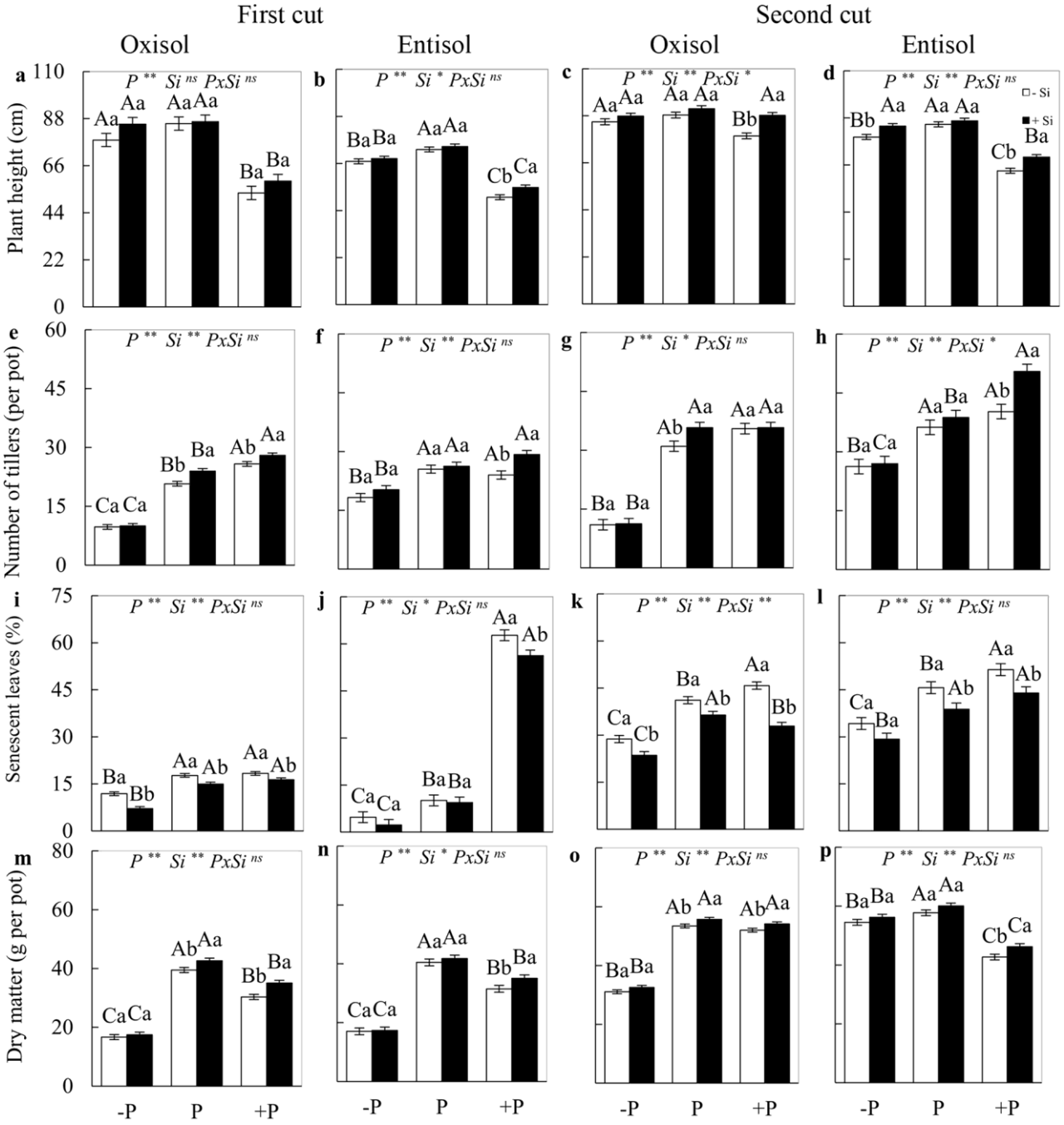


Figure 4. Plant height, number of tillers, rate of leaf senescence, and biomass production in the grazing strata, in the first (**a,b,e,f,i,j,m,n**) and second cuts (**c,d,g,h,k,l,o,p**), in the forage plant *M. maximus* cv. BRS Zuri cultivated under phosphorus levels of deficiency (− P), adequacy (P), and excess (+ P) in Oxisol and Entisol, in the absence (− Si) and presence (+ Si, 1.5 mmol L^{-1}) of silicon. Ns, * and ** correspond to the non-significant F-test, significant at 5 and 1%, respectively. Means were tested by the SNK test at 5% error probability. Uppercase letters compare means between nutritional levels and lowercase letters compare the effect of Si. Bars represent the standard error of the mean, n = 4.

P deficiency by decreasing the C content of the plants compared to those under sufficient or adequate levels of P reflected in a decrease in the C:N ratio of the forage in both soils and cuts, except for the second cut in plants grown in Entisol. The decrease in C content in P-deficient plants observed in this study is similar to that reported for another species (*Holcus lanatus*)[74], which confirms the essential role played by P in the assimilation of C, as it regulates photosynthesis by acting as substrate, product, and/or effector of enzymes of the C4 pathway in mesophyll cells[68,75]. Thus, even with a possible recycling of P in deficient plants[8], it is not enough to meet the demand of the plant organs generating nutrient deficiency, and its damage is well documented in photosynthetic efficiency[47].

Changes in C:N:P stoichiometric ratios in deficient plants resulted in greater P use efficiency compared to plants grown under P sufficiency. This is natural in plants grown in soils with restricted P contents due to mechanisms such as membrane remodeling with P-free lipids (such as galacto and sulfolipids)[70] or due to the preservation of P in inorganic forms, facilitating its remobilization[76]. However, there was a decrease in the use efficiencies of N and C because the conversion of N and C into biomass depends on P cellular homeostasis, as it is essential to the physiological and biochemical processes in plant cells, being a component of nucleic acids and membrane lipids, as well as a mediator of the energy metabolism[77,78].

The efficiency of plants to use absorbed nutrients to compose its tissues has a direct influence on biomass production[61,79]. Therefore, P deficiency in relation to P-sufficient plants reduced nutritional homeostasis and the use efficiency of C and N, affecting forage plant growth in both cycles and in the two soils studied, with a decrease in dry matter production dries of 50 and 31% in plants grown in Oxisol and Entisol, respectively. These losses have been commonly reported in Poaceae cultivated under low levels of P[44,80], limiting the productive capacity of pastures in tropical soils[3,4].

Another important nutritional disorder in plants is P toxicity. It is still little reported in forage grasses, especially in crops without silicate fertilization, which is the condition of most pastures in the world. In this research, it was clearly evident that the high dose of P applied reflected in high average levels of P in the plant, reaching approximately 18.3 and 44.2 g kg^{-1} compared to the treatment under P sufficiency, which presented 7.2 and 19.1 g kg^{-1} of P in plants grown in Oxisol and Entisol, respectively. It should be noted that the lower P content in plants grown in Oxisol compared to Entisol is probably due to the greater adsorption of the element in Oxisol, reducing P availability in the soil and its absorption by the plant[80]. The opposite occurred in Entisol, which provided high levels of P in the plant due to the low clay content in this soil, giving it a low adsorption capacity for phosphate and greater availability for the plant, with a greater risk of toxicity in the plants[81,82].

It is worth mentioning that the stress resulting from excess P in the plant stimulated the absorption of residual Si from the soil by the forage plant (as it occurred under P deficiency). This confirms that the plant uses the strategy of absorbing Si even at low levels in the soil, which may be a plant defense mechanism to mitigate stresses[24,83]. An aspect not yet reported in forage plants is the effect of toxicity or excess P on C:N:P stoichiometry. It was evidenced in this research that the excess P in relation to the sufficiency of P affected the C:N:P stoichiometric ratios in the forage, with a decrease in the C:P, N:P , and C:N ratios in the two studied soils. The C:N ratio is highlighted for decreasing on average 28 and 49% in plants grown in Oxisol and Entisol, respectively. This reduction was due to the combination of a lower C content and a higher N content in plants under excess P, inhibiting the activation of RubBisCO by decreasing photosynthesis[15,84].

In addition, we also showed that lower C:P and N:P ratios may indicate that C and N can limit P toxicity in the plant. Although there was a greater N uptake, the generated stoichiometric imbalance limits the use of nutrients[85]. Thus, the loss of C:N:P homeostasis had nutritional consequences on the plant, as it decreased the use efficiencies of P, C, and N in plants grown in both soils and cuts because the conversion of nutrients into biomass depends on the possibility and/or capacity of the plant to maintain sufficient concentrations while maintaining in stoichiometric equilibrium in the tissues[19,86].

As a result of the decrease in nutrient use efficiencies, excess P reduced plant growth, decreasing plant height and increasing the rate of leaf senescence in plants cultivated in both soils, thus causing a 24% decrease in dry matter production in the two soils and two cuts of forage cultivated in Entisol, while causing a 23% decrease in the first cycle of plants cultivated in Oxisol. Thus, the physiological damage of P toxicity (especially in photosynthesis)[17,84] was previously induced by nutritional disturbances in elemental homeostasis.

Reflections of P imbalance were observed for the first time in the species *M. maximus*. P toxicity begins with an excess of thin tillers and leaves with reduced length, not very rigid and decumbent (Fig. 5a,b). In addition, there was chlorosis in older leaves, with purplish spots that progress to necrosis from the apex to the base in the leaf blade (Fig. 5c), bein similar to what was described in leaves of wheat and rice plants under P toxicity[84,87].

Thus, the observed results allow accepting the first and second hypotheses tested, as it was shown that P imbalances modify the C:N:P stoichiometry of the forage and that P toxicity caused a greater stoichiometric imbalance especially in plants cultivated in a sandy soil (Entisol). Therefore, the risk of facing P toxicity is high for forages grown in Entisol, requiring a rigorous management of this nutrient.

Benefits of Si in mitigating stress under P deficiency and toxicity in grass forage. Si is a well- known element to attenuate different abiotic stresses in many crops. However, in forage plants, studies evaluating P deficiency were carried out only in hydroponic cultivation[36,44], and there is a lack of reports of crops in different soils, especially regarding P toxicity. This is worrying, as forage crops are grown in different soils worldwide, with vast areas cultivated in Oxisol and Entisol. Thus, it is important to know if Si is really capable of mitigating these stresses under these cultivation conditions.

Initially, it was evident that plants cultivated under P deficiency in Entisol and that received the application of Si nanoparticles presented an increase of 21% in the P content in relation to those that did not receive Si. It is important to note that the levels of Si in the plant were higher in deficient plants than in plants under P sufficiency as a in response to stress. Therefore, a higher Si content in the soil, and consequently in the plant, has the ability to positively regulate the gene expression of P transporters, in addition to favoring the availability of P in the soil by stimulating the exudation of malate and citrate in Poaceae[88], decreasing the adsorption and favoring the uptake of P by the plant. In this context, the use of Si can favor a greater use of the P present in the soil by pastures, which is essential, since nutrient reserves are finite[89] 25% of the land cultivated with pastures has soils with low P content[1,4].

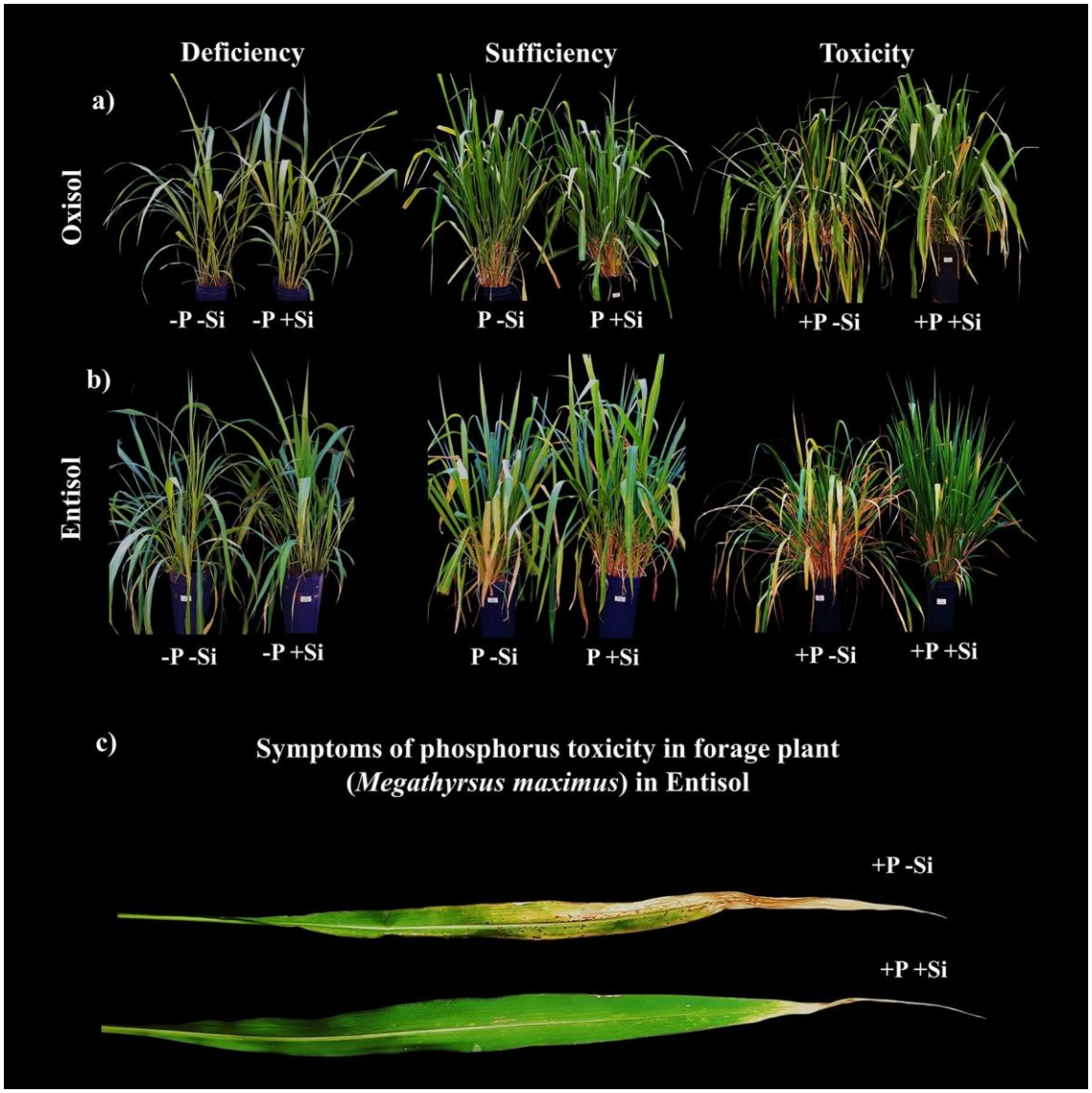


Figure 5. Visual aspects of *M. maximus* cv. Zuri under phosphorus deficiency (− P), sufficiency (P), and toxicity (+ P) combined with the absence (− Si) and presence of Si (+ Si) nanoparticles grown in Oxisol (**a**) and Entisol (**b**); details of symptoms of P toxicity in *M. maximus* in the absence and presence of Si (**c**).

Additionally, Si promoted a decrease in C:P and N:P ratios in the two cycles in Entisol, thus promoting a 9% increase in the P use efficiency by the plant. This was also reflected in greater C use efficiency in the second forage cut in both soils. Complementarily, we carried out a Pearson correlation analysis between the studied variables and the DM production of the deficient plants, and we observed that the use efficiencies of C ($r = 0.996^{*}$) and P ($r = 0.991^{*}$), as well as the C:P ratio ($r = 0.986^{*}$) were the ones that most contributed to DM production in both soils. A similar action was observed in rice plants deficient in N, in which Si promoted greater nutritional homeostasis, contributing to the efficient use of nutrients[35]. The benefits of Si in the balance of C:N:P stoichiometry were not enough to increase the efficiency of N use in the forage in the two cuts and in the two soils. Consequently, there was no increase in the number of tillers or in dry matter production by plants deficient in
P. However, other authors have observed this effect of Si in other pastures[46] and in sorghum[47]. It is possible that the effect of Si on C:N:P homeostasis did not reach a sufficient level to favor greater accumulation of biomass and mitigate P deficiency in the forage within the growth cycle studied. Considering the potential of Si presented in our study, we reinforce the need for further research aimed at studying the mitigating action of Si on P-deficiency stress in Poaceae plants.
It was verified that P toxicity was severe in plants that did not receive Si, showing a limiting nutritional disorder. In this research, we observed that in plants cultivated under excess P, the increase in the absorption of the Si applied to the soil in the form of nanosilica reduced the P content

in the two cuts of the forage cultivated in Entisol, as well as in the second cut in Oxisol, revealing that Si negatively modulates P absorption in conditions of excess. One of the possible ways to attenuate P toxicity by Si is the modulation of the gene expression of P transporters[90], which has already been demonstrated in rice[8] and depends on the translocation and accumulation of Si in the shoot[91]. Forages have a good capacity for Si absorption, as they are a Si-accumulating plants[29], especially when the element is supplied in the form of nanosílica[92].

The increase in Si absorption in relation to its absence in P-deficient plants caused changes in stoichiometric ratios in the forage, especially in the second cut of the plant cultivated in Entisol, with lower C:P and N:P ratios, which is due to the greater P uptake. Furthermore, Si increased the C:N ratio in the forage in both cuts in Entisol, improving stoichiometric homeostasis. Therefore, for the first time there is a report on the potential of Si to modify C:N:P stoichiometry in forage plants cultivated under excess P, but this depends on the soil used for cultivated, as it stood out more in Entisol, probably due to the greater severity of macronutrient toxicity. Research on the effects of Si on C:N:P stoichiometry in stressed plants[93], of water deficit in sugarcane[43,55,94], and of the effect of Si in the forage plant *M. maximus* are recent[38].

The effects of Si in relation to its absence on the C:N:P homeostasis of forage plants cultivated under P toxicity was sufficient to increase nutritional efficiency, highlighting the efficiency of N use, providing an average increase of 18% in this efficiency, in the two cycles and soils. There was also an increase in the use efficiency of C and P depending on the forage cut. These added effects on nutritional efficiency were sufficient to favor forage growth under excess P by increasing height and number of tillers in both soils, consequently increasing forage dry matter production. In Pearson's correlation analysis, we observed that the use efficiencies of C ($r = 0.996^{*}$), P ($r = 0.979^{*}$) and N ($r = 0.945^{*}$) in Entisol, and the efficiencies use of C (0.996^{*}), and N ($r = 0.949^{*}$) and plant height ($r = 0.901^{*}$) in Oxisol, were the ones that most contributed to the increase in DM in plants under P toxicity.

An important aspect favored by Si to attenuate P toxicity and plant growth was its strong and constant effect of decreasing the rate of leaf senescence in all soils and growth cycles. It is possible that this effect of Si on leaf senescence may be related to the increase in N use efficiency, as this nutrient increases the period when leaves are photosynthetically active[78] and also deletes genes related to mechanisms for the induction of senescence[95]. This effect of Si in reducing leaf senescence is little studied, being only reported in plants cultivated under water deficit, such as rice[96] and sorghum[97], and under sulfur deficiency, such as in barley plants[95]. In this paper, this effect was visually noticed (Fig. 5a,b,c).

It was also possible to visually notice the benefits of Si in mitigating P toxicity, since the damage caused by this previously described nutritional disorder was not observed when the plants received Si (Fig. 5), which presented better plant architecture, as already observed in rice plants[98] due to greater rigidity in the plant tissues[73]. In parallel, another benefit of Si in the plant would be its effect of increasing the energy in plant metabolism, which would favor the antioxidant defense mechanisms of plants due to P toxicity, providing components for the Poaceae cell wall, ensuring structural resistance, and reducing the need for lignin synthesis (which demands a high energy content)[99,100]. This energy can be used in the organic synthesis of plant defense compounds against stress.

Our results indicate that forages are sensitive to P toxicity, causing an imbalance of C:N:P stoichiometry in the plant, and that the use of nanosilica via fertigation can mitigate this stress, making the pasture productive again and providing environmental implications. Excess P in the soil is at risk of contaminating water systems[101–103], and with forage cultivation under fertigation with Si, the P extracted from the soil would be continuously exported in the forage, without risk to the environment.

Thus, the third hypothesis of this research can be partially accepted, since fertigation with Si enabled to attenuate the excess P in both soils, but its benefits were not sufficient to mitigate P deficiency in the evaluated period. This reinforces in an unprecedented way that Si is more effective to attenuate P toxicity in relation to P deficiency in this species.

Benefits of Si in forage plants under P sufficiency. Surprisingly, it was observed that in plants cultivated under P sufficiency, the supply of Si resulted in a change in stoichiometry, balancing the C:N and N:P ratios, especially in forages cultivated in Oxisol, also balancing the C:P ratio in Entisol in the second cut. Therefore, the potential of Si to increase nutritional efficiency in forages is unveiled due to greater stoichiometric homeostasis, especially of C:N and N:P. These changes in stoichiometry resulted in an increase in the use efficiency of P and N in the two forage cuts with sufficient P, associated with a decrease in the rate of senescent leaves and an increase in tillering. Consequently, there was an increase of approximately 5% in the dry matter production of plants cultivated in Oxisol. In Entisol, stoichiometric changes were restricted and were not sufficient to increase dry matter production in plants under sufficiency of P.

The role played by silicon as a facilitator of the balance of mineral nutrients in the plant and a mediator of morphological and biochemical changes[104,105] may explain the increase in plant growth even without nutritional stress. Furthermore, high levels of Si in the shoots, such as those found in this study, favor the expression of the benefits of Si to plants, with recent studies reporting production gains due to stoichiometric balance and efficiency in the use of macronutrients such as N and P in different species cultivated without stress, such as forage plants cultivated in a hydroponic system[36,44], sugarcane[37,106], and sorghum [107].

These results have an important practical implication, as they allow indicating this beneficial element via fertigation for the cultivation of forage without P imbalances, especially if cultivated in Oxisol in an irrigated system.

5 Conclusions and future perspective

Fertigation with Si nanoparticles promotes the absorption of the element by the forage, improves C:N:P homeo- stasis and the nutritional efficiency of plants cultivated under P deficiency and excess P, and reduces plant senescence regardless of P level, attenuating the stress caused especially by P toxicity in Entisol and in Oxisol, as well as in plants without nutritional stress grown in Oxisol.

The supply of Si increases the dry mass production of plants in the excessive state of P grown in Entisol, and also in plants grown under adequate and excessive states of P in Oxissol. Leaf senescence showed a lower value with addition of Si in plants grown in Oxisol in the three nutritional states of P.

The research revealed that using Si via fertigation triggers modifications in C:N:P stoichiometry that are relevant to the cultivation of *M. maximus* cv. Zuri, although the magnitude of the effects depends on the growth cycle, soil, and P nutritional status.

This study opens the way to expand research on the potential of Si via fertigation in forages of other species and also in other soils, having global implications in view of the occurrence of P deficiency and toxicity, which undermine the sustainability of forage cultivation in many countries.

Data availability

Datasets generated or analyzed during the present study are available from the corresponding author upon reasonable request.

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Author contributions

C.C.F.M. wrote the main text of the manuscript; D.S.A. assisted in conducting the experiments and statistical analyses; R.M.P. guided nutritional analyzes and the revision of the manuscript; A.M.Z. and D.J.F. helped to adapt methodologies for conducting the experiments; and M.C.P. contributed with laboratory structure and analysis.

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Competing interests

The authors declare no competing interests.

Additional information

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RESEARCH Open

Nanosilica enhances morphogenic and chemical parameters of *Megathyrsus maximus* grass under conditions of phosphorus deficiency and excess stress in different soils

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Abstract

Phosphorus (P) imbalances are a recurring issue in cultivated soils with pastures across diverse regions. In addition to P deficiency, the prevalence of excess P in soil has escalated, resulting in damage to pasture yield. In response to this reality, there is a need for well-considered strategies, such as the application of silicon (Si), a known element for alleviating plant stress. However, the influence of Si on the morphogenetic and chemical attributes of forage grasses grown in various soils remains uncertain. Consequently, this study aimed to assess the impact of P deficiency and excess on morphogenetic and chemical parameters, as well as digestibility, in Zuri guinea grass cultivated in Oxisol and Entisol soils. It also sought to determine whether fertigation with nanosilica could mitigate the detrimental effects of these nutritional stresses. Results revealed that P deficiency led to a reduction in tiller numbers and grass protein content, along with an increase in lignin content. Conversely, P excess resulted in higher proportions of dead material and lignin, a reduced mass leaf: stem ratio in plants, and a decrease in dry matter (DM) yield. Fertigation with Si improved tillering and protein content in deficient plants. In the case of P excess, Si reduced tiller mortality and lignin content, increased the mass leaf:stem ratio, and enhanced DM yield. This approach also increased yields in plants with sufficient P levels without affecting grass digestibility. Thus, Si utilization holds promise for enhancing the growth and chemical characteristics of forage grasses under P stress and optimizing yield in well-nourished, adapted plants, promoting more sustainable pasture yields.

Keywords Silicon fertigation, Zuri guinea grass, Phosphorus nutritional stresses, Lignin, Tillering

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1 Background

Yield in pastoral ecosystems worldwide is susceptible to phosphorus (P) limitation, particularly in tropical regions where deficiencies are prevalent [1]. In these regions, extensive weathering, and the high phosphate adsorption capacity of soils diminish nutrient availability, particularly in clayey soils [2]. This necessitates phosphate fertilization to sustainably boost forage yield [3]. Conversely, in intensive agriculture, the frequent application of high doses of phosphorus (P) fertilizers, whether conventional or organic, can result in excessive P accumulation within plants, surpassing the quantities exported from the fields [4]. This leads to nutritional imbalances and an overabundance of P within plant tissues [5, 6]. The risk of P excess is further exacerbated in soils with a sandy texture (clay content < 15%), where phosphate availability is heightened due to relatively low element adsorption in the soil [2].

Within plants, the cellular balance of inorganic phosphate (Pi) plays a fundamental role in converting nutrients such as carbon (C) and nitrogen (N) into biomass, as P serves vital metabolic and structural functions [5, 7]. Phosphorus imbalances compromise plant physiological processes [8], consequently affecting the morphogenic processes that determine forage growth. For instance, disruptions in P levels within the plant can diminish leaf and stem appearance and elongation [9, 10], as well as plant tillering [11–13], ultimately reducing forage yield and pasture sustainability.

The repercussions of P imbalances within plants extend beyond growth rates and biomass yield to influence for- age quality. Forage grasses encompass carbohydrates, proteins, lipids, fibers, lignin, minerals, and vitamins, all of which significantly impact herd productivity [14]. Nutritional imbalances can alter these components, potentially affecting the nutritional value of the pasture [15, 16]. However, further research is needed to comprehensively understand these effects.

Given the global prevalence of P imbalances in plants [1, 4], there is an urgent need for strategies to mitigate these losses. Research efforts have been directed toward finding more efficient and sustainable methods for phosphate nutrition in forage plants [17]. One emerging option for addressing these imbalances involves silicon (Si), with initial reports suggesting promise in mitigating nutritional deficiencies [18]. However, these studies have primarily focused on soilless hydroponic cultivation [19, 20], leaving the role of Si in the morphogenetic responses of grasses under P deficiency when cultivated in soil unexplored. Moreover, the effects of excess P on grasses remain largely unknown, including its impact on plant morphogenesis, necessitating further investigation. It is conceivable that Si may also contribute to alleviating excess P, given its known benefits to this plant group (Poaceae) when subjected to other nutritional stresses [21, 22].

It is important to note that the potential benefits of Si in stress mitigation hinge on the plant's high uptake of the element, which, in turn, depends on the source used. Recent advancements in nanotechnology have introduced the option of nanoparticulate silicon [23], which holds the potential to enhance Si uptake due to the monomeric size of SiO_2 particles that remain stable in solution [24, 25]. Consequently, there is an expectation that employing this Si source may offer promising prospects for mitigating nutritional stress, warranting further investigation.

To shed light on the effects of P imbalances in forage grasses and the potential benefits of Si in alleviating these stresses, it is crucial to address the following questions: (i) How does damage resulting from P deficiency and excess affect the morphogenesis of *Megathyrsus maximus* cv. Zuri grass and impede P yield? (ii) Does it influence chemical parameters and the digestibility of plant biomass? (iii) Is nanosilica fertilization an efficient strategy?

In other words, does it enhance Si uptake by the plant, thereby mitigating the damage caused by P deficiency and excess through improvements in plant morphogenesis and forage quality when cultivated in both clayey and sandy soils?

If these hypotheses are substantiated, it will mark the first comprehensive understanding of how this forage grass species responds to morphogenic changes when subjected to P deficiency or excess and how this affects forage quality. Furthermore, it may indicate the utility of employing nanoparticulate Si in forage cultivation to ameliorate issues related to P deficiency or excess in soils of varying textures, thereby bolstering the sustain- able cultivation of this species in regions grappling with P imbalances.

2 Methods

Experimental design and cultivation environment

Two experiments were conducted with *Megathyrsus maximus* cv. Zuri, cultivated in Oxisol (Experiment 1) and Entisol (Quartzipsamment) (Experiment 2) [26] under greenhouse conditions. These experiments were carried out at São Paulo State University, Jaboticabal, Brazil, spanning from October 2021 to April 2022. Through- out this period, six defoliation intervals were imposed, corresponding to six growth cycles. Cultivation occurred under full natural light conditions. Inside the greenhouse, the average maximum air temperature reached 47 ± 5 °C, while the average minimum temperature was 22 ± 5 °C, with an average relative humidity of 50 ± 10%.

The soils were collected from the surface layer of the uncultivated area, in the 0 to 20 cm layer, and the samples were air-dried and passed through a 6-mm mesh sieve. Both experiments followed a 3 × 2 factorial design, encompassing three phosphorus nutritional states: deficient (no P application), sufficient (200 mg dm^{-3} of P) [27], and excessive (600 mg dm^{-3} of P). These states were combined with the absence of silicon (Si) application (no Si) and the presence of Si (1.5 mM Si solution) [28]. The experiments were arranged in a completely randomized design with four replications. Each experimental unit consisted of a plastic pot with a volume of 7.2 L (dimensions: height 32 cm, bottom base 14 × 14 cm, and top 16 × 16 cm), filled with Oxisol or Entisol samples, each pot containing two plants.

Characterization of soils and application of treatments

Soil samples were collected from native forests and subsequently subjected to chemical analysis following established procedures [29]. The results for Oxisol and Entisol, respectively, were as follows: pH $CaCl_2$ = 3.8 and 4.3; organic matter (OM) = 34 and 9.0 mg dm^{-3}; P in resin extractor = 12 and 2 mg dm^{-3}; K = 1.4 and 3.0; Ca = 6 and 3.0; Mg = 2 and 1.0 mmolc dm^{-3}; H + Al = 85 and 16; and cation exchange capacity (CEC) = 94 and 20.3 mmolc dm^{-3}. Silicon contents were determined [30], yielding the following outcomes: 3.0 and 1.0 g dm^{-3} for Oxisol and Entisol, respectively. Granulometric analysis, conducted according to [31], provided the following results for Oxi- sol and Entisol, respectively: 51 and 94% sand, 6 and 1% silt, and 43 and 5% clay, with texture [32] sandy clay (Oxi- sol) and sand (Entisol).

To address soil requirements, liming was carried out using limestone with a total neutralization power of 125%, consisting of CaO (58.5%) and MgO (9%), to correct acidity and increase base saturation to 70% [29]. Forty days after liming, phosphorus (P) was incorporated into the soil at varying rates: 0, 200 [27], and 600 mg dm^{-3} of P, administered in the form of triple superphosphate, corresponding to the deficiency, sufficiency, and excess P treatments, respectively. Additionally, 225, 50, 5, and 0.5 mg dm^{-3} of K, S, Zn, and B were applied to both soil types. The sources used were potassium chloride (52.4% K), calcium sulfate dihydrate (18% S), zinc sulfate heptahydrate (35% Zn), boric acid (17% H_3BO_3), and iron chelate (EDDHA) (6% Fe). Nitrogen (300 mg dm^{-3}) was provided incrementally

during each regrowth period in the form of urea (45% N), with subsequent irrigation. In Entisol, an additional 5 mg dm^{-3} of Fe was required.

Sowing was directly performed in the soil using seeds from the Zuri grass cultivar, developed by the Brazilian Agricultural Research Corporation and commercially acquired. Each pot contained two plants, which under- went a standardization cut at 17 cm above ground level 30 days after sowing, marking the commencement of the data collection phase. In the case of the treatment deficient in Entisol (0 mg dm^{-3} of P), an additional 4 mg dm^{-3} of P was applied on the day of standardization to facilitate minimal plant growth, whereas Oxisol did not necessitate such intervention for minimal plant development. Irrigation management was conducted to maintain soil water retention at 70%, monitored by daily pot weighing and compensating for water losses due to evapotranspiration [33, 34].

Silicon application occurred daily from the sowing date, utilizing a 1.5 mmol L^{-1} Si solution [28]. Colloidal nanosilica served as the Si source, characterized by particle sizes ranging from 8.5 to 9.7 nm, a specific surface area of 300 m^2 g^{-1}, and a pH of 10.5. The same volume of solution was applied across all treatments, with the daily volume determined based on the treatment with the lowest water demand. On average, 102 and 69 mg dm^{-3} of Si were administered during each forage regrowth in Oxisol and Entisol, respectively. In treatments without Si application, irrigation was performed using deionized water. Cuts were executed when plants under P sufficiency reached a height of 70 cm, leaving a residual biomass of 30 cm in height [35].

Variables analysed

Morphogenic and structural variables

Growth monitoring encompassed six regrowth cycles of the plants. In each regrowth phase, two tillers per pot were meticulously selected and distinguished with colored ribbons. These tillers were examined every three days, focusing on the exposure of ligules, stem length, and the length of leaf blades in various states: expansion, expanded, or undergoing senescence. At the end of each growth cycle, the following parameters were assessed immediately before plant cutting: number of leaves per tiller, number of tillers per pot, count of live and dead leaves, and tiller diameter, with measurements performed using a digital caliper.

Following data collection, the subsequent variables were computed in accordance with [10]: leaf appearance rate (LA, leaves per tiller per day), leaf elongation rate (LE, measured in millimeters per day), number of live leaves per tiller, stem elongation rate (SE, expressed in millimeters day^{-1}), and stem diameter (SD, measured in millimeters). Tillering was also evaluated, considering the following parameters: number of tillers per pot, tiller appearance rate (TA = number of new tillers per total tillers alive in the previous cycle)/days of regrowth, tiller mortality rate (TM = number of dead tillers per total tillers alive in the previous cycle)/number of regrowth days, and tiller survival rate (TS = 1-TM) [36, 37].

Yield and morphological fractions

The average dry matter (DM) yield was determined through six collections of biomass from the plant's grazing stratum [35]. In each collection, the morphological components, including leaf blades, stems, and dead material, were isolated from the biomass and measured in grams of fresh weight. This material was then placed in paper bags and subjected to drying in an

oven with forced air circulation (maintained at 65 ± 5 ºC) until a constant mass was achieved. Subsequently, the dry matter (DM) content of the leaf blades, stems, and dead material was determined. Finally, the percentage composition of each morphological component, the mass leaf blade:stem ratio, and the total DM yield (in grams per pot) were calculated.

P and Si contents

P and Si contents in DM (composite samples with subsamples of the five growth cycles analyzed) of the grazing stratum were determined. To determine P, the sample was subjected to nitric-perchloric digestion, with a spectrophotometer reading at 420 nm [38]. Si extraction was carried out by alkaline digestion in hydrogen peroxide at 120ºC [39], and determined by spectrophotometer reading at 410 nm after colorimetric reaction with ammonium molybdate [30]. P and Si contents were expressed in g kg^{-1}.

Chemical composition of forage

The processed material underwent milling using a Willey-type mill, enabling the determination of percentages for neutral detergent fiber (NDF), acid detergent fiber (ADF), and lignin in the dry mass [40, 41]. This data was used to calculate hemicellulose (the difference between NDF and ADF) and cellulose (the difference between ADF and lignin) contents. Additionally, the percent- ages of mineral matter (MM), non-fiber carbohydrates (NFCs), and crude protein (PB% = N content x 6.25, with N determined using a LECO Truspec CHNS analyzer) (AOAC, 2012) were computed. In vitro dry matter digestibility (IVDM) was also assessed [42]. The following equation was employed to estimate total digestible nutrients (TDN%): TDN (%) = Deg + (1.25*EE) – MM, where Deg represents degradability, 1.25 is the correction factor, EE signifies ether extract, and MM denotes mineral matter.

Statistical analyses

The data were subjected to assessments of normality, homogeneity, and the independence of residuals [43, 44]. Subsequently, analysis of variance was conducted using the F test (with $p < 0.05$). In cases where significant differences among means were detected, Tukey's post hoc test ($p < 0.05$) was employed for comparisons. These statistical analyses were carried out using the SPEED Stat version 2.8 software [45].

3 Results

Phosphorus and silicon contents

A significant interaction PxSi ($p < 0.05$) was observed for P and Si contents in plants. In the absence of Si, the deficiency and excess of P in the soil in relation to the adequate state caused a decrease and increase in the P content of the plant, respectively, which occurred in both soils (Fig. 1a, b), without changes in the levels of Si independent of the P state (Fig. 1c, d).

In the presence of Si, the P content was reduced in plants under excess P in both soils, and decreased in plants under adequate P status in Entisol, but there was no change in the P content of deficient plants when they received Si (Fig. 1a, b). Furthermore, the Si content increased in plants across all P states in both soils when they received nanosilica fertilization (Fig. 1c, d). The Si content was higher in plants deficient in P in Oxi- sol (Fig. 1c) and in P deficiency and excess in Entisol (Fig. 1d).

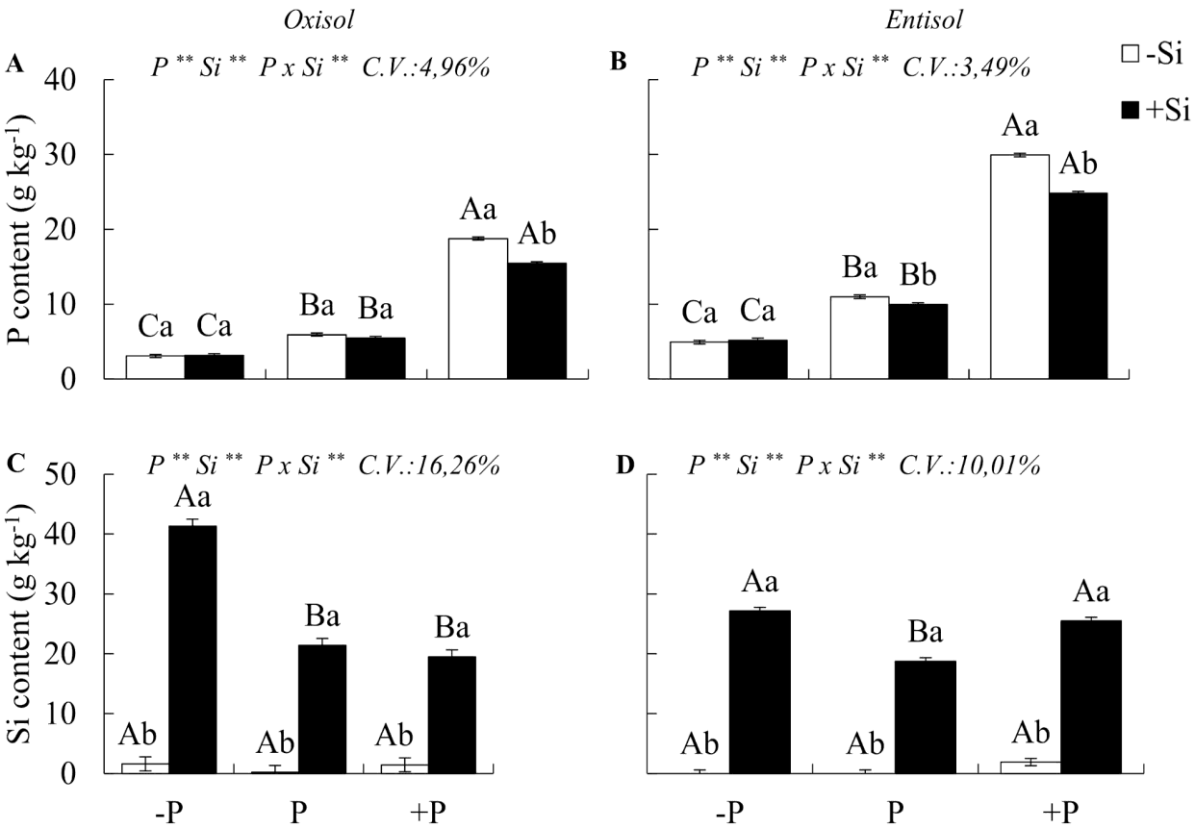


Fig. 1 Phosphorus content and silicon content of Zuri guinea grass cultivated under different phosphorus levels of deficiency (- P), adequacy (P), and excess (+ P) in Oxisol (A, C) and Entisol (B, D) in absence (-Si) and presence of silicon (+ Si, 1.5 mmol L^{-1}). Ns, *, ** refer to F test not significant, significant at 5 and 1%, respectively. Nutritional states are compared in uppercase letters, and the effect of Si in lowercase letters (Tukey test, $p < 0.05$). Bars correspond to the standard error of the experiment mean

Morphogenic and structural characteristics

A significant interaction PxSi ($p < 0.05$) was observed for most of the studied morphogenetic and structural variables (Fig. 2a-j), except for leaf elongation in Oxisol and stem diameter and leaf appearance rate in Entisol. In Oxisol, P deficiency compared to the adequate state led to an increase in leaf appearance rate and the number of live leaves per tiller (Figs. 1e and 2a). It also resulted in increased stem elongation and diameter compared to plants under P sufficiency (Fig. 2g and 1i).

Additionally, phosphorus deficiency reduced the tiller mortality rate in the Oxisol (Fig. 2c). In Entisol, P deficiency decreased the tiller appearance rate (Fig. 1b), and the number of tillers per pot in the forage, both in Oxisol (55%) and Entisol (35%) (Fig. 3a-h).

In contrast, compared to P sufficiency, excess P increased the rate of leaf appearance and leaf elongation while decreasing the number of live leaves per tiller in both soils (Fig. 2a-f). Stem elongation increased in plants under P excess in Oxisol. However, stem diameter decreased in both soils (Fig. 3 g-j). Excess P also raised the tiller appearance rate in both soils, leading to higher tiller numbers. Nevertheless, it also increased the tiller mortality rate in Oxisol and Entisol (Fig. 3a-h).

A significant interaction between P and Si was observed for the variables leaf appearance, number of leaves per tiller, and stem elongation in both soils, and leaf elongation in Entisol and stem diameter in Oxisol (Fig. 2a-j). In Oxisol, under P deficiency, the presence of Si,

compared to its absence, resulted in a decrease in the number of live leaves per tiller (Fig. 2e) and an increase in the tiller appearance rate, which did not occur in Enti- sol (Fig. 3a, b). In Entisol, Si application to forage under P deficiency increased leaf appearance and elongation rates, decreased stem elongation, and increased stem diameter (Fig. 2b, d, h, j).

Under excess P application in Oxisol, the presence of Si, compared to its non-application, led to a decrease in the leaf appearance rate and stem elongation (Fig. 2a, g). Furthermore, it increased the number of live leaves per tiller and stem diameter (Fig. 2e, i). In Entisol with excess P, plants that received Si showed a decrease in appearance and leaf elongation rates, as well as stem elongation (Fig. 2b, c, g), and an increase in the number of live leaves and stem diameter (Fig. 2f, i).

In both soils, Si fertilization in plants under excess P resulted in a decrease in the tiller mortality rate and an increase in the number of tillers per pot, along with an increase in the tiller survival rate in Entisol (Fig. 3a-h). In P sufficiency in Oxisol, the presence of Si increased the number of live leaves per tiller (Fig. 2e) and the number of tillers per pot (Fig. 3 g). Meanwhile, in Entisol, the plants with sufficient P showed a decrease in leaf and stem elongation rates (Fig. 2d, g).

Morphological composition and dry matter production

A significant interaction PxSi ($p < 0.05$) was observed for the morphological variables, specifically the percentage of the leaf blade and dead material in both soils, and for the stem percentage in Entisol, but not for dry matter yield (Fig. 4a-j).

When compared to P sufficiency, *M. maximus* plants grown in Oxisol under P deficiency exhibited an increase in the green leaf blade (19%) and stem (100%) percent- ages, along with a decrease in the leaf:stem ratio (49%) and dead material (100%). This led to a notable 39% decrease in DM yield (Fig. 4a, c, e, g, i). Similarly, in Entisol, when compared to P-sufficient plants, those subjected to P deficiency showed an increase in the leaf blade (9%) and a decrease in dead material, resulting in a 20% reduction in DM yield (Fig. 4b, d, f, h, j). However, the presence of Si had no significant effect on the morphological variables and DM yield in plants under P deficiency in the studied soils.

Cultivation under excess P without Si, in contrast to P sufficiency, resulted in a decrease in the green leaf blade (19% and 27%) and an increase in dead material (45% and 71%) in Oxisol and Entisol, respectively. It did not signifi- cantly influence the stem fraction of the plants but did increase the leaf:stem ratio in both soils (Fig. 4a-h). In Entisol, excess P led to a 14% reduction in final DM yield, which was not observed in Oxisol (Fig. 5i, j).

M. maximus plants under P excess that received SiO_2 nanoparticulate experienced an increase in the leaf blade (29% and 26%) and the mass leaf:stem ratio, as well as a decrease in dead material (84% and 67%) in Oxisol and Entisol, respectively (Fig. 4a-f). Furthermore, in plants with P sufficiency and Si supplementation compared to those without Si, there was an increase in the leaf blade (16% and 7%) and the mass leaf:stem ratio and a decrease in dead material (88% and 55%) in Oxisol and Entisol, respectively. Fertilization with Si increased the total DM yield of forage in both P excess (9% and 18%) and P suf- ficiency (8% and 5%) in Oxisol and Entisol, respectively (Fig. 4i, j).

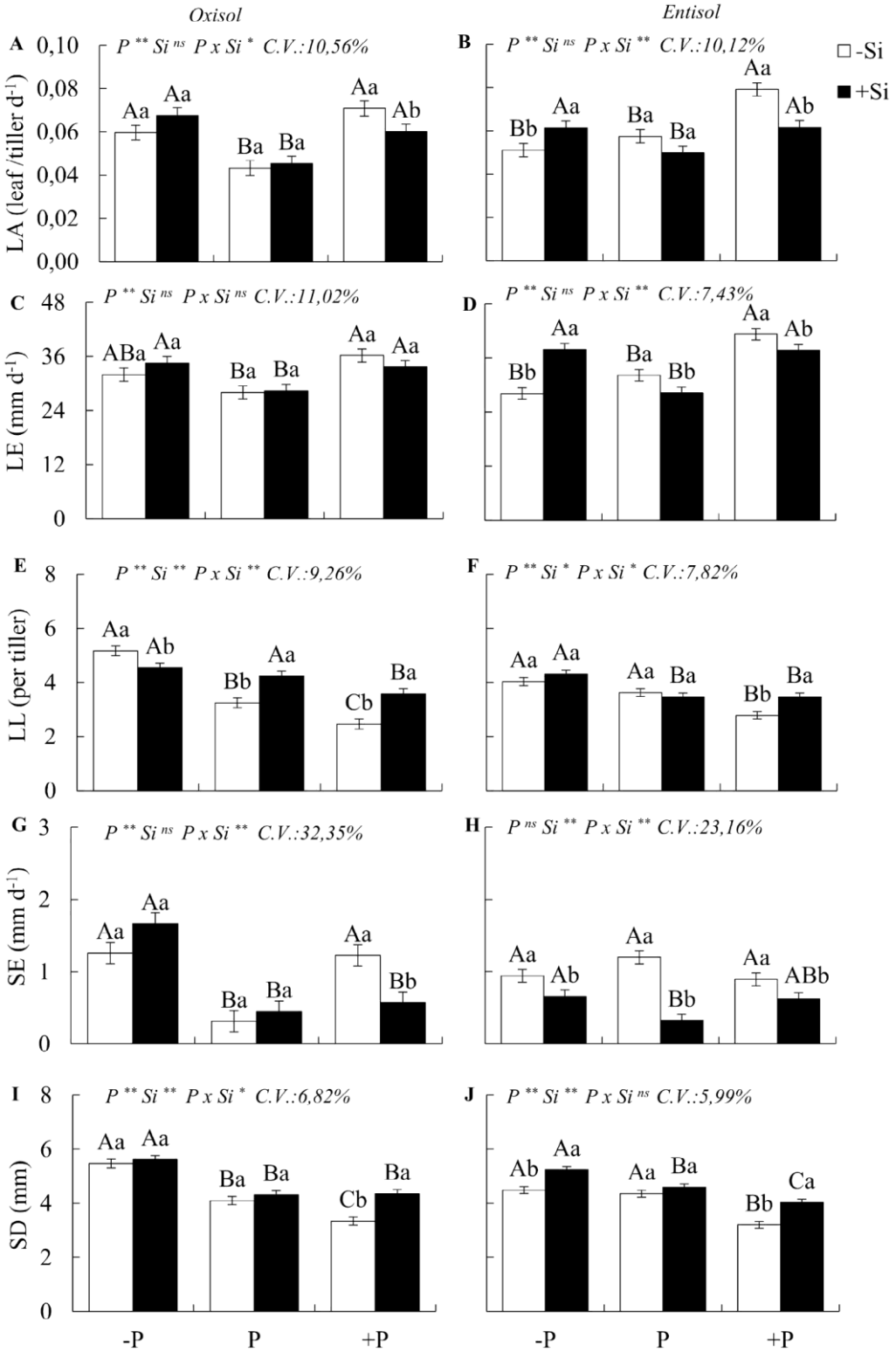


Fig. 2 Leaf appearance rate (LA), leaf elongation rate (LE), number of live leaves per tiller (LL), stem elongation rate (SE), and stem diameter (SD) of Zuri guinea grass under different phosphorus levels deficiency (-P), sufficiency (P), and excess (+ P) in Oxisol (A, C, E, G, and I) and Entisol (B, D, F, H, and J) in the absence (-Si) and presence of silicon (+ Si, 1.5 mmol L^{-1}). Ns, *, ** denote the F test results as not significant and significant at 5 and 1%, respectively. Nutritional states are compared using uppercase letters, and the effect of Si is compared in lowercase letters (Tukey test, $p < 0.05$). Bars represent to the standard error of the experiment mean

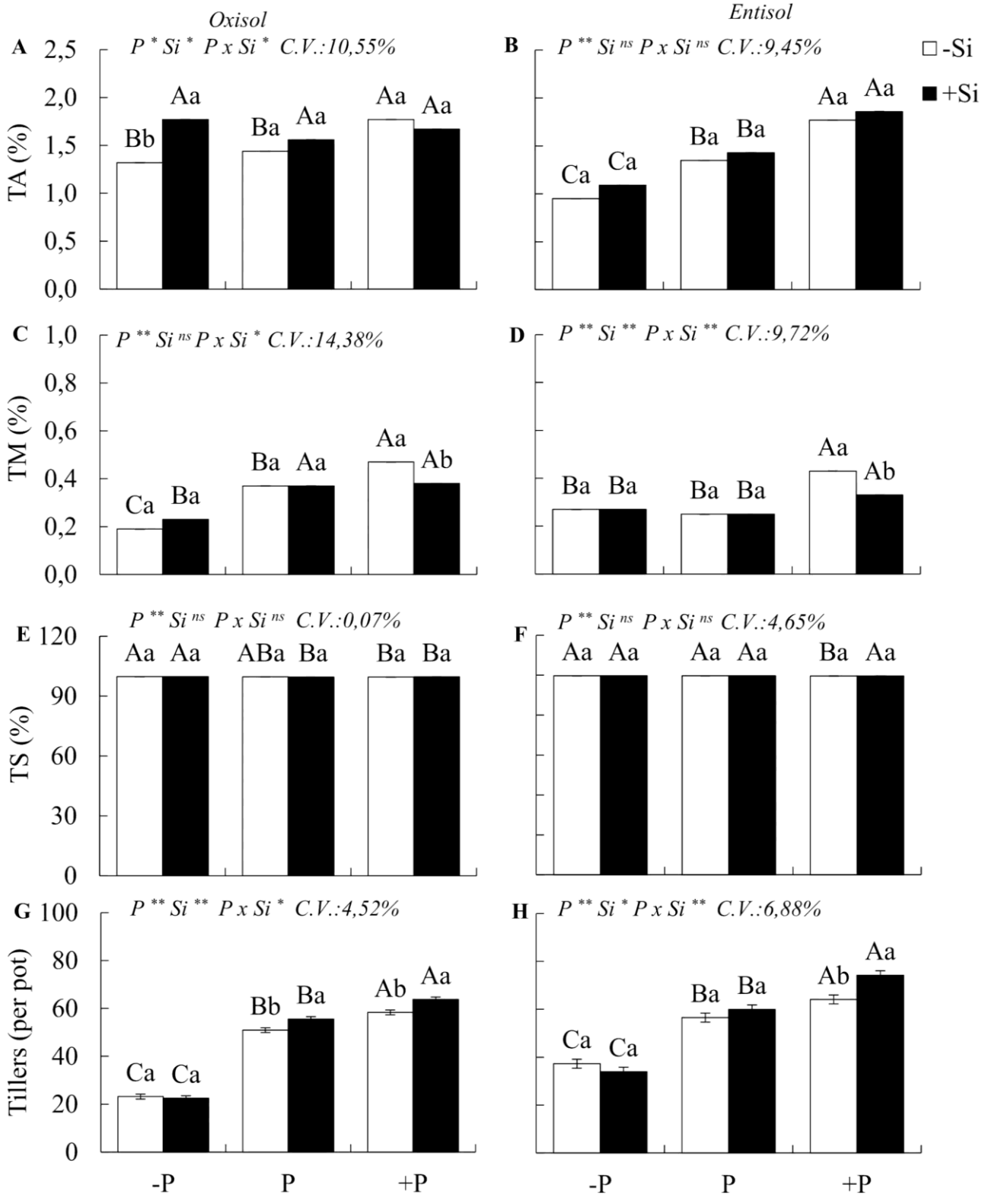


Fig. 3 Tiller appearance rate (TA), tiller mortality rate (TM), tiller survival rate (TS), and number of tillers per pot of Zuri guinea grass under different phos- phorus levels: deficiency (-P), sufficiency (P), and excess (+ P) in Oxisol (A, C, E, and G) and Entisol (B, D, F, and H) in the absence (-Si) and presence of sili- con (+ Si, 1.5 mmol L^{-1}). Ns, *, ** denote the F test results as not significant and significant at 5 and 1%, respectively. Nutritional states are compared using uppercase letters, and the effect of Si is indicated with lowercase letters (Tukey test, $p < 0.05$). Bars represent the standard error of the experiment mean

Chemical composition of forage

The results concerning variables related to chemical com- position, fiber, and DM digestibility revealed a significant interaction PxSi ($p < 0.05$), but only for the percentage of lignin and mineral matter in both soils, and for non-fiber carbohydrates in Oxisol (Figs. 5a-h and 6a-h).

Under P deficiency in Oxisol, when compared to plants with adequate P status, *M. maximus* exhibited an increase in the percentage of lignin, a decrease in non- fiber carbohydrates, and an increase in mineral matter, with no significant effect on the CP content or DM digestibility (Figs. 5 and 6a, c, e and g). Conversely, in Entisol, deficiency did not significantly influence fiber composition or the percentage of non-fiber carbohydrates. However, it resulted in a 5.1% decrease in CP con- tent and a reduction in mineral matter (Figs. 5 and 6b, d, f and h).

Under P excess, as compared to Oxisol sufficiency, the plants displayed a decrease in non-fiber carbohydrates and an increase in CP (15.4%) and mineral matter (Figs. 5g and 6a and c). In contrast, under Entisol conditions, excess P led to a decrease in hemicellulose (28.5%) and mineral matter, coupled with an increase in lignin (1.1%), CP (28.6%), and DM digestibility (Figs. 5b and f and 6b, d and h).

With the addition of Si, plants experiencing P deficiency in relation to nutrient sufficiency exhibited increased CP content (4.9% and 9.4% in Oxisol and Enti- sol, respectively) and mineral matter (Fig. 6a-d), with no significant impact on fiber composition or digestibility. In cases of excess P in plants cultivated in Oxisol, Si fertilization resulted in increased non-fiber carbohydrates and mineral matter. In Entisol, there was a decrease in lignin (1.3%) and an increase in CP content (12.4%), as well as mineral matter. The presence of Si in conditions of P sufficiency, as opposed to its absence, led to a reduction in the percentage of lignin in both soils (1.0%). Further- more, it increased the CP content in Oxisol (4.1%) and Entisol (9.7%) and elevated the mineral matter in Oxisol. Regardless of the P nutritional status, Si fertilization had no impact on TDN percentage or in digestibility.

4 Discussion

P imbalances and Si absorption

P deficiency and excess were clear in both soils, con- firmed by the low and high content in the plant, respectively, in relation to plants in an adequate state of the nutrient (Fig. 1a, b). The low levels of P available in weathered soils led to the occurrence of deficiency, and the dose applied to cause excess P increased its content in the plant in both soils, reaching 18.8 and 29.9 g kg^{-1} in cultivated plants in Oxisol and Entisol, respectively. The same dose of P caused a greater increase in the nutrient content in the plant in Entisol, due to the greater availability of phosphate in this soil compared to Oxisol, which has a higher clay content [2]. Thus, in sandy soil the risk of P toxicity in plants under excessive fertilization is greater than in clayey soil.

Nanosilica fertigation was efficient in increasing the Si content in plants compared to non-application. This increase in Si content was more prominent in P deficiency plants in both soils, and also in excess P in Entisol, revealing that Si is an element required by plants subjected to P imbalances, in a similar way to abiotic stresses [46, 47]. It is pertinent to admit that Si can reduce the risk of P toxicity in soils under nutrient excess, given its action in decreased P content of plants in both soils. The Si mechanisms involved in this regulation still need to be elucidated, especially for its action as a regulator of the expression of P transporters [48].

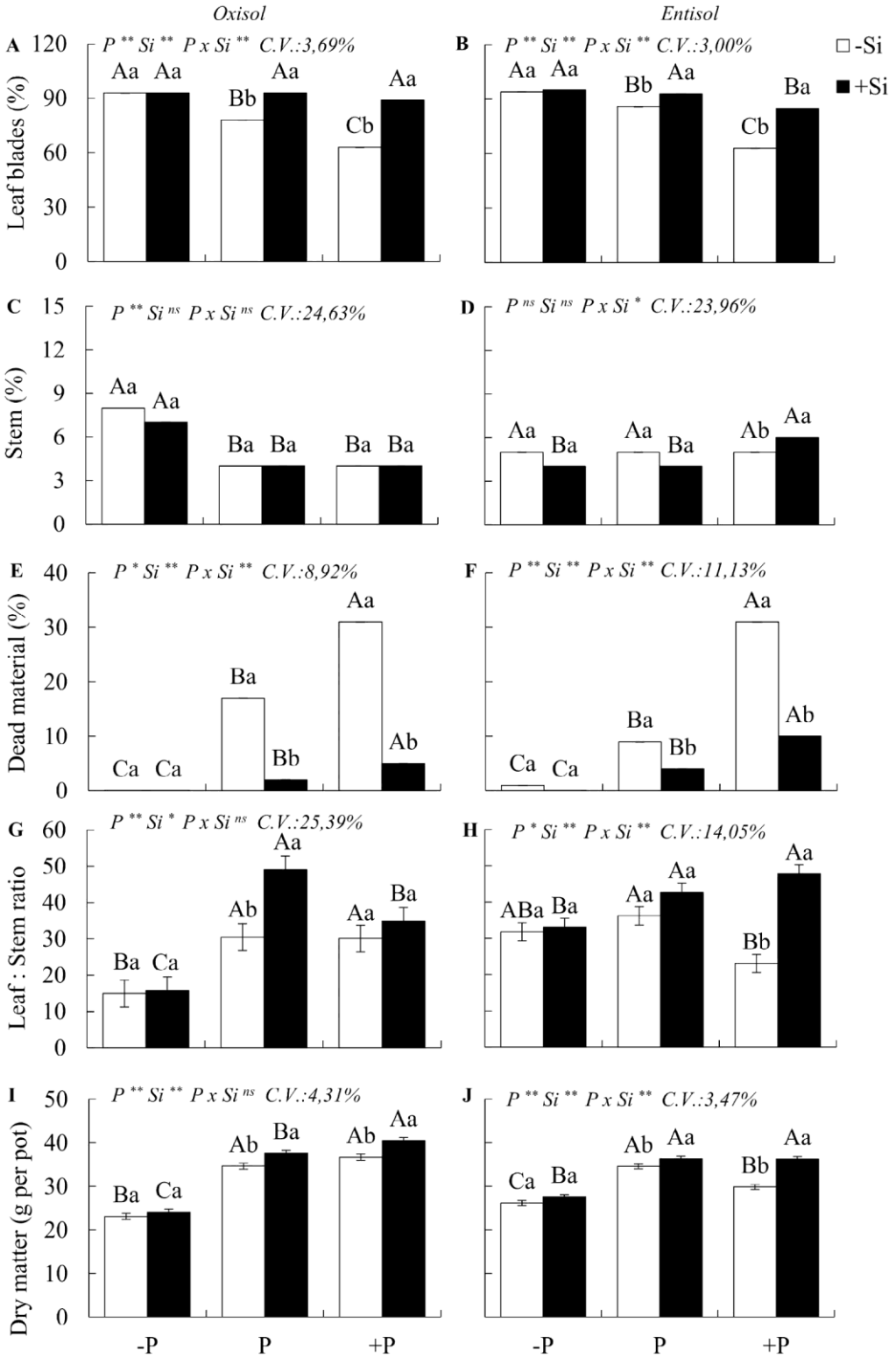


Fig. 4 Percentage of leaf blade, stem, dead material, mass leaf:stem ratio, and dry matter yield of Zuri guinea grass under different phosphorus levels: deficiency (-P), sufficiency (P), and excess (+P) in Oxisol (**A, C, E, G**, and **I**) and Entisol (**B, D, F, H**, and **J**) in the absence (-Si) and presence of silicon (+ Si, 1.5 mmol L^{-1}). Ns, *, ** denote the F test results as not significant and significant at 5 and 1%, respectively. Nutritional states are compared using uppercase letters, and the effect of Si is indicated with lowercase letters (Tukey test, $p < 0.05$). Bars represent the standard error of the experiment mean

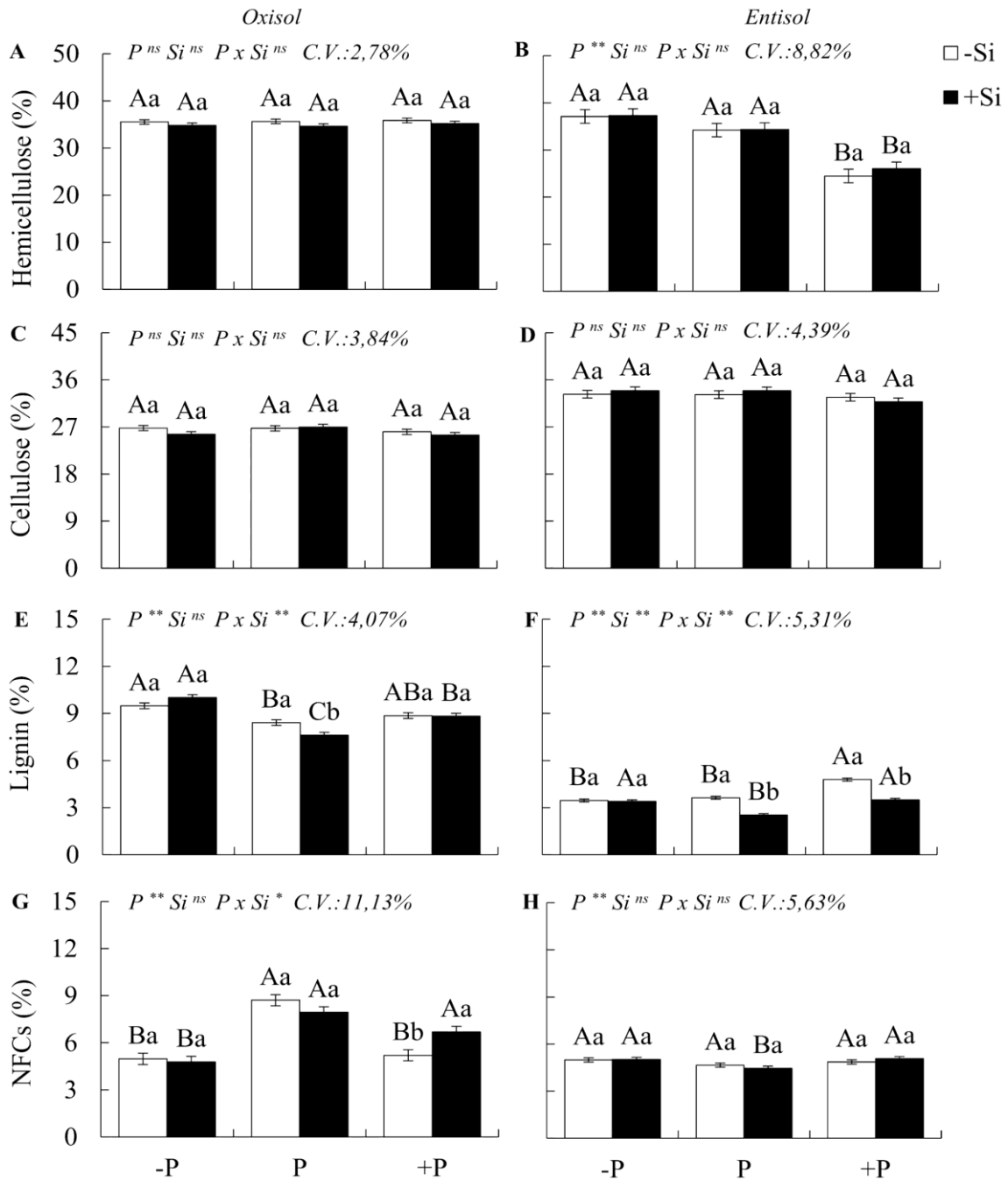


Fig. 5 Percentage of hemicellulose, cellulose, lignin, and non-fiber carbohydrates (NFCs) in the dry matter of Zuri guinea grass cultivated during six regrowth cycles under different phosphorus levels: deficiency (-P), sufficiency (P), and excess (+ P) in Oxisol (A, C, E, and G) and Entisol (B, D, F, and H) in the absence (-Si) and presence of silicon (+ Si, 1.5 mmol L^{-1}). Ns, *, ** denote the F test results as not significant and significant at 5 and 1%, respectively. Nutritional states are compared using uppercase letters, and the effect of Si is indicated with lowercase letters (Tukey test, $p < 0.05$). Bars represent the standard error of the experiment mean

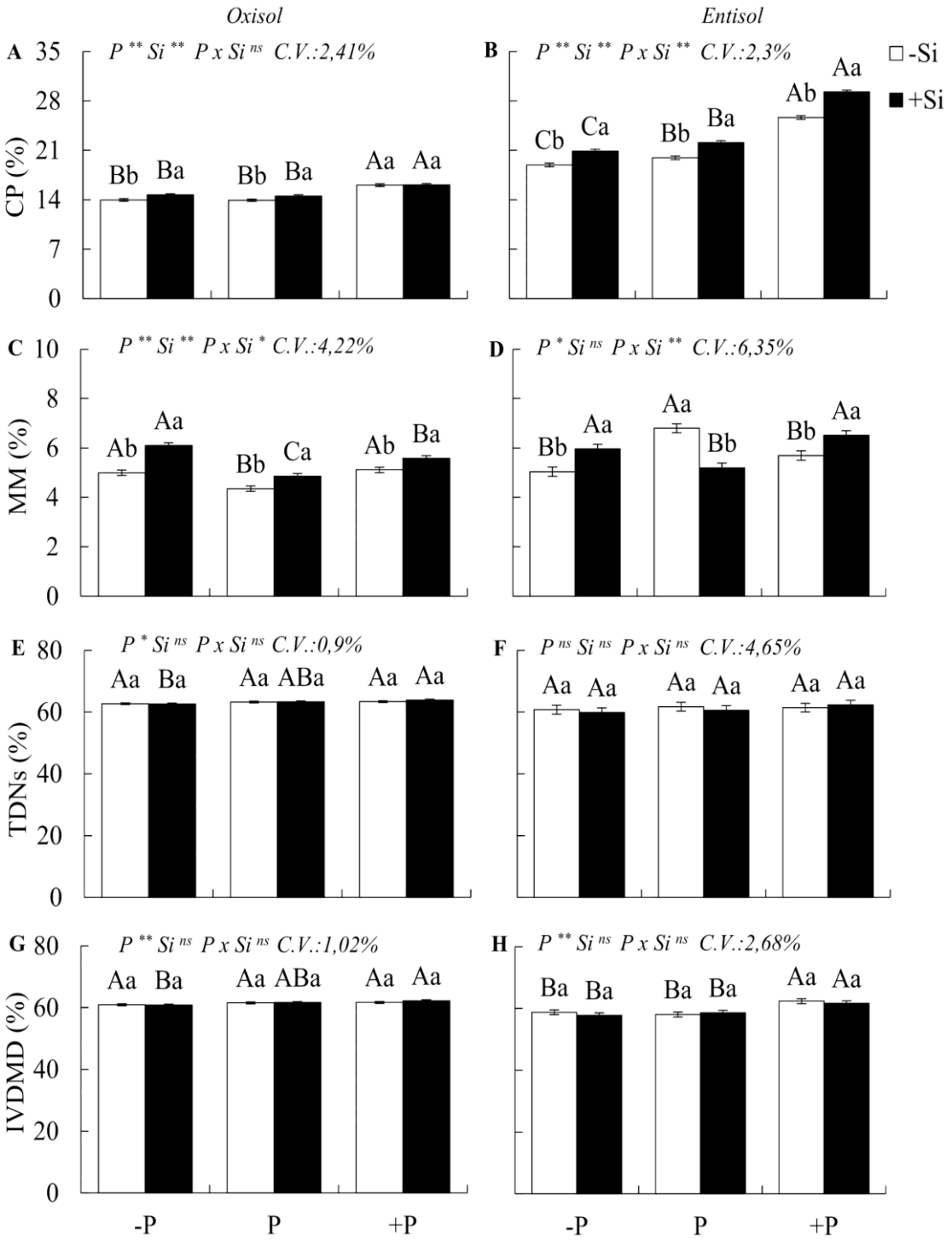


Fig. 6 Percentage of crude protein (CP), mineral matter (MM), total digestible nutrients (TDNs), and in vitro dry matter digestibility (IVDMD) of Zuri guinea grass, cultivated during six regrowth cycles under different phosphorus levels: deficiency (-P), sufficiency (P), and excess (+ P) in Oxisol (**A, C, E**, and **G**) and Entisol (**B, D, F**, and **H**) in the absence (-Si) and presence of silicon (+ Si, 1.5 mmol L^{-1}). Ns, *, ** denote the F test results as not significant and significant at 5 and 1%, respectively. Nutritional states are compared using uppercase letters, and the effect of Si is indicated with lowercase letters (Tukey test, $p < 0.05$). Bars represent the standard error of the experiment mean

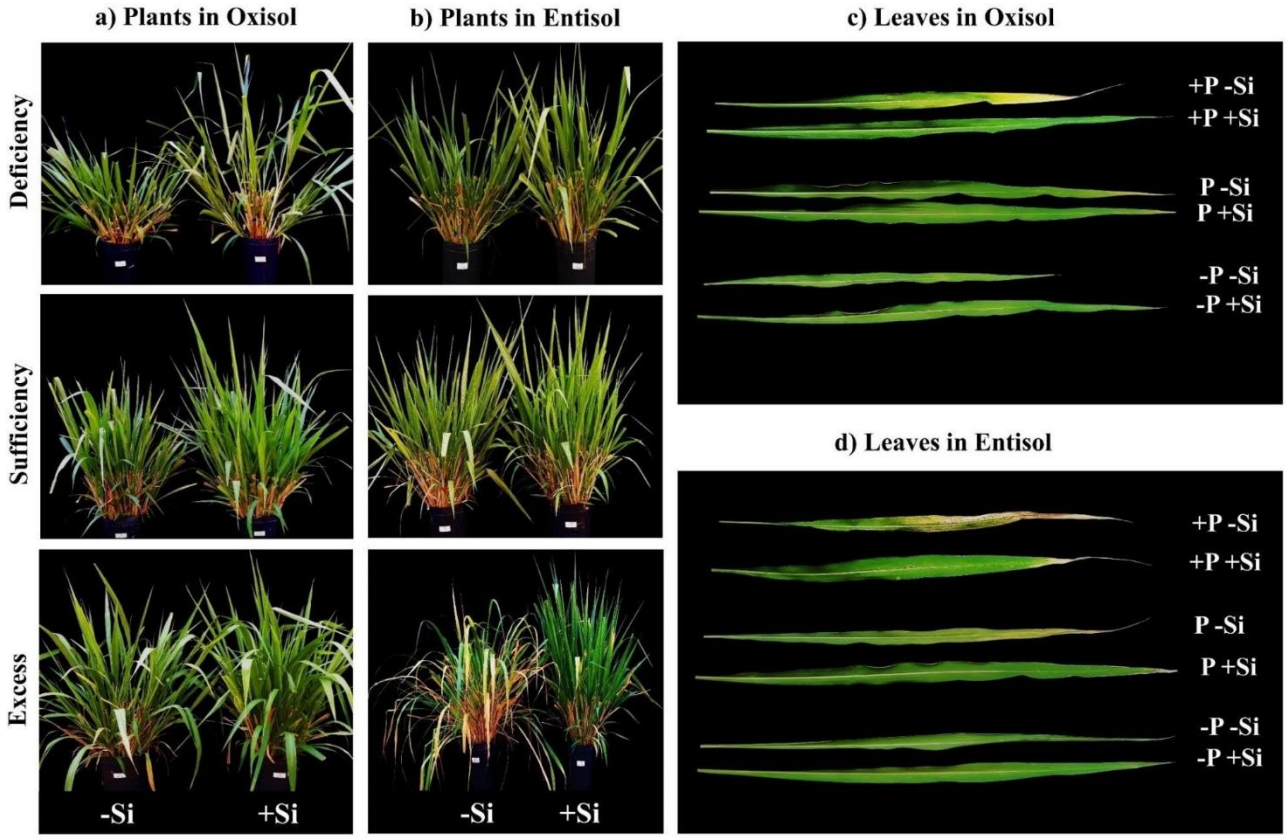


Fig. 7 Plant phenotype and visual aspects of the leaf blades of *M. maximus* cv. Zuri grown under conditions of phosphorus deficiency, sufficiency, and toxicity, combined with the absence (-Si) or presence of Si nanoparticles (+ Si, 1.5 mmol L^{-1}) in Oxisol (a, c) and Entisol (b, d) at the end of the fifth re- growth cycle

Deficiency and excess of P without the use of Si in pasture morphogenesis and yield

While the effects of phosphorus (P) deficiency on grasses have been well-documented [1, 3, 49], there is relatively limited research focusing on the morphogenic processes of grasses used in pastures under P deficiency [50, 51]. This is a notable gap in the literature because understanding how nutritional disorders of P affect these plants and how they respond morphogenetical to such stress is crucial.

In our study, we observed several strategies employed by *M. maximus* to cope with P deficiency, which was evident in plants cultivated in both soils studied. Compared to plants under P sufficiency, those experiencing P deficiency increased the number of live leaves per tiller without decreasing leaf elongation rates. However, this strategy came at the cost of a significant reduction in tiller appearance rate and the overall number of tillers, resulting in diminished biomass yield.

The growth and tillering dynamics of forage grasses involve morphogenic processes crucial for both forage yield and pasture longevity [11]. Our findings shed light on the morphogenetic strategies employed by *M. maximus* to mitigate the effects of P deficiency in both clayey (Oxisol) and sandy (Entisol) soils. In Entisol, the morphophysiological changes in *M. maximus* under P deficiency manifested as a reduced tiller appearance rate due to decreased cell division and expansion. This out- come aligns with observations made in perennial *Lollium* grasses [52].

The decrease in tillering observed under macronutrient deficiency occurred in both soils. However, in Oxisol, plants responded by increasing appearance rates and leaf elongation. This difference may be attributed to a more severe degree of P deficiency in the plants grown in Oxisol, possibly prompting a more efficient utilization of the available nutrient. It is known that under P deficiency, plants can allocate more P to essential metabolic processes [53, 54]. Additionally, while each tiller has a genetically predetermined number of leaves [55], leaf elongation is a trait influenced by genotype-environment interactions in forage grasses [56], as we observed in relation to P.

The reduction in tillering had a severe impact on forage yield, a common occurrence in grasses under P deficiency [12, 54, 57]. The reduced yield of nutritionally deficient plants was anticipated, considering they were grown in weathered soils with low available P content (12 and 2 mg dm^{-3} in Oxisol and Entisol, respectively). This limitation compromises cell division and hinders net photosynthesis rates [7, 49].

Interestingly, the decrease in DM yield due to P deficiency was 18% more pronounced in Oxisol than in Entisol. This difference may be explained by the fact that plants in Entisol likely utilized the small amount of added P (4 mg dm^{-3}) more efficiently to enable minimal growth, which accounted for only 2% of the recommended dose [27]. However, this was sufficient to mitigate the severity of P deficiency to a certain extent in Entisol, which has a lower phosphate adsorption capacity [2, 49, 51].

Plants cultivated under excess P exhibited impairments, possibly stemming from disrupted cellular phosphate (Pi) homeostasis. This imbalance affects essential P-related functions in plants, leading to decreased photosynthesis and biomass yield [5, 8]. Our study suggests, for the first time, that an excess of P in the soil disrupts the balance between C, N, and P in grasses, subsequently hindering the efficient utilization of these nutrients [58]. However, there is still a limited number of studies describing the effects of excess P on grasses, even in nutrient solutions [59]. Thus, our study may represent one of the first attempts to identify morphogenic responses of forage grasses to excess P in different soils.

Our research provides a deeper understanding of the morphogenic mechanisms of *M. maximus* and highlights the plant's response strategies when exposed to excess P compared to plants with adequate P levels in both soils. Surprisingly, we found that the forage, when subjected to toxic P levels, increased leaf appearance and elongation rates but simultaneously maintained a reduced number of live leaves on each tiller. Consequently, this led to an increase in tiller appearance and numbers, albeit with smaller diameters, higher tiller mortality rates, lower percentages of live leaf blades, higher amounts of dead material, and ultimately reduced dry matter yield.

In contrary to P deficiency, excess P accelerates the growth dynamics of *M. maximus.* However, the higher tiller mortality observed in plants under excess P in both soils may result not only from the increased stimulus to cell division processes due to P excess but also from the synergistic effects between P and N. Under P excess, plants can absorb higher quantities of N, contributing to increased tissue renewal [60, 61]. [54] also noted that tissue renewal processes in Massai grass (*M. maximus* x *M. infestum*) are accelerated with increasing phosphorus doses, even in the absence of toxic P levels.

Early leaf senescence and associated losses were observed in plants grown under both P deficiency and excess. However, excess P only significantly impacted total DM yield in Entisol, which aligns with the higher phosphate availability in sandy soils [2]. Moreover, in soils rich in oxidic clays like Oxisol, the availability of P decreases with prolonged exposure to adsorption sites [62]. Thus, the implications of excess P in pastures are even more concerning when considering sandy soils, partially supporting our initial hypothesis. Although both P imbalances altered the growth and tillering of plants in both soils, only the excess of P reduced the DM yield of Zuri grass when cultivated in sandy soil.

Deficiency and excess of P without the use of Si in the morphological, chemical composition and nutritional value of forage

Our observations indicate that P imbalances also induce changes in the morphogenic and structural characteristics, chemical composition, and nutritional value of *M. maximus* grass. However, although P deficiency resulted in increased hemicellulose and decreased protein in plants grown in one soil type (Entisol) and increased lignin and mineral content, while decreasing non-fibrous carbohydrates in another soil type (Oxisol), these changes did not significantly impact the total digestible nutrients (TDN) and in vitro dry matter digestibility (IVDMD) of the grasses cultivated in both soils. The notable increase in lignin content in P-deficient plants grown in Oxisol is a known effect observed in plants exposed to abiotic and biotic stress as part of their natural defense mechanisms [63]. However, it is a costly strategy in terms of energy expenditure for the plant [64].

The lack of an effect of P deficiency on digestibility can be attributed to the fact that these plants maintained a greater number of young leaves. This occurred because plants in this condition typically had fewer tillers, which prompted an increase in leaf blade and stem yield in response to stress. Furthermore, plants under P deficiency exhibited delayed leaf senescence, which had a positive impact on forage digestibility.

In the case of plants subjected to P deficiency in Entisol, one notable effect was the reduction in the plant's crude protein (CP) content. This CP fraction includes protein nitrogen (true protein) and non-protein nitrogen, such as amino acids and amines, which are crucial for animal nutrition [65]. The decrease in protein levels in these plants was attributed to the fact that P is essential for ribonucleic acid (RNA), a requirement for the translation process in protein synthesis [7]. Moreover, P-deficient plants experience reduced nitrogen (N) uptake, which is vital for protein formation [66, 67].

Another effect of P deficiency in plants grown in Oxisol was the increase in mineral matter content. This increase may have resulted from higher elemental concentrations in the dry matter, given that these plants exhibited less growth and biomass yield compared to adequately nourished plants (Fig. 7a, b). Alternatively, the increase in mineral matter could be attributed to the uptake of residual silicon (Si) from the soil. Stressed plants often release exudates into the rhizosphere, promoting the dissolution of phytoliths within organic matter [68], thus releasing Si.

In summary, pastures of *M. maximus* under P deficiency produced less dry matter compared to well-fertilized pastures, and while they exhibited lower protein content, it did not negatively affect digestibility.

Another significant nutritional concern arises with the issue of excess P in the grass. However, the effects of excess P on the nutritional value of the plant had remained largely unexplored until our study. We observed that excess P initially decreased the mass leaf:stem ratio due to the reduced percentage of live leaf blades, a phenomenon previously described by [10]. These visual symptoms, such as chlorosis and necrotic spots on the leaves (Fig. 7c, d), mark the onset of P toxicity in this species, which eventually progresses to complete leaf necrosis. These symptoms result from biochemical disruptions in plant tissues caused by excessive P, including photosynthesis inhibition and increased lipid peroxidation [8], along with accelerated senescence and reduced photosynthetically active areas. This ultimately leads to decreased dry matter accumulation [9, 69], resulting in biomass loss, as grazing animals typically select green leaf blades with greater nutritional value [70, 71].

That excess P, similar to P deficiency, resulted in a higher lignin content in *M. maximus*, serving as a strategy to mitigate nutritional stress, consistent with findings from [72]. This underscores the variability in fiber lignin content associated with nutrient inputs [14]. However, even with increased lignin content, we visually noted that plants under P stress, especially those under P excess, did not attain a phenotype resembling well-nourished P plants, which typically exhibit well-developed, green leaf blades, characteristic of most forage grasses (Fig. 7a-d).

Although higher lignin content may affect fiber digestibility by ruminants [63, 73], our study did not find any significant impact on dry matter digestibility despite P imbalances. This can be explained by the fact that the lignin primarily consisted of non-core lignin, mainly composed of low molecular weight phenolic compounds released from the cell wall through hydrolysis. These compounds are typically represented by ester-linked p-hydroxycinnamic acids, as opposed to core lignin, which features highly condensed cell wall phenylpropanoid polymers that resist microbial degradation in the rumen [74, 75].

The increase in CP content observed in plants under excess P in Entisol can be attributed to P's essential role in protein synthesis. However, it is crucial to note that this may also be related to the fact that P stimulates N uptake [60]. Nevertheless, the higher protein content in plants under P excess results in nutrient loss, as these nutrients cannot be efficiently redistributed within the plant for metabolic processes or used by grazing animals that typically avoid consuming dead leaves.

Considering the results discussed, our study partially confirms the second hypothesis. While P imbalances did indeed alter the chemical composition of the plant, they did not affect forage digestibility. However, the significant reduction in biomass yield caused by excess P and early leaf senescence ultimately compromises the availability of high-quality pasture [70].

Benefits of Si in the morphogenesis and production of plants with deficiency, sufficiency, and excess P

This study has provided a comprehensive understanding of the detrimental effects of P imbalances on forage, which significantly impact extensive cultivation areas of these species worldwide. Given these findings, there is an urgent necessity to develop strategies for mitigating this damage without harming the environment.

The use of Si can be synergistic with P uptake by plants as silicates compete with phosphate for adsorption sites, which increases available phosphate in the soil [19, 76]. However, the effects of Si on the morphogenesis of forage plants, especially with the use of innovative sources of the element, such as nanosilica, are unknown, and it is opportune to further research on this topic, which motivated this study.

The benefits of silicon in the morphogenesis of P-deficient forage were somewhat limited, as it only increased the tiller appearance rate in plants grown in Oxisol and resulted in an increase in the appearance rate, leaf elongation, and stem diameter in plants grown in Entisol. However, these improvements in morphogenesis induced by silicon under P deficiency were insufficient to significantly enhance plant dry mass yield in the two soils studied. This may be attributed to the fact that there was no significant increase in the number of tillers, which represents the basic unit of grass yield [10].

In hydroponic studies, silicon has been shown to alleviate P deficiency in wheat and rice [77, 78]. However, these studies involve more rigorous control of P levels in the culture medium (nutrient solution), which generates a more severe deficiency in plants compared to soil cultivation. There are indications that the beneficial effects of silicon are more pronounced under severe stress conditions [79]. Furthermore, advanced forage regrowth cycles may exacerbate P deficiency in the soil due to nutrient export in the biomass, potentially enhancing the benefits of silicon in plants. Nonetheless, this remains a subject for future research [51].

Concerning the role of silicon in plants with excess P, this is an uncharted territory in this species, as P excess is less widespread compared to P deficiency. Nevertheless, it is essential to initiate research in this area. Our study revealed that silicon triggers certain morphogenic processes in the plant to counteract the damage caused by excess P in *M. maximus*, which was observed in plants cultivated in both soils. However, this was accompanied by a decrease in the appearance rate of new leaves due to the control of tissue flow within the plant. This led to an increase in the number of live leaves per tiller and a decrease in stem elongation rate, ultimately favoring greater tiller numbers and thicker tiller diameters. These improvements in plant growth and structure translated into an increase in plant dry mass yield in Entisol.

However, it should be noted that in plants grown in Oxisol with the P dosage used, it was not possible to induce P toxicity due to this soil's high capacity for P adsorption. Therefore, since P toxicity did not manifest in plants grown in this soil, it was not feasible to investigate the mitigating effects of silicon in such a scenario. Nevertheless, the risk of P toxicity in Oxisol remains relatively low, and further research using higher P doses (> 600 mg dm^{-3} of P equivalent to 1200 kg ha^{-1} of P) may be required, as Oxisol's maximum P adsorption capacity is approximately 575 mg dm^{-3} and may vary depending on other soil properties, such as organic matter content [2].

Considering these results obtained in plants cultivated in Entisol, it is plausible that mitigating the dam- age caused by excess P in *M. maximus* may have similar benefits in other species [76, 80]. In a study involving rice plants cultivated in a nutrient solution with excess P, silicon was found to downregulate the gene expression of phosphate transporters, thereby reducing phosphate uptake by the plant [48]. This mechanism may be one of the ways silicon mitigates P excess in grasses and war- rants further investigation.

Studies involving silicon typically focus on stress conditions, with the prevailing belief that silicon benefits only stressed crops, offering no advantages to non- stressed plants [79]. However, our study evaluated the effects of silicon on the morphogenesis of plants under P sufficiency, i.e., plants without stress. We observed an increase in the number of live leaves per tiller and the number of tillers in plants grown in Oxisol, as well as a decrease in stem elongation in plants grown in Entisol.

These positive effects of Si reflected an increase in DM production in *M. maximus* in both soils, possibly due to different Si mechanisms reported in grasses, such as the promotion of adequate nutritional homeostasis to pro- vide an increase in the efficiency of N and P use [20, 47, 81, 82], even in plants without stress [83]. Our results corroborate the fact that Si can influence the morphology of plants [23], mainly in Si-accumulating species [84], and can improve the productivity of non-stressed plants and mitigate nutritional stress.

In conclusion, it was clear that the utility of silicon for *M. maximus* cultivation depends on the presence or absence of stress, the type of stress, and the soil class. Silicon can offer benefits to *M. maximus* in regions world-wide, whether it covers areas without nutritional stress in sandy or clayey soils or addresses areas with excess P, particularly in sandy soils, thus making it a valuable tool for sustainable agricultural yield [80]. Furthermore, it can be used in areas with excess P, especially in sandy soils, enabling its use in agriculture. This discovery confirms the important role of Si as a tool for more sustainable agricultural production [46].

Benefits of Si on the morphological and chemical composition and nutritional value of forage

An issue of concern within the scientific community regarding silicon's presence in forage is its potential role as an anti-nutritional element in animal feed [85]. Furthermore, it remains unclear whether silicon has a beneficial or detrimental effect on forage quality under various cultivation conditions, including areas with ample soil fertility or those with phosphorus (P) deficiency or excess. This is a pressing concern because, as we have observed, silicon may significantly influence morphogenesis and plant growth. However, these advantages would be futile if there were substantial losses in forage quality, ultimately affecting the performance of animals consuming such forage.

In an effort to address this question, our study demonstrated that the use of nanosilica in P-deficient plants did not result in alterations to the morphological or fiber composition of *M. maximus*. Instead, it led to increased crude protein (CP) and mineral matter content. This increase in protein content can be attributed to silicon's role in enhancing the uptake of both P [78] and nitrogen (N) [86], both of which are integral to protein synthesis in plants. This finding is of paramount importance due to the significance of protein for the ruminal microbiota's activity [14].

The increase in mineral matter in the presence of silicon reflects the uptake of this beneficial element by stressed plants [19, 77]. Notably, utilizing silicon in these plants did not hinder forage digestibility, possibly because silicon did not induce lignification. Nevertheless, it is worth noting that P-deficient wheat subjected to silicon exhibited enhanced lignin synthesis [87], indicating that species may adopt varying strategies for mitigating stress, involving silicon in cell wall composition and/or activating enzymes related to lignin synthesis, which should be elucidated in future studies.

This study unequivocally demonstrates that the introduction of silicon into *M. maximus*, even under P deficiency, does not compromise the forage's nutritional value. This is a highly practical revelation, as most pastures cultivated in tropical regions contend with P-deficient soils [1] and could immensely benefit from the sustainable application of this element. In regions with excess P, incorporating silicon also yielded promising outcomes for M. maximus. This resulted in improved morphological composition of the plant, with reduced dead material and increased leaf blade fractions in both soil types. Additionally, it's noteworthy that there was a decrease in the tiller mortality ratema pivotal factor for pasture persistence [11]. Importantly, it should be highlighted that, in line with observations in other crops subjected to excess P [88, 89], silicon supplementation in *M. maximus* grown under P excess led to reduced lignin content in the fiber and increased CP and mineral matter content, especially in plants cultivated in Entisol.

While some advantages of lignin have been reported for stressed plants, such as enhanced leaf architecture [90] and the antioxidative action of phenolic precursors against reactive oxygen species [91], it is not considered a favorable strategy for forage plants since lignin is an anti- nutritional component for ruminants [75]. Our study confirmed that in *M. maximus*, silicon does not promote lignin synthesis, even in plants exposed to excess P. This may be attributed to the plant's utilization of silicon at a low energy cost for cell wall composition, effectively substituting lignin's role in plant tissue support, ultimately leading to reduced lignin synthesis [92].

Therefore, the significant contribution of nanosílica fertilization to the improvement of morphological and chemical composition in forage grasses was evidenced, even under excess P. As such, our third hypothesis was partially confirmed, as nanosilica fertilization mitigated the stress associated with excess P without compromising forage quality. Moreover, it is evident that silicon application in plants with sufficient P nutrition led to decreased lignin content, which may enhance fiber digestibility [63], and joins other promising results in grasses without nutritional stress [92]. Additionally, our study revealed that silicon supplementation increased protein content in plants with optimal P nutrition, corroborating findings observed in Zuri (*M. maximus*) and Ipyporã *(Urochloa ruziziensis* x *U. brizantha*) grasses following silicate fertilization [28].

However, plants tend to absorb silicon in greater quantities when subjected to stress [93]. Consequently, the decrease in forage lignin content under P sufficiency likely stemmed from a slight increase in silicon content. Similar findings were reported in rice plants and sorghum without stress, indicating a negative correlation between silicon accumulation and lignin synthesis [88, 89], a relationship consistent with our observations under P sufficiency. Further investigations into the connection between silicon fertilization and lignin biosynthesis in grasses are imperative, including studies involving properly nourished plants, as results appear to be contingent on the crop and growing conditions.

In conclusion, these results underscore the advantages of silicon fertilization in forage grasses under P stress or with adequate nutrition. This practice optimizes the integrated soil-forage-animal system, resulting in the improved formation of pastures, recognized as the most economically efficient food source for animal yield according to [14]. Thus, the use of Si can help recover the potential productive of pastures, with a more efficient use of productive resources, improving the productivity and sustainability of pasture production.

5 Conclusions and future perspectives

In summary, this study provides novel insights into the underlying causes of growth reductions in *M. maximus* cv. Zuri when subjected to both P deficiency and excess P in two tropical soils. Furthermore, we elucidate the plant's morphogenic and structural adaptive strategies to mitigate these stresses, all while maintaining forage quality.

Moreover, we demonstrate that the application of SiO_2 nanoparticles fosters enhanced equilibrium within the plant's growth and senescence processes, mitigating bio- mass yield loss, particularly in plants cultivated under excess P in sandy soil. Additionally, SiO_2 nanoparticle fertilization increases yields under P sufficiency in soils with varying textures without compromising digestibility. Future research endeavors should delve into Si-specific mechanisms, employing metabolomic approaches to better understand Si's role in alleviating damage caused by P excess in grasses and optimizing yields in non-stressed plants. This investigation should also explore Si's impact on reducing plant senescence, which was notably observed in this study. Furthermore, examining Si's potential in ameliorating P deficiency in forage grasses warrants exploration, given the observed potential to enhance the growth and protein content of deficient plants, including testing with different Si sources and doses, to find the economic viability of their use.

Abbreviations

ADF	Acid detergent fibre	C	Carbon
CP	Crude protein		
DM	Dry matter		
LA	Leaf appearance rate		
LE	Leaf elongation rate		
MM	Mineral matter		
NDF	Neutral detergent fibre		
N	Nitrogen		
NFCs	Nonfiber carbohydrates		
P	Phosphorus		
SE	Stem elongation rate		
SD	Stem diameter		
Si	Silicon		
TA	Tiller appearance rate		
TDN	Total digestible nutrients		
TM	Tiller mortality rate		
TS	Tiller survival rate		

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Authors' contributions

CCFM conducted the experiments and wrote the paper. DSA assisted in conducting the experiments, statistical analysis and formatting figures. AMZ, DJF, and MCP performed laboratory analyzes and provided direction for the approach. RMP designed the research and revised the manuscript. All authors read the final manuscript.

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Data Availability: The datasets generated and/or analysed in this study are available from the corresponding author upon reasonable request.

Declarations

Competing interests: The authors declare no competing interests.

Research involving plants: The experimental research was carried out in accordance with relevant institutional, national, and international guidelines and legislation. It does not involve an endangered species.

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CAPÍTULO 4 - Fertirrigação com nanosílica na atenuação de estresse por deficiência ou excesso de nitrogênio em gramínea forrageira cultivada em dois solos

RESUMO - As plantas forrageiras são cultivadas sob diversos solos e manejos, ficando vulneráveis à deficiência ou ao excesso de nitrogênio (N). Ensaios em solução nutritiva indicam que esses estresses alteram a estequiometria elementar prejudicando a eficiência nutricional e a produção de massa seca (MS) das culturas, podendo ser mitigado pela fertirrigação com silício (Si). Porém, não se sabe como isso ocorre em gramíneas forrageiras cultivadas em diferentes solos. Foram analisados os prejuízos nutricionais e produtivos causados pela deficiência ou excesso de N em capim Zuri (*M. maximus*) cultivado em dois solos, e os benefícios da fertirrigação com Si (1,5 mM) na atenuação dos prejuízos. Observou-se alterações na estequiometria elementar, prejudicando a eficiência de uso de N, carbono, fósforo e enxofre, e diminuindo a eficiência fotossintética das plantas em ambos estresses de N. Porém, o excesso de N reduziu a produção de MS apenas em solo arenoso. A fertirrigação com nanosílica (1,5 mM de Si) promoveu absorção do Si, regulando a estequiometria C:N:P:S e melhorando a eficiência nutricional das plantas estressadas em Latossolo Vermelho distroférrico típico (argiloso) e em Neossolo Quartzarênico distrófico típico (arenoso). Isso culminou em menor extravasamento celular, mantendo melhor índice de cor verde e menor senescência foliar em plantas sob deficiência, excesso ou suficiência de N. Assim, houve melhora na eficiência fotossintética das plantas sob excesso de N em Neossolo, aumentando sua produção. Conclui-se que a fertirrigação com nanosílica pode atenuar danos causados pelas desordens de N ou de P em capim Zuri, mitigando a perda na produção de forragem na forrageira sob excesso de N cultivada em solo arenoso.

Palavras-chave: desequilíbrios nutricionais; eficiência nutricional; estequiometria elementar; *Megathyrsus maximus*, nanopartículas de Si

Fertigation with nanosilica in attenuating stress due to nitrogen deficiency or excess in forage grass grown in two soils

ABSTRACT - Forage plants grown under different soils and management, making them vulnerable to deficiency or excess of nitrogen (N). Tests in nutrient solution indicate that these stresses alter the elemental stoichiometry, impairing the nutritional efficiency and production of dry mass (DM) of crops, which can be mitigated by fertigation with silicon (Si). However, it is not known how this occurs in forage crops grown in different soils. The nutritional and productive losses caused by deficiency or excess of N in Zuri grass (*M. maximus*) cultivated in two soils were analyzed, and the benefits of fertigation with Si (1.5 mM) in mitigating the losses. Changes in elemental stoichiometry were observed, impairing the efficiency of use of N, carbon, phosphorus and sulfur, and decreasing the photosynthetic efficiency of plants under both N stresses. However, excess N reduced DM production only in Entisol (Quartzipsamment). Fertigation with nanosilica (1.5 mM Si) promoted Si absorption, regulating the C:N:P:S stoichiometry and improving the nutritional efficiency of stressed plants in Oxisol (clayey) and in Entisol (sandy). This culminated in less cell extravasation, better maintaining a higher green color index and less leaf senescence in plants under N deficiency, excess or sufficiency. Thus, there was an improvement in the photosynthetic efficiency of plants under N excess in Neossolo, increasing their production. It is concluded that fertigation with nanosilica can mitigate damage caused by N or P disorders in Zuri grass, mitigating the loss in forage production in forage under excess N grown in sandy soil.

Keywords: nutritional nitrogen stress; pasture, nutritional efficiency; elementary stoichiometry; Si nanoparticles

1 Introdução

O cultivo de espécies forrageiras de alto potencial de produção de biomassa (Poaceae) permite produzir proteína animal de alto valor biológico com menor pressão sobre os recursos naturais, além de beneficiar os sistemas agrícolas integrados, com importante papel em economias em desenvolvimento (Martin et al., 2020; Fuglie et al., 2021; Muñoz-Ulecia et al., 2023). Os pastos estão presentes em aproximadamente 22% da superfície terrestre livre de gelo, sobre diversos tipos de solo com variados manejos de sua fertilidade (Phelps e Kaplan, 2017), possibilitando a ocorrência de desequilíbrios nutricionais tais como deficiência ou excesso de nitrogênio (N) no solo (Delevatti et al., 2019; Phohlo et al., 2022; Melo et al., 2023a).

As gramíneas forrageiras com alto potencial produtivo como as do gênero *Megathyrsus*, apresentam demanda significativa de N (Euclides et al., 2022), nutriente estrutural que compõem centenas de compostos orgânicos na planta (Prado, 2021; Hawkesford et al., 2023). É relevante ter ótima concentração no tecido foliar para que haja ótima conversão de carbono (C), fósforo (P), enxofre (S), demais nutrientes e recursos ambientais em biomassa por meio da fotossíntese.

A deficiência ou o excesso de N pode prejudicar a homeostase C:N:P:S nos tecidos vegetais, um fator importante para a ótima eficiência de uso dos nutrientes pelas plantas (Elser et al., 2010; Costa et al., 2024) e ao mesmo tempo induz estresse oxidativo e degrada os pigmentos fotossintéticos diminuindo a taxa de fotossíntese (Mu e Chen, 2021), limitando o perfilhamento, o alongamento de folhas e o desenvolvimento radicular da planta (Farhan et al., 2024).

Ao contrário do que ocorre em sistemas extensivos, nos pastos manejados intensivamente sem critérios técnicos adequados, as fertilizações com N podem ser elevadas (Mallory e Griffin, 2007; He et al., 2009; Oliveira et al., 2017), podendo causar toxicidade às plantas quando predomina na forma de amônio (NH_4^+) (Goyal e Huffaker, 1984), ou elevar o acúmulo de nitrato (NO_3^-) na forragem com efeitos tóxicos ao metabolismo dos ruminantes (Holman et al., 2019). Os impactos da fertilização excessiva de N em gramíneas forrageiras ainda são uma incógnita, havendo raros ensaios (Barhoumi, 2017), pois, as pesquisas tem focado na deficiência de N, embora

majoritariamente com substrato inerte (Zhu et al., 2014; Deus et al., 2020; Araújo et al., 2022).

A matriz dos solos tropicais sob efeito da calagem apresenta cargas predominantemente negativas, assim, solos argilosos com maior capacidade de troca de cátions que os arenosos, retém mais íons NH_4^+ do que NO_3^- (Nieder et al., 2011; Beusch et al., 2019). Considerando que os contaminantes dos fertilizantes, como o biureto presente na ureia, podem prejudicar a nitrificação quando aplicado em doses elevadas (Xue et al., 2022), o risco de toxidez de NH_4^+ no solo arenoso seria maior, pois, mais NH_4^+ ficaria livre em solução após a fertilização. O nitrato por sua vez pode lixiviar mais rapidamente no solo arenoso, favorecendo sua deficiência (Hussain et al, 2022), mas em pastagens fertirrigadas essa lixiviação é minimizada (Azad et al., 2020). Nesse contexto, a aplicação de altas doses de fertilizantes pode causar acúmulo excessivo no solo e na planta. No entanto, é preciso elucidar essas questões e como isso afeta os pastos.

Uma estratégia para minimizar os prejuízos causados pelos desequilíbrios nutricionais é a utilização de silício (Si), pois, auxilia nos processos de combate ao estresse oxidativo, melhorando a integridade de pigmentos fotossintetizantes, e o equilíbrio C:N:P nos tecidos (Carvalho et al., 2022; Costa et al., 2022; Melo et al., 2023b). Diante disso, a sua aplicação é importante pois, é comum teores disponíveis de Si relativamente baixo nos solos, principalmente em solos tropicais altamente lixiviados devido ao processo de dessilicação (Camargo e Keeping, 2021; Dutra et al., 2023).

Os estudos com Si para atenuar estresses nutricionais estão restritos aos cultivos hidropônicos a partir do uso predominante do silicato de potássio visto em algumas espécies como arroz (Deus et al., 2020), forrageiras (Buchelt et al., 2020; Araújo et al., 2022), e cana-de-açúcar (Oliveira et al., 2022), mas essa fonte é sensível a polimerização. Para diminuir esse problema tem surgido fontes provenientes de nanopartículas de Si e podem potencializar a absorção devido ao tamanho diminuto de partículas, estabilidade em solução e facilidade de aplicação em sistemas fertirrigados (Wang et al., 2022; Awad-Allah, 2023). No entanto, faltam estudos em

condição de solo para aferir a eficiência das nanopartículas de Si na atenuação de deficiência ou toxicidade de N em gramíneas forrageiras cultivadas em diferentes solos tropicais.

Considerando os danos biológicos causados pela subdosagem ou superdosagem de N em gramíneas forrageiras cultivadas em solos contrastantes, e que os mecanismos de atenuação desses danos pela aplicação de nanosílica ainda são desconhecidos, é pertinente investigar algumas hipóteses: (I) os desequilíbrios de N alteram a homeostase e a eficiência nutricional de gramínea forrageira cultivada em diferentes solos; (II) o uso de superdosagem de N pode ser mais danoso à gramínea cultivada em solos de textura arenosa e; (III) a aplicação de nanosílica promove absorção de Si e atenuação dos danos causados pelos desequilíbrios nutricionais, com destaque para toxicidade de N em capim *M. maximus* cv. Zuri em Latossolo Vermelho distroférrico típico e Neossolo Quartzarênico distrófico típico ao melhorar a homeostase entre C, N, P e S, a eficiência nutricional e fotossintética, e diminuir a perda na produção de matéria seca. Se as hipóteses se confirmarem, serão esclarecidos os danos da subdosagem e superdosagem de N na planta cultivada em diferentes solos, e se a utilização do Si se será mais efetiva na deficiência ou no excesso de N em dois solos contrastantes.

Diante do exposto, os objetivos deste estudo foram avaliar os prejuízos causados pela deficiência e pelo excesso de N no solo, e se uso da nanosílica é benéfico para mitigar os dois estresses nutricionais em *M. maximus* cv. Zuri cultivada em solos de texturas contrastantes.

2 Material e métodos

2.1 Condições de cultivo

Foram desenvolvidos dois experimentos independentes e simultâneos com a espécie *Megathyrsus maximus* cv. Zuri, sendo um em Latossolo Vermelho distroférrico típico, textura argilosa, e outro em Neossolo Quartzarênico distrófico típico, textura arenosa (Santos et al., 2018) em casa de vegetação na Universidade Estadual Paulista “Júlio Mesquita Filho” (UNESP – Jaboticabal, Brasil). O período experimental

compreendeu cinco ciclos de crescimento das plantas, aproximadamente 180 dias a partir da semeadura. Durante esse período foram monitoradas diariamente a temperatura e a umidade relativa do ar no interior da casa de vegetação utilizando um termo-higrômetro. Os registros foram de temperatura do ar foram a média máxima de 47 ± 5 °C, média mínima de 22 ± 5°C, e umidade relativa do ar média igual a 50 ± 10%.

2.2 Desenho experimental e instalação

Em cada experimento foram testados 6 tratamentos em esquema fatorial 3x2, com 4 repetições, e delineamento inteiramente casualizado. Foram combinados três estados nutricionais de N: deficiente (30 mg dm^{-3}), suficiente ou adequado (300 mg dm^{-3}) (Malavolta et al.,1981) e excessivo (600 ou 800 mg dm^{-3}), com ausência de Si (sem aplicação) e presença de Si (1,5 mM). A unidade experimental constituiu-se de duas plantas em um vaso plástico de 7L com altura de 32 cm, base inferior 14 x 14 cm e superior 16 x 16 cm. Os vasos foram preenchidos com 6 kg de amostra de Latossolo e 8 kg de amostra de Neossolo coletadas na camada superficial de área não cultivada, nos municípios de Jaboticabal/SP e Araraquara/SP, respectivamente. As amostras foram previamente peneiradas (malha 6 mm).

Amostras dos solos foram analisadas quimicamente para fins de fertilidade (Raij et al., 2001) e obtenção do teor de Si (Korndorfer et al., 2004), com os seguintes resultados para Latossolo Vermelho e Neossolo Quartzarênico, respectivamente: pH em CaCl2 =3,8 e 4,3; MO (matéria orgânica) = 34 e 9,0 mg dm^{-3}; P no extrator resina = 12 e 2 mg dm^{-3}; K=1,4 e 3,0; Ca = 6 e 3,0; Mg = 2 e 1,0 mmolc dm^{-3}; H+Al = 85 e 16; T (capacidade de troca de cátions) = 94 e 20,3 mmolc dm^{-3}; V (saturação por bases) = 10 e 21% e Si= 3,0 e 1,0 g dm^{-3}. Amostras dos solos passaram por análise granulométrica (Donagema et al., 2011), constando os seguintes resultados para Latossolo e Neossolo, respectivamente: 51 e 94% de areia, 6 e 1% de silte e, 43 e 5% de argila.

Realizou-se aplicação de calcário magnesiano (poder de neutralização total:125%, CaO: 58,5%, MgO: 9%) para elevar a saturação por bases a 70% (Raij et

al., 2001). Procedeu-se a homogeneização das amostras de solo de cada vaso com a quantidade de calcário correspondente às doses de 2,25 e 0,48 g dm^{-3} em Latossolo e Neossolo, respectivamente, cumprindo um período de incubação de 40 dias com os solos úmidos antes da semeadura.

A fertilização foi realizada após o período de reação do calcário, incorporando nos solos secos de cada parcela as quantidades de cloreto de potássio, superfosfato triplo, sulfato de cálcio di-hidratado, sulfato de zinco heptahidratado, ácido bórico correspondentes às doses de 150, 200, 50, 5 e 0,5 mg dm^{-3} de K, P, S, Zn e B, bem como quelato de ferro (EDDHA) (5 mg dm^{-3} de Fe) em Neossolo (Malavolta et al., 1981). Após o terceiro corte foi realizada adubação potássica de manutenção com 75 mg dm^{-3} de K. O nitrogênio (ureia) foi aplicado nas doses de 30, 300 e 800 mg dm^{-3} de N em Latossolo, e 30, 300 e 600 mg dm^{-3} de N em Neossolo para estabelecer os estados deficiente, adequado e excessivo de N, respectivamente. No estado excessivo de N, a dose foi parcelada em três aplicações durante cada período de rebrotação das plantas, sempre incorporada com irrigação.

A semeadura foi realizada depositando 20 sementes de *M. maximus* Zuri diretamente no solo de cada parcela, em um sulco circular de 1 cm de profundidade. O desbaste foi realizado após a emergência mantendo-se duas plantas por vaso, e aos 30 dias após a semeadura realizou-se o corte de uniformização, deixando todas as plantas com altura de 17 cm, em relação ao nível do solo no vaso.

2.3 Condições hídricas e fornecimento de silício

Para determinar a capacidade de retenção de água (CRA) dos solos foram preenchidos dois vasos com cada tipo de solo, sendo os mesmos submetidos a saturação em recipiente com água por 24h. Ao serem retirados do ambiente de saturação, os vasos foram cobertos com filme plástico e mantidos em drenagem livre. Após a drenagem, amostras dos solos foram secas em estufa, permitindo determinar a CRA por diferença entre as massas de solo drenado (úmido) e seco. A irrigação foi realizada mantendo os solos em 70% de sua CRA, procedendo a pesagem diária dos

vasos ao final da tarde, seguida da reposição da água perdida por evapotranspiração (Boaretto et al., 2014; Oliveira Filho et al., 2021).

O fornecimento de Si deu-se desde a semeadura até o último corte das plantas, aplicando uma solução de 1,5 mmol L^{-1} de Si (Buchelt et al., 2021), preparada com nanosílica coloidal (partículas de 8,5 a 9,7 nm, área superficial específica de 300 m^2 g^{-1} e pH 10,5). Todos os tratamentos receberam o mesmo volume de solução de Si diariamente, sendo esse volume definido diariamente com base no tratamento de menor demanda hídrica, a partir da pesagem dos vasos. O volume aplicado de solução de Si foi contabilizado, e correspondeu a uma lâmina média diária de 18 e 13 mm nos experimentos em Latossolo e em Neossolo, respectivamente.

Nos tratamentos com maior demanda hídrica, a irrigação foi completada com água deionizada, e nas parcelas que não receberam Si, a irrigação foi realizada sempre com água destilada e deionizada. As coletas de biomassa do estrato pastejável foram realizadas sempre que as plantas sob suficiência de N atingiam 70 cm de altura, deixando uma biomassa residual de 30 cm de altura (Barbosa et al., 2021).

2.4 Variáveis analisadas

2.4.1 Índices de extravasamento de eletrólitos e de cor verde

Para analisar o extravasamento de eletrólitos retirou-se cinco discos foliares (6 mm) do terço médio da folha mais recentemente expandida das plantas, e em seguida foram colocados em béquer com 20 mL de água deionizada em temperatura ambiente (~25 °C) por duas horas. A leitura da condutividade elétrica inicial (EC_1) foi então aferida com condutivímetro manual (TDS-3). As amostras foram autoclavadas por 20 min a temperatura de 121 °C, e após resfriarem (temperatura ambiente) fez-se a leitura da condutividade elétrica final (CE_2). O índice de extravasamento de eletrólitos foi estimado pela fórmula: $EL = EC_1 / EC_2 \times 100$ (Dionisio-Sese e Tobita, 1998).

O índice de cor verde foi aferido utilizando medidor de clorofila portátil (OptiSciences® CCM -200). O terço médio da folha mais recentemente expandida de cada planta foi posicionada no equipamento, que retorna valores proporcionais à

concentração de clorofila na amostra. Ambas avaliações foram realizadas ao final de cada ciclo de rebrotação, um dia antes da coleta de massa, obtendo-se a média ao final do período experimental.

2.4.2 Eficiência quântica do fotossistema II (Fv/Fm)

A Fv/Fm foi estimada medindo-se a fluorescência da clorofila entre 7h e 9h da manhã, após ambiência da porção da lâmina foliar a ser analisada, que ficou por 30 min no escuro sob o clipe do aparelho. A análise realizada por meio da excitação da clorofila pela luz vermelha pulsante (3.500 µmol) emitida por fluorímetro portátil (Opti-Sciences Os30P) (Lichtenthaler et al., 2005). As aferições foram realizadas no terço médio da folha mais recentemente expandida, em cada planta ao final do quinto ciclo de rebrotação.

2.4.3 Biométricas e produtivas

Ao final de cada ciclo de crescimento quando as plantas sob suficiência de N atingiam altura de 70 cm (Barbosa et al., 2021), realizou-se a contagem do número de perfilhos (perfilhos por vaso), e do número de folhas vivas e senescentes para obter o percentual de folhas senescentes por vaso. Imediatamente antes de realizar o corte das plantas era aferida a altura das plantas (cm) considerando o comprimento desde a base até a inflexão das folhas totalmente desenvolvidas.

A produção média de matéria seca (MS) foi determinada ao realizar a coleta de biomassa do estrato pastejável das plantas ao final dos cinco ciclos de rebrotação. No último ciclo, após a coleta de parte área procedeu-se a avaliação da densidade de raízes. O bloco de solo e raízes foi retirado do vaso e colocado sobre uma bandeja. Em seguida, um cilindro metálico de 269 cm^3 foi cravado no centro do bloco até o preenchimento do mesmo. O solo foi retirado do cilindro e lavado até obtenção das raízes livres de solo.

As amostras de parte área e de raízes foram lavadas em solução detergente (0,1% v:v) e água destilada sucessivamente, e em seguida foram acondicionadas em sacos de papel e levadas à estufa com circulação forçada de ar (65 ± 5 ºC) até atingir massa constante. Assim foi obtida a produção de massa seca (MS) de cada ciclo de

rebrota, e ao final do período experimental calculou-se a média dos cinco ciclos (MS, g por vaso). Com os dados de MS de raízes obtidos, calculou-se a densidade de raízes (Densidade de raízes, g cm^{-3}) = MS de raízes (g) /volume do cilindro (cm^3).

2.4.4 Teores de nutrientes e Si

Foram determinados os teores de C, N, P, S e Si na matéria seca do estrato pastejável, que foi triturada em moinho tipo Willey. Para isso utilizou-se uma amostra composta por alíquotas de mesmo volume de cada ciclo analisado. Os teores de C e N foram determinados em analisador elementar LECO Truspec CHNS. P e S foram determinados em extrato nítrico-perclórico, sendo o P por colorimetria (vanadato e molibdato) e o S (SO_4^-) por turbidimetria (cloreto de bário) ambos com leitura em espectrofotômetro a 420 nm (Malavolta et al., 1997). O Si foi extraído por digestão alcalina em peróxido de hidrogênio a 120 ºC (Kraska e Breitenbeck, 2010), e determinado em espectrofotômetro a 410 nm após reação colorimétrica com molibdato de amônio (NH_4^+) (Korndorfer et al., 2004). O teor de cada elemento foi expresso em g kg^{-1}.

2.4.5 Homeostase estequiométrica e eficiência de uso de nutrientes

Utilizando os teores dos nutrientes e de Si na MS foram calculadas as razões estequiométricas C:Si, C:N, C:P, N:P e C:S, e as eficiências de uso de C (EUC), de N (EUN), de P (EUP) e de S (EUS), obtidas por meio do quociente do quadrado da matéria seca e o teor do nutriente (Korndorfer et al., 2004).

2.4.6 Registros fotográficos

Foram obtidas imagens fotográficas comparativas da parte aérea e do sistema radicular das plantas sob os tratamentos de deficiência, suficiência e excesso de N, na ausência ou presença de Si, como material suplementar para observação de sintomas e do aspecto geral das plantas.

2.5 Análise estatística

Os dados foram submetidos a análise de variância pelo Teste F ($p<0,05$), após sua análise quanto aos pressupostos de normalidade, homogeneidade e independência dos resíduos (Jarque e Bera, 1980; Bartlett, 1937). Quando teste F foi significativo, as médias foram comparadas pelo Tukey ($p<0,05$), utilizando o software estatístico SPEED Stat versão 2.8 (Carvalho et al., 2020). Foi realizada uma análise de correlação de Pearson entre as variáveis ($p<0,05$), gerando uma matriz para os estados de deficiência, suficiência ou excesso de N. As correlações positivas estão destacadas em escala de azul, e as correlações negativas em escala de vermelho. A análise foi realizada utilizando o programa R versão 4.4.3.

3 Resultados

3.1 Teores de Si, N, C, P e S na massa seca

Houve interação significativa NxSi ($p<0,05$) para os teores de nutrientes e Si na MS em ambos solos estudados (Fig 1, a-j). Em ausência de Si nas plantas deficientes em N observou-se um aumento no teor de Si (Latossolo), diminuição nos teores de N, C e S, e aumento no teor de P em ambos solos, em comparação com as plantas sob suficiência de N. Na condição de excesso de N em relação ao estado suficiente, os teores de N e S foram aumentados, enquanto o teor de C das plantas diminuiu em ambos solos, com aumento no teor de P das plantas em Neossolo.

Na presença de Si, as plantas sob deficiência em relação à suficiência de N apresentaram aumento no teor de Si e P, e diminuição no teor de N e C em ambos solos. Nas plantas sob excesso de N houve aumento no teor de N em ambos solos, sendo que em Neossolo ocorreu também incremento nos teores de Si, P e S, e diminuição do teor de C das plantas sob excesso de N em comparação com a suficiência de N (Fig 1 a-j).

A aplicação de Si em relação à sua ausência aumentou nos teores de Si nas plantas em todos os estados de N, com diminuição nos teores de N na suficiência e no excesso de N, e diminuição no teor de P na deficiência e excesso de N em ambos solos. Outro efeito da fertilização com nanosílica foi a diminuição no teor de C das

plantas sob suficiência de N em ambos solos, e na deficiência de N em Neossolo, mas houve aumento no teor de C nas plantas sob excesso de N em Neossolo (Fig 1 a-j).

3.2 Razões estequiométricas

A interação NxSi foi significativa ($p<0,05$) para a maioria das razões estequiométricas analisas em ambos solos, com exceção das razões C:P e N:P em Neossolo, e da razão C:S em Latossolo (Fig 2, a-i). Em ausência de Si, a deficiência de N em relação à suficiência causou diminuição nas razões C:Si, C:P e N:P, com aumento nas razões C:N e C:S em ambos solos, enquanto sob excesso de N houve diminuição nas razões C:Si, C:N, C:P, e C:S, e aumento na razão N:P em Latossolo e Neossolo. Na presença de Si, a deficiência de N promoveu diminuição na C:Si em Latossolo, diminuição nas razões C:P e N:P, e aumento nas razões C:N e C:S em ambos solos, em relação à suficiência de N.

A fertilização com Si em relação à sua ausência fez diminuir a razão C:Si nos três estados de N em ambos solos, e causou aumento na razão C:N nas plantas sob deficiência de N em Neossolo. Além disso, notou-se aumento na razão C:P das plantas sob deficiência de N em Latossolo, e no excesso de N em ambos solos. Plantas sob excesso de N em Latossolo que receberam Si apresentaram ainda aumento na razão N:P, enquanto a razão C:S aumentou nos estados adequado e excessivo de N em Latossolo, e também no deficiente e no excessivo em Neossolo (Fig 2, a-i).

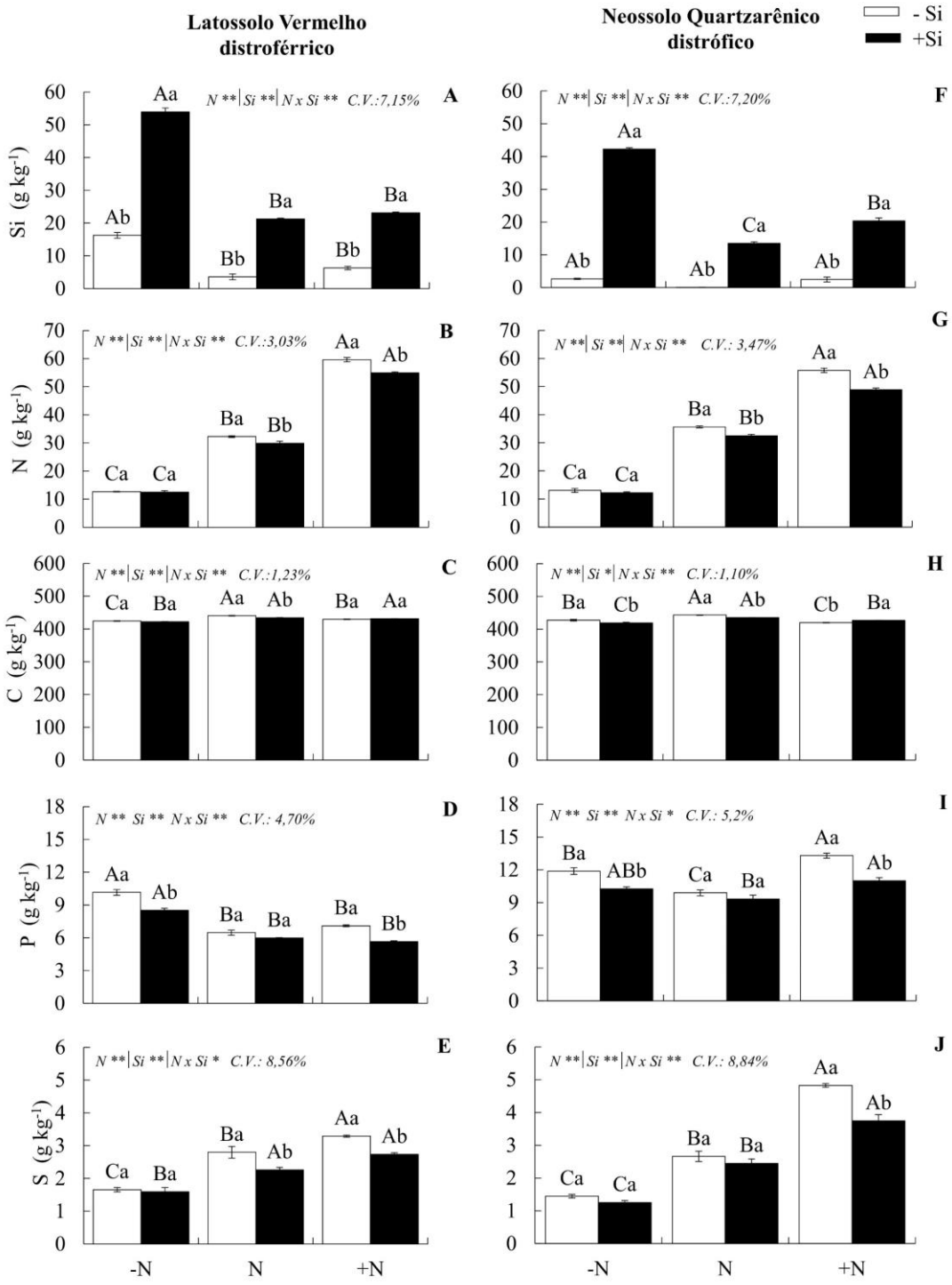


Fig. 1 Teores de Si, C, N, P e S em capim *M. maximus* cv. Zuri cultivado sob estados deficiente (-N), suficiente (N) e excessivo de nitrogênio (+N) fertirrigadas com silício (+Si) ou sem fertirrigação de Si (-Si), em Latossolo (a, b, c, d, e) e Neossolo (f, g, h, i) (Médias de cinco ciclos de crescimento). Ns, * e ** correspondem ao teste F não significativo, significativo a 5 e 1%, respectivamente. Letras minúsculas indicam diferenças do Si dentro de cada estado de N, e letras maiúsculas indicam diferenças nos estados de N de acordo com a condição de Si (teste Tukey, $p<0,05$)

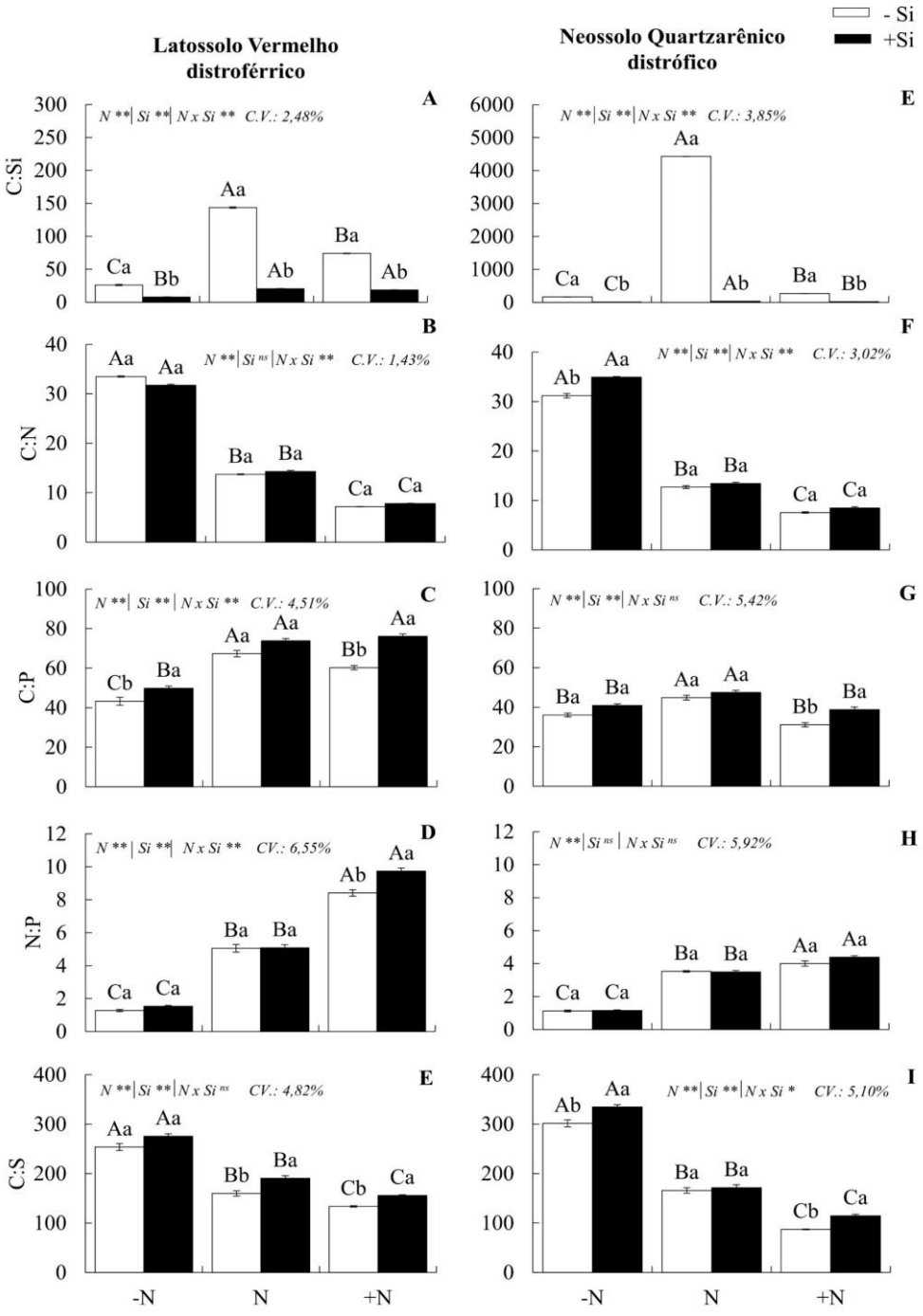


Fig. 2 Razões estequiométricas C:Si, C:N, C:P, N:P e C:S em capim *M. maximus* cv. Zuri cultivado por cinco períodos de rebrotação sob estados deficiente (-N), suficiente (N) e excessivo de nitrogênio (+N) fertirrigadas com silício (+Si) ou sem fertirrigação de Si (-Si), em Latossolo (a, b, c, d, e) e em Neossolo (f, g, h, i) (Médias de cinco ciclos de crescimento). Ns, * e ** correspondem ao teste F não significativo, significativo a 5 e 1%, respectivamente. Letras minúsculas indicam diferenças do Si dentro de cada estado de N, e letras maiúsculas indicam diferenças nos estados de N de acordo com a condição de Si (teste Tukey, $p<0,05$)

3.3 Eficiência de uso de C, N, P e S

Houve interação NxSi significativa ($p<0,05$) para a EUP em ambos solos, para EUC em Neossolo, e para NUE em Latossolo (Fig 3, a-h). Em ausência de Si as plantas de capim Zuri deficientes em N apresentaram aumento na NUE e diminuição em EUC e EUP, em ambos solos, sem alteração na EUS em comparação com plantas adequadamente nutridas com N. Em plantas sob excesso de N houve diminuição em EUN, EUP e EUS em ambos solos. A EUC também diminuiu em Neossolo, mas não em Latossolo.

Na presença de Si houve nas plantas deficientes em N em relação à suficiência do nutriente um aumento na EUN e diminuição em EUC e EUP em ambos solos, com prejuízo também na EUS em Latossolo. Na condição de excesso de N, foram diminuídas EUN e EUS em Latossolo e Neossolo, enquanto em Neossolo houve diminuição em EUC e EUP, em comparação com plantas sob suficiência de N.

Quando se comparada a presença de Si em relação à sua ausência observa-se um aumento em EUN, EUP e EUS na deficiência, na suficiência e no excesso de N em Latossolo e Neossolo, com aumento também na EUC em plantas sob suficiência e excesso de N em ambos solos, mas não na deficiência de N (Fig 3, a-h).

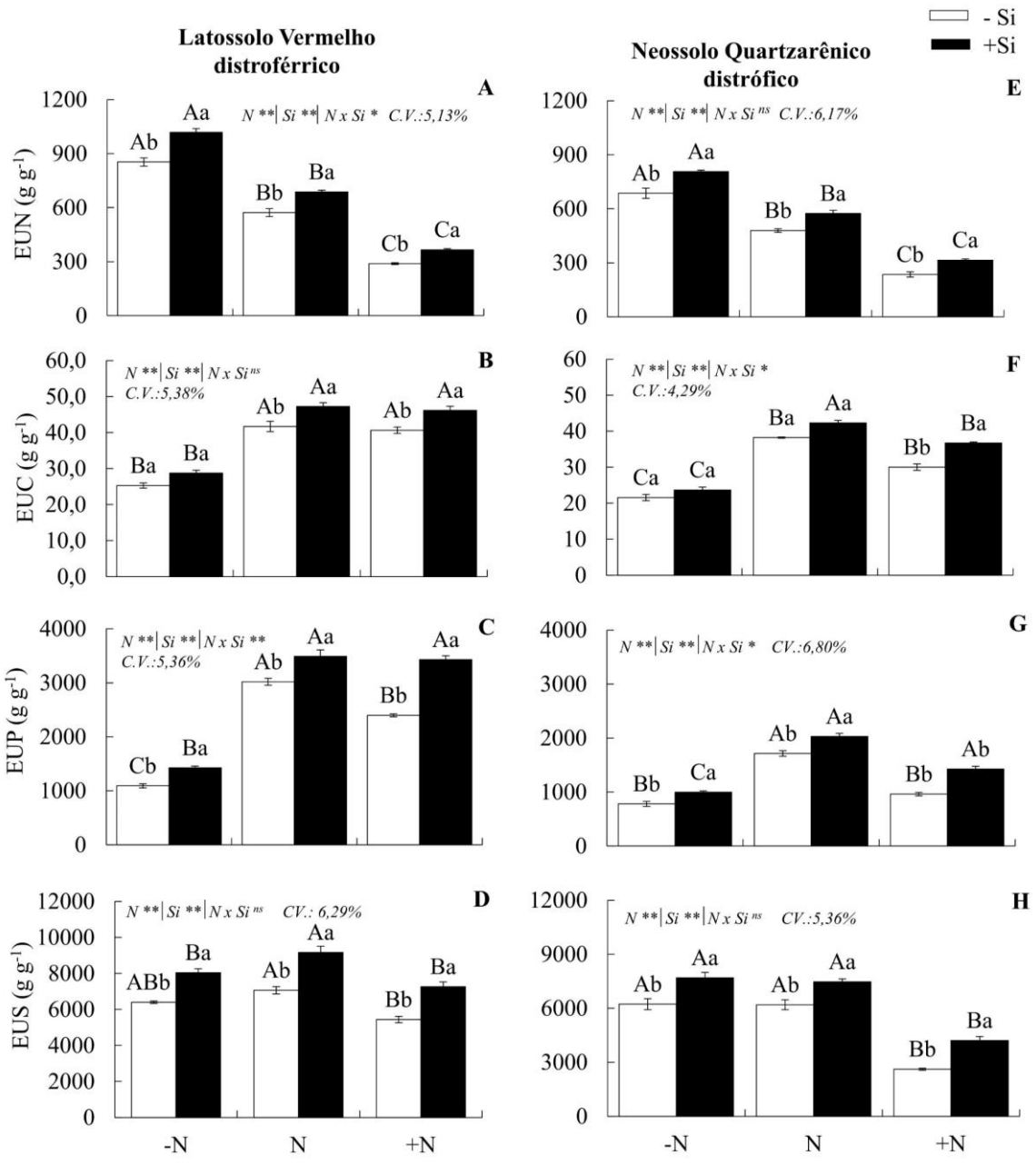


Fig. 3 Eficiências de uso de N (EUN), de C (EUC), de P (EUP) e de S (EUS) em capim *M. maximus* cv. Zuri cultivado por cinco períodos de rebrotação sob estados deficiente (-N), suficiente (N) e excessivo de nitrogênio (+N) fertirrigadas com silício (+Si) ou sem fertirrigação de Si (-Si), em Latossolo (a, b, c, d) e em Neossolo (e, f, g, h) (Médias de cinco ciclos de crescimento). Ns, * e ** correspondem ao teste F não significativo, significativo a 5 e 1%, respectivamente. Letras minúsculas indicam diferenças do Si dentro de cada estado de N, e letras maiúsculas indicam diferenças nos estados de N de acordo com a condição de Si (teste Tukey, $p<0,05$)

3.4 Índice de cor verde, extravasamento de eletrólitos e eficiência do FSII

As variáveis índice de cor verde e eficiência quântica do fotossistema II (FSII) apresentaram interação significativa NxSi ($p<0,05$), o que não se verificou para o índice de extravasamento de eletrólitos (Fig 4, a-f). Sob ausência de Si o índice de cor ver das plantas deficiente em N diminuiu em Latossolo e em Neossolo, e sob excesso de N essa diminuição ocorreu apenas nas plantas cultivadas em Neossolo. A eficiência quântica do PSII diminuiu em ambos solos, em comparação com as plantas sob suficiência de N.

Na presença de Si, o índice de cor verde ainda diminuiu sob deficiência de N em ambos solos em comparação com a suficiência de N. As plantas sob excesso de N apresentaram diminuição no índice de cor verde e na eficiência quântica do PSII em Neossolo, em relação às plantas cultivadas sob estado adequado de N. Quando se comparada a presença de Si com sua ausência, observa-se um aumento no índice de cor verde das plantas sob deficiência ou excesso de N em Latossolo e em Neossolo, diminuição do extravasamento de eletrólitos e aumento na eficiência quântica do PSII nas plantas sob excesso de N em ambos solos (Fig 4, a-f)

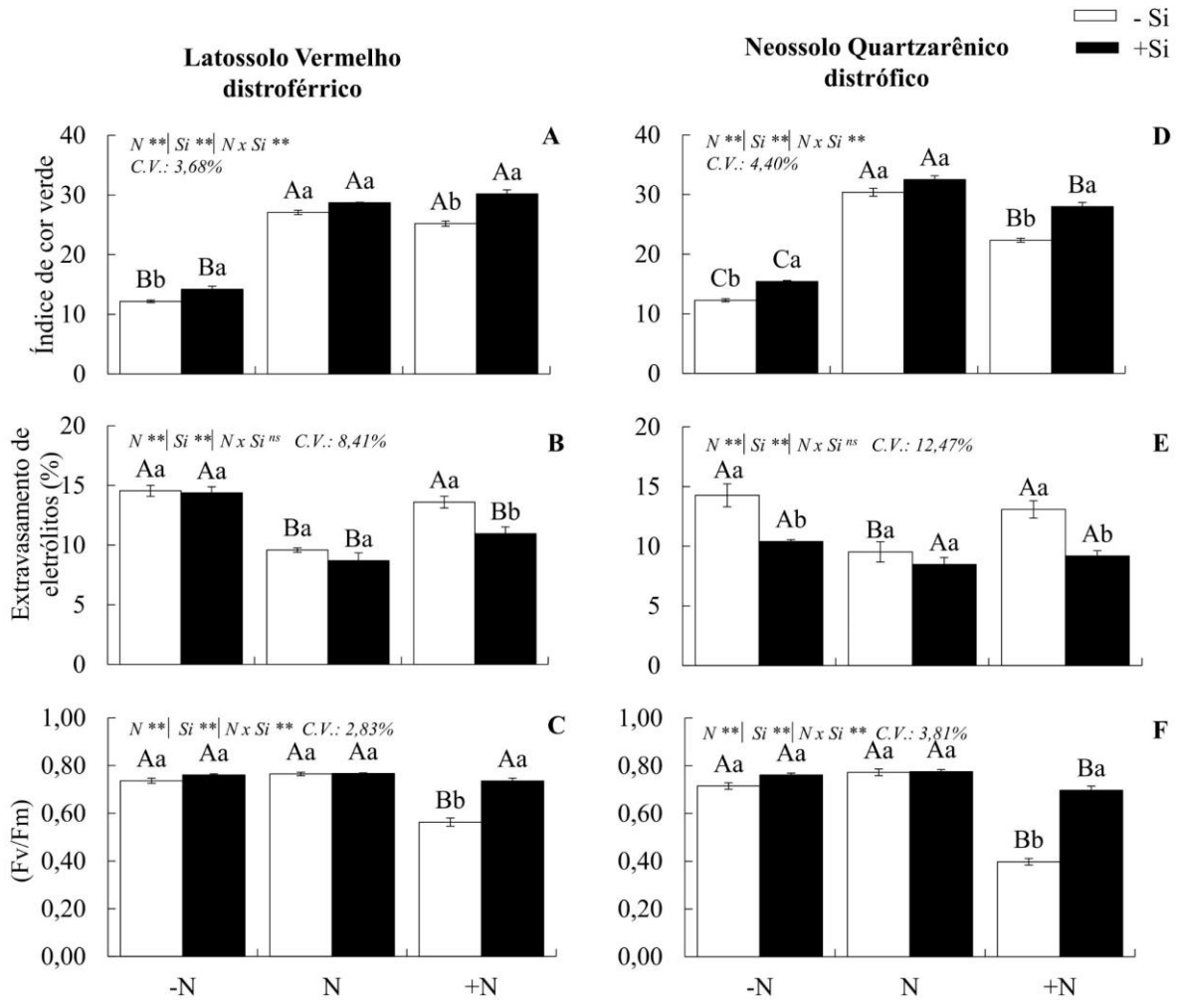


Fig. 4 Índice de cor verde e índice de extravasamento de eletrólitos (médias de cinco ciclos de crescimento) e eficiência quântica do fotossistema II (no quinto ciclo de crescimento) em plantas de capim Zuri cultivadas sob estados deficiente (-N), suficiente (N) e excessivo de nitrogênio (+N) fertirrigadas com silício (+Si) ou sem fertirrigação de Si (-Si), em Latossolo (a, b, c) e em Neossolo (d, e, f). Ns, * e ** correspondem ao teste F não significativo, significativo a 5 e 1%, respectivamente. Letras minúsculas indicam diferenças do Si dentro de cada estado de N, e letras maiúsculas indicam diferenças nos estados de N de acordo com a condição de Si (teste Tukey, $p<0,05$)

3.5 Parâmetros biométricas e produtivos

A interação NxSi foi significativa ($p<0,05$) para as variáveis: altura de planta em Latossolo, percentual de folhas senescentes em ambos solos, MS do estrato pastejável e densidade de raiz em Neossolo (Fig 5, a-j). Comparando os estados nutricionais na ausência de Si, observou-se na deficiência de N em relação ao estado adequado uma diminuição na altura de planta, no número de perfilhos (52 e 58%) e na MS produzida em (42 e 46%) em Latossolo e Neossolo, respectivamente. Sob excesso de N as plantas apresentaram diminuição na altura, no número de perfilhos (47 e 25%), e na densidade de raiz (55 e 62%) em relação ao estado adequado de N, em Latossolo e Neossolo, respectivamente, bem como diminuição na MS produzida (25%) em Neossolo. Observou-se ainda um aumento na senescência foliar sob excesso de N em relação ao estado adequado, de 11 e 28% em Latossolo e Neossolo, respectivamente (Fig 5, a-j).

Na presença de Si observou-se nas plantas sob deficiência ou excesso de N diminuição na altura, no número de perfilhos e na MS em ambos solos, em relação às plantas sob suficiência de N. No excesso de N também houve diminuição na densidade de raízes em ambos solos, diminuição na MS produzida em Neossolo (15%) em comparação com a suficiência de N.

Na presença de Si em comparação com sua ausência as plantas deficientes em N apresentaram diminuição no percentual de folhas senescentes (11 e 16%) em Latossolo e Neossolo, respectivamente. Nas plantas sob excesso de N houve aumento na altura de plantas (7 e 10%), número de perfilhos (19 e 15%), densidade de raízes (41 e 38%) e MS produzida (12 e 19%), bem como diminuição no percentual de folhas senescentes (18 e 23%) em Latossolo e Neossolo (Fig 5, a-j).

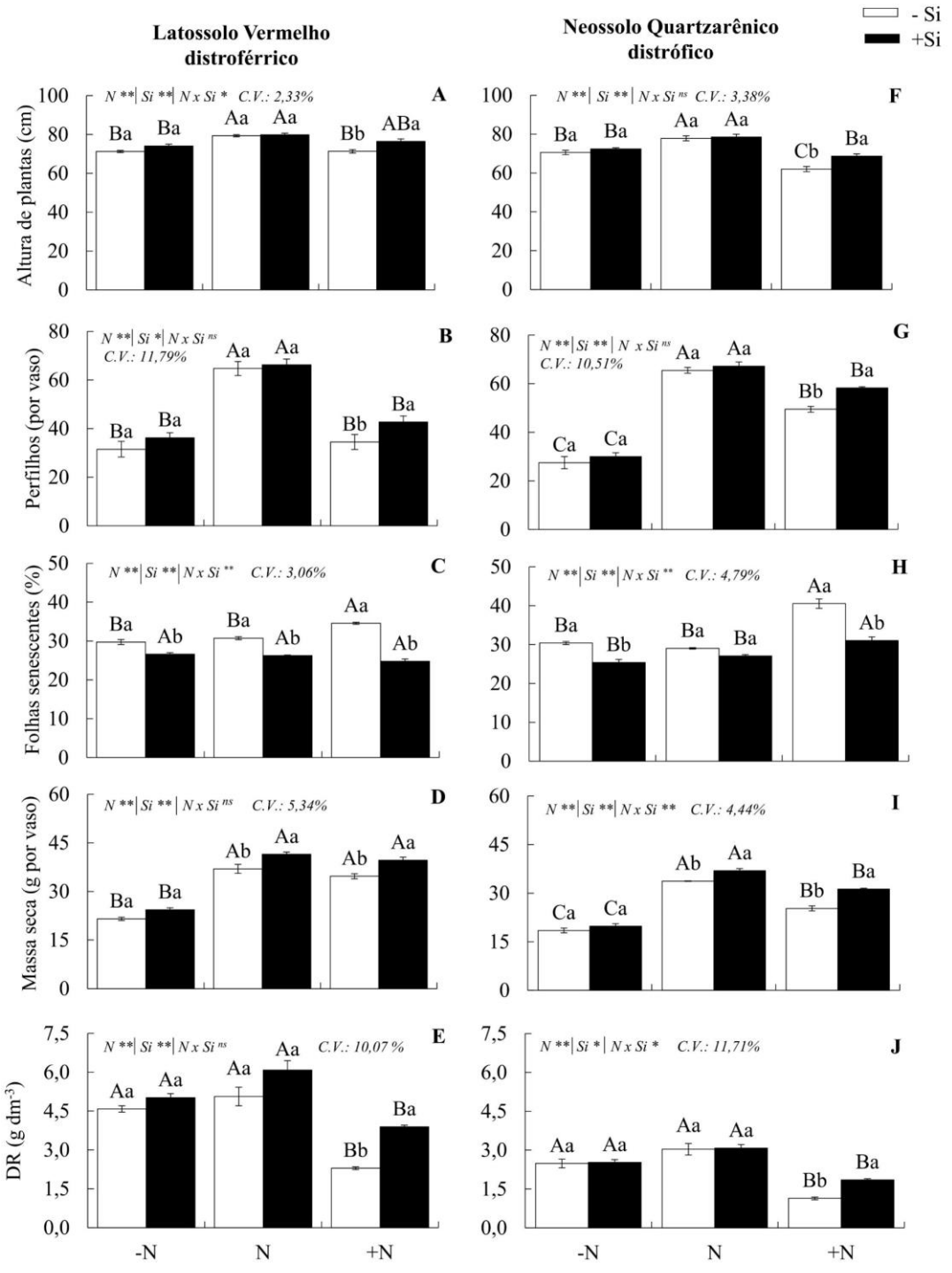


Fig. 5 Altura de planta, número de perfilhos, percentual de folhas senescentes, massa seca do estrato pastejável e densidade de raízes (DR) em plantas de capim Zuri cultivadas sob estados deficiente (-N), suficiente (N) e excessivo de nitrogênio (+N) fertirrigadas com silício (+Si) ou sem fertirrigação de Si (-Si), em Latossolo (a, b, c, d, e) e em Neossolo (f, g, h, i, j) (Médias de cinco ciclos de crescimento). Ns, * e ** correspondem ao teste F não significativo, significativo a 5 e 1%, respectivamente. Letras minúsculas indicam diferenças do Si dentro de cada estado de N, e letras maiúsculas indicam diferenças nos estados de N de acordo com a condição de Si (teste Tukey, $p<0,05$)

3.6 Análise de correlação

As matrizes da correlação de Pearson (Fig 6 a-f) permitem observar que na deficiência de N em Latossolo (Fig 6 a) houve forte relação positiva do teor de Si com a EUP (r = 0,88*), com o índice de cor verde (r = 0,80*) e com a MS (r = 0,79*), e houve fortes relações negativas da MS com o teor de C (r = -0,86*) e com a relação C:Si (r = -0,78*). Em Neossolo (Fig 6 b), a matéria seca foi relacionada positivamente com a EUC e a EUP (r = 0,98*; r = 0,88*), e o teor de Si com o índice de cor verde (r = 0,97*). Vale destacar algumas relações negativas, entre o extravasamento celular e o número de perfilhos (r = -0,86*), e entre a relação C:Si e o índice de cor verde (r = -0,94*).

Na condição de suficiência de N em Latossolo (Fig 6 c) foram observadas relações positivas entre a relação C:Si e o percentual de folhas senescentes (r = 0,95*), e entre a eficiência de uso de N e de C (r = 0,92*), com relações negativas entre teor de Si e folhas senescentes (r = -0,95*), entre a razão C:Si e a eficiência de uso de S (r = -0,90*), e entre razão C:Si e índice de cor verde (r = -0,94*). Em Neossolo, o teor de Si apresentou relação positiva com EUN e EUC (r = 0,69*), com o índice de cor verde (r = 0,71*), e com a MS (r = 0,62*).

Sob excesso de N em Latossolo (Fig 6 e) observa-se forte relação positiva das eficiências de uso (EUP, EUN e EUS) com a matéria seca (r = 0,97*, r = 0,96*, r = 0,95*), e também relação positiva entre teor de Si e MS (r = 0,85*). Foram encontradas relações negativas entre teor de Si e teor de N (r = 0,91*), e entre teor de Si e percentual de folhas senescentes (r = 0,94*). Em Neossolo (Fig 6 d), houve relação positiva entre do teor de Si com a matéria seca (r = 0,91*) e com a eficiência do FSII (r = 0,87*), e relação negativa entre a senescência foliar e a matéria seca (r = - 0,96*).

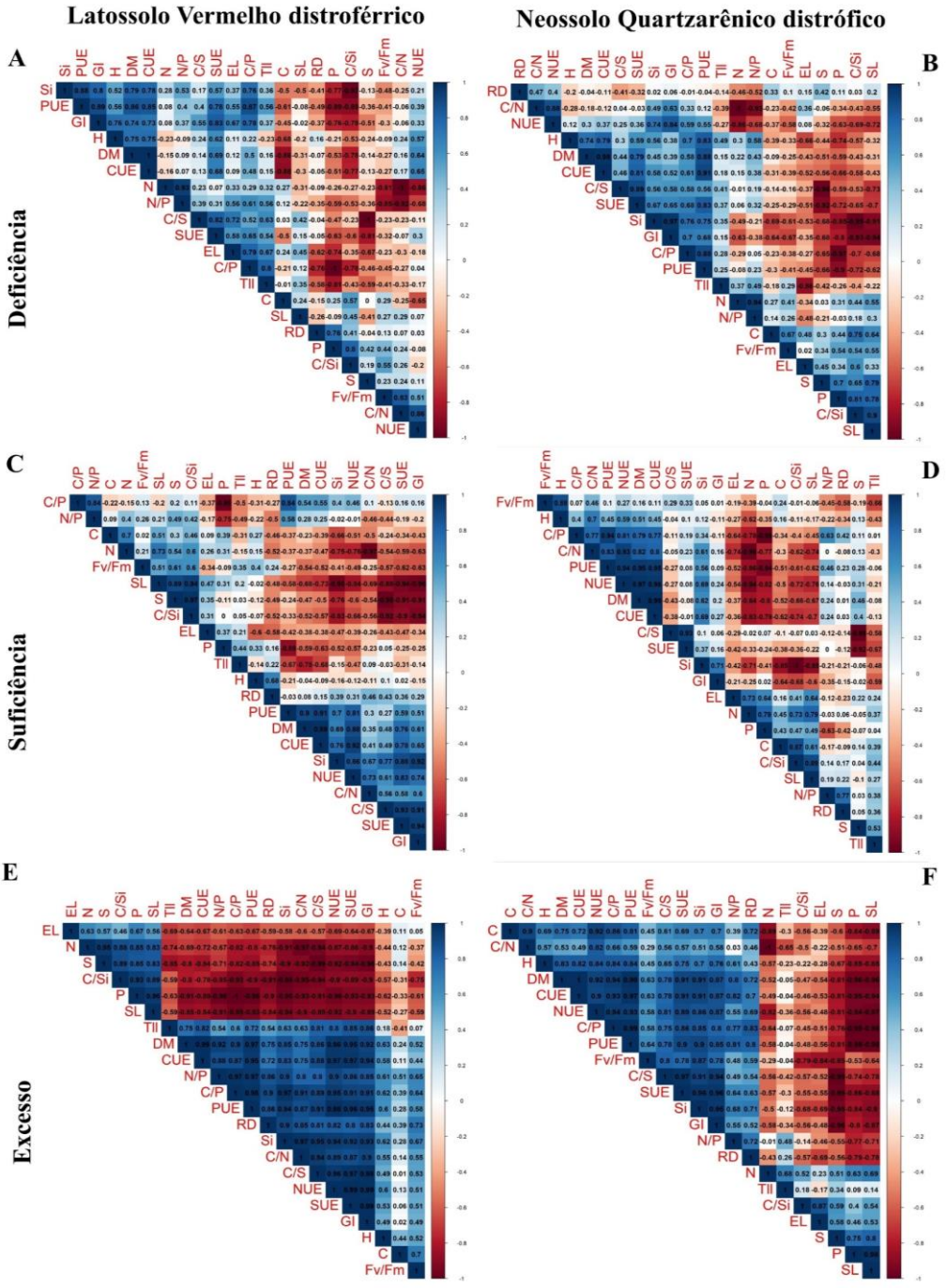


Fig. 6 Correlação de Pearson (p<0,05) entre as variáveis teores de carbono, nitrogênio, fósforo, enxofre, silício (C, N, P, S, Si), razões estequiométricas (C:N, C:Si, C:P e N:P), eficiências de uso de C, N, P e S (CUE, NUE, PUE, e SUE), índice de cor verde (green index, GI), extravasamento de eletrólitos (electrolyte leakage, EL), eficiência do PSII (Fv/Fm), altura de planta (H), número de perfilhos (TIL), folhas senescentes (senescentes leaves, SL), massa seca (dry matter, DM) e densidade de raízes (root density, RD) nos estados de deficiência, suficiência e excesso de N em Latossolo Vermelho distroférrico (a, c, e) e Neossolo Quartzarênico distrófico(b, d, f) incluindo os dados de ausência e presença de Si.

4 Discussão

4.1 Deficiência e excesso de N prejudicam a assimilação de C e a eficiência nutricional em *M. maximus*

A limitação de N causada pelos baixos teores do nutriente no solo impõe às plantas forrageiras diversos prejuízos, causando o declínio da produção de forragem (Rueda et al., 2020). Foi constatado que o cultivo de *M. maximus* sob a menor dose de N (30 g dm^{-3}) em Latossolo e Neossolo resultou em baixo teor médio de N na MS (12,5 g kg^{-1}) quando comparado ao estado de suficiência de N (33,8 g kg^{-1}). Isso indica que mesmo solos argilosos, geralmente com maior teor de matéria orgânica que os solos arenosos, não conseguem sustentar a demanda de N de gramíneas forrageiras, exigindo fertilizações assertivas para otimizar a produção e perenidade dos pastos (Euclides et al., 2022).

A aplicação de alta dose de N no tratamento de excesso elevou substancialmente o teor de N (N total) nas plantas em ambos solos (>55 g kg^{-1}), com vários efeitos adversos que configuram um estado de toxicidade de N. Sabe-se que existe um efeito tóxico da absorção exagerada de N-NH_4^+ em diversas espécies cultivadas, mas sem evidências de que o acúmulo de N-NO_3^- possa ser tóxico às plantas (Campos et al., 2020; Hawkesford et al., 2023) quando há adequada atividade de bactérias nitrificantes (Dal Molin et al., 2020). No entanto, a nitrificação pode ser prejudicada pelo uso de dose excessiva de ureia devido a presença de biureto como contaminante, que além de ser tóxico para as plantas (Ochiai et al., 2023) impacta negativamente nas bactérias nitrificantes no solo (Mikkelsen, 2007; Xue et al., 2022; MAPA, 2018). Além disso, ocorre inclusive liberação de íons NH_4^+ durante a degradação microbiana do biureto no solo (Ochiai et al., 2020). Portanto, há poucas evidências de uma toxicidade direta da ureia, e em vez disso ela deve ser indireta a partir do acúmulo de NH_4^+. Essa via deverá ser esclarecida em próximos estudos, mas de fato observou-se que a fertilização excessiva com ureia causou danos expressivos em *M. maximus*.

A alteração do estado de N das plantas pela deficiência ou excesso de N no solo prejudicou a assimilação de C, pois o N é essencial à biossíntese de clorofila e

enzimas envolvidas na fotossíntese (Mu e Chen, 2021). Com a menor assimilação de C e alterações nos teores de N, P e S, houve perda da homeostase C:N:P:S em *M. maximus* sob ambos desequilíbrios de N, verificada por meio das alterações nas razões C:N e C:P das plantas em Latossolo e Neossolo, e flutuação das razões C:S e N:P. Consequentemente, a eficiência de uso do C foi diminuída tanto na deficiência quanto sob excesso de N, pois, a capacidade da planta em converter os nutrientes em biomassa (Siddiqi e Glass, 2008), é influenciada pela homeostase elementar (Elser et al., 2010; Costa et al., 2022; Melo et al., 2023b).

As plantas deficientes em N apresentaram mecanismo de aumentar a EUN, mas sob excesso de N o efeito foi contrário, diminuindo sua eficiência de uso, o que é uma resposta regulatória natural em função da disponibilidade de N (Perchlik e Tegeder, 2017). Porém, a EUP sob deficiência ou excesso N em ambos solos também foi comprometida, reafirmando a importância do equilíbrio N:P na utilização do P pelas plantas (Raven, 2012; Xiao et al., 2024). Portanto, foi confirmada a hipótese levantada de que os desequilíbrios de N alteram a homeostase e a eficiência de uso de nutrientes *M. maximus* em Latossolo Vermelho distroférrico e em Neossolo Quartzarênico distrófico.

Uma particularidade observada nas plantas sob excesso de N em ambos solos foi o aumento no teor de S, que corrobora a sinergia entre N e S, de modo que a maior oferta de N pode induzir a regulação positiva de genes relacionados a absorção de S (Hesse et al., 2004), sem, no entanto, desconsiderar algum efeito de concentração nas plantas cultivadas em Neossolo. Contudo, houve perda do equilíbrio C:S que pode comprometer o desempenho de funções vitais do S como constituinte de aminoácidos, proteínas e sulfolipídios, por exemplo (Li et al., 2020a).

A diminuição da cor verde verificada nas plantas deficientes ou sob excesso de N deve-se primeiramente à necessidade de teores adequados de N e de seu uso eficiente para manter a síntese de clorofila (Mu e Chen, 2021). Além disso, o estresse oxidativo indicado pelo aumento no extravasamento celular, sinaliza a peroxidação lipídica das membranas (Deus et al., 2020), causando sintomas como clorose e necrose nos tecidos.

O índice de cor verde pouco mais baixo nas plantas sob deficiência de N não prejudicou a eficiência do PSII em *M. maximus,* semelhante ao observado em *Cynodon dactylon* (Li et al., 2020b), embora tenha sido observado diminuição no teor de C e baixa eficiência de uso de C nessa condição. Por outro lado, o excesso de N diminuiu a eficiência do FSII, indicando um efeito da toxidez de amônio que é o desacoplamento da fotofosforilação devido a perda do gradiente de prótons transmembrana nos cloroplastos (Prado, 2021). Não foi descartado um possível dano do biureto aos cloroplastos nas plantas sob excesso de N, pois isso foi observado em plântulas de arroz (Zhang et al., 2023), e de fato observamos danos foliares em *M. maximus* sob fertilização excessiva de N (ureia) principalmente em Neossolo (Fig 5 c, h; Fig 1 a, c material suplementar).

Os desequilíbrios de N podem alterar também o desenvolvimento do sistema radicular das plantas, porém, em *M. maximus* a diminuição da densidade de raízes foi prejudicada apenas sob fornecimento excessivo de N, devido à diminuição do alongamento e ramificação das raízes (Li et al., 2013; Hawkesford, 2023). Somados os danos, as plantas de *M. maximus* tiveram a produção de biomassa diminuída sob deficiência em Latossolo (42%) quanto em Neossolo (46%), e sob excesso de N em Neossolo (25%), ressaltando a importância de uma nutrição adequada de N nas pastagens (Oliveira et al., 2020; Schulz et al., 2023).

Portanto, as pastagens cultivadas em solos arenosos podem ser mais suscetíveis aos danos causados pelo excesso da ureia do que as cultivadas em solos argilosos tropicais, corroborando com a segunda hipótese estudada, de que os danos causados pela deficiência e excesso de N, podem variar conforme o tipo de solo. Em Latossolo, os danos biológicos do excesso de N não prejudicaram significativamente a produção de biomassa, pois a eficiência de uso de C e o índice de cor verde das plantas não foram alterados sob excesso de N. Essa maior resiliência ao excesso de N pode estar relacionada a uma menor toxicidade de $N\text{-}NH_4^+$, pois, quanto maior interação do biureto presente na ureia com as partículas minerais e orgânicas do solo, menor sua ação deletéria sobre as bactérias nitrificantes no solo (Mikkelsen, 2007), resultando em menor acúmulo de amônio em Latossolo em relação ao Neossolo.

4.2 Mecanismos da nanosílica na mitigação de estresses por deficiência e excesso de N em gramínea forrageira

A fertilização com Si é promissora para atenuação de estresses nutricionais em gramíneas cultivadas em solução nutritiva (Silva e Prado, 2021; Araújo et al., 2022; Buchelt et al., 2021). Uma premissa para o êxito dessa prática inédita para essa espécie é que a fonte e a forma de aplicação promovam a uma ótima absorção do Si pela planta e isso foi evidenciado com uso da nanosílica pois aumentou o teor de Si na parte aérea de *M. maximus* cultivada em diferentes solos (Fig 1 a, f).

Dentre os fatores que favoreceram a absorção do Si seria fato das gramíneas serem plantas acumuladoras de Si (Mitani-Ueno e Ma, 2021), e as propriedades da nanosílica com partículas diminutas de SiO_2 e alta estabilidade em solução sem polimerização (Souza Júnior et al., 2022; Awad-Allah, 2023). Além disso, a absorção da nanosílica é de baixo custo energético, pois, é transportada pela via apoplástica até a endoderme, e somente então atuam LSi1 e LSi2 (transporte ativo dependente de ATP) no transporte pela endoderme, chegando à parte aérea pelo fluxo transpiratório do xilema (Mathur e Roy, 2020).

As plantas sob deficiência de N fertirrigadas com Si apresentaram menores alterações na homeostase C:N:P:S (Fig 2), havendo incremento no teor de Si e diminuição nos teores de C e de P. Isso não se deve ao efeito de concentração pois, não houve alteração da MS pela aplicação de Si na deficiência de N e sim uma alteração na estequiometria do C na presença de Si. Isso foi anteriormente observado por Neu et al. (2017) em plantas de trigo, e pode favorecer o equilíbrio de nutrientes nos tecidos de gramíneas forrageiras sob estresses abióticos (Rocha et al., 2022; Melo et al., 2023b).

A partir do maior equilíbrio estequiométrico na presença de Si, as plantas deficientes em N apresentaram melhores eficiências de uso de N, de P e de S em ambos solos (Fig 3), o que propiciou aumento no índice de cor verde, diminuição no extravasamento celular (Fig 4) e menor senescência foliar (Fig 5). Assim, a homeostase na estequiometria elementar mediada pelo Si confirma-se como um importante fator para uma maior eficiência nutricional em plantas cultivadas sob baixa

nitrogenada em diferentes solos, similar ao elucidado para desequilíbrios de P em gramínea forrageira (Melo et al., 2023b).

O maior índice de cor verde (clorofila) e a menor senescência foliar das plantas deficientes em N quando receberam Si, resultam da eficiência de uso do N que foi otimizada, indicando melhora na síntese e/ou preservação da clorofila. Esse efeito do Si no índice de clorofila das gramíneas foi descrito no cultivo hidropônico com omissão de N (Deus et al., 2020; Araújo et al., 2022), mas agora sabe-se que ocorre também quando a deficiência é imposta pelo solo, propiciando plantas mais verdes e com menor senescência foliar (Fig 5 c, h).

Assim, a fertirrigação com Si induziu relações fortes indicando melhorias em aspectos bioquímicos das plantas deficientes (Fig 6 a, b). Ficou clara a relação positiva do teor de Si no índice de cor verde em Latossolo (r = 0,80**) e em Neossolo (r = 0,97**). O índice de cor verde por sua vez foi influenciado pela EUS (r = 0,83**) em Latossolo, que melhorou a partir da homeostase C:S (r = 0,82**), enquanto em Neossolo a EUN foi importante para incrementar o índice de cor verde (r = 0,84**), resultante do maior equilíbrio na razão C:N (r = 0,88**). Com esses efeitos, o teor de Si influenciou positivamente a produção de MS pelas plantas deficientes em N em Latossolo (r = 0,79**) e em Neossolo (r = 0,45*), mas seus benefícios não foram suficientes para o aumento da produção. A justificativa seria que não houve melhora na EUC das plantas deficientes (Fig 3 b, f), uma variável de alta relação com a produção de MS em Latossolo (r = 1,0**) e em Neossolo (r = 0,98**, Fig 6 a, b).

As plantas de capim Zuri cultivadas sob excesso de N e fertirrigadas com Si tiveram melhora no equilíbrio das razões C:P, C:S e N:P devido ao aumento no teor de C e diminuição nos teores de P e S (Fig 2). Efeitos de concentração/diluição são insuficientes para justificar essas alterações, pois não houve grande oscilação na MS (Fig 5). Isso sugere um efeito regulatório do Si na absorção de N quando em excesso no solo, e embora ainda não esteja totalmente claro, alguns estudos indicam que há uma ação do Si na regulação da expressão de transportadores de nutrientes como N, P e S, relatados em extensa revisão (Pavlovic et al., 2021). Observou-se que os danos na homeostase elementar do capim Zuri são minimizados na presença de Si,

corroborou fortemente para as eficiências de uso do N, C, P e S na gramínea cultivada sob excesso de N em ambos solos (Fig 3).

O mecanismo do Si em diminuir o índice de extravasamento celular no excesso de N em ambos solos, pode ser relacionado com seus benefícios na homeostase estequiométrica do C. Esse elemento contribui para uma maior resistência das células (Rivero-Marcos et al., 2023), pois, se deposita formando uma dupla camada cutícula-silício-cutícula na parede celular (Souza Júnior et al., 2023), dispensando em parte a síntese de compostos complexos de C. Isso é evidenciado pela diminuição da razão C:Si nas plantas fertilizadas com nanosílica (Fig 2 a, e), e essa substituição de C por Si pode resultar em saldo energético para a planta (Hao et al., 2020).

A melhor eficiência de uso de nutrientes e o possível saldo energético gerados pela incorporação do Si pode ter favorecido a síntese de compostos ou enzimas antioxidantes que combatem a espécies reativas de oxigênio (Oliveira et al., 2019), diminuindo o dano oxidativo na planta. Soma-se a isso, o fato que o excesso de N pode aumentar o teor de amônio na zona radicular e essa toxicidade pode ter sido neutralizada pois, a literatura indica em diferentes espécies que o Si atenua a toxicidade amoniacal (Leal et al., 2021; Campos et al., 2020) favorecendo a planta.

O fornecimento de Si aumentou a tolerância de *M. maximus* à toxicidade de N em Neossolo, com aumento na sua eficiência fotossintética, que refletiu em incrementos no número de perfilhos, na altura de plantas e na densidade de raízes induzindo incremento de 12 e 19% na produção de biomassa das plantas cultivadas em Latossolo e Neossolo, respectivamente (Fig 5). Assim, houve forte relação entre o teor de Si e a produção de MS das plantas sob excesso de N cultivadas em Latossolo ($r = 0,85^{**}$) e Neossolo ($r = 0,91^{**}$) (Figura 6 e,f).

O que mais explica o aumento da produção de MS nas plantas com excesso de N cultivadas em Latossolo na presença de Si seriam os incrementos na eficiência de uso dos nutrientes (EUC: $r = 0,99^{**}$; EUP: $r = 0,97^{**}$; EUN: $0,96^{**}$; EUS: $0,95^{**}$) induzidos pelas modificações das razões estequiométricas (N:P $r = 0,90^{**}$; C:P $r = 0,97^{**}$). Isso ocorreu de forma semelhante no Neossolo pois houve relações positivas do teor de Si com a eficiência de uso dos nutrientes (EUC: $r = 0,91^{**}$; EUN: $r = 0,86^{**}$;

EUP: r = 0,90**) e com as razões estequiométricas (C:P r = 0,85**, C:S r = 0,91**). Vale destacar o efeito do Si na diminuição da senescência foliar, com relação negativa entre Si e senescência em Latossolo (r = -0,94**) e em Neossolo (r = -0,90**), reforçando o papel do Si na diminuição da senescência foliar, o que foi observado visualmente nas plantas (Fig 1, material suplementar) e corrobora com o maior índice de cor verde das plantas em ambos solos quando receberam Si (Fig 4 a, b).

Portanto, a terceira hipótese testada foi parcialmente confirmada, pois, a aplicação de nanosílica promoveu a absorção de Si e atenuação de danos causados pelos desequilíbrios de N, mitigando a toxicidade de N em Neossolo devido principalmente ao mecanismo de melhorar a homeostase entre C, N, P e S, otimizando a eficiência nutricional e a fotossíntese, e aumentando a produção de matéria seca. Porém, os benefícios nutricionais e fisiológicos do Si observados na deficiência de N não foram suficientes para atenuar o prejuízo na MS em ambos solos.

A relevância do Si para aumentar a tolerância da forrageira ao excesso de N-ureia no solo ocorre sem risco ambiental por ser um elemento atóxico no sistema solo-planta. Assim, o uso do Si na fertirrigação de pastos surge como estratégia de custo econômico-ambiental favorável para melhorar a eficiência de uso de N em sistemas manejados intensivamente, em relação a outras alternativas como o uso de ureia com inibidores de nitrificação, sendo pertinente o desenvolvimento de novas pesquisas para comparar essas tecnologias em diferentes espécies de forrageiras.

4.3 Ação da nanosílica em poácea forrageira sob suficiência de N

A ênfase da utilização do Si como elemento benéfico tem sido dada a atenuação de estresses, no entanto, alguns estudos indicam que o Si pode otimizar a produção de gramíneas forrageiras sem estresse nutricional, e ainda sem prejudicar o valor nutritivo da forragem, pois o Si atua em processos importantes como a eficiência de uso de N em *M. maximus* (Melo et al., 2023c; Buchelt et al., 2023). No presente estudo a fertilização com nanosílica incrementou o teor de Si nas plantas em estado de suficiência de N, e isso ocorreu juntamento com a diminuição no teor de C, e na razão C:Si das plantas em ambos solos.

Esses resultados indicam uma possível substituição do C pelo Si na parede celular (Neu et al., 2017), fortalecendo-a com menor custo energético em comparação a síntese de compostos estruturais de C (Hao et al., 2020). Isso seria um benefício do Si em plantas sem estresse de N, direcionando mais energia para o metabolismo, e de fato foi observado que as plantas apresentaram melhora na eficiência de uso de nutrientes em Latossolo (EUN: r = 0,86**; EUS: r = 0,88**; EUC: r = 0,76**) e em Neossolo (EUC e EUN: r = 0,69*; EUP: 0,56*), relacionadas positivamente com a MS (Fig 6), contribuindo para aumentar a produção de MS em 10 e 8% em Latossolo e Neossolo, respectivamente. Esse ganho na MS em plantas sem estresse nutricional representa um importante ganho de produtividade das pastagens utilizando uma prática sem impacto ambiental que é a aplicação de Si.

Além do benefício direto na produção de MS, a fertirrigação com Si foi efetiva em diminuir a senescência foliar pois em plantas cultivada em Latossolo e em Neossolo a senescência foliar apresentou relação negativa com o teor de Si (r = -0,95**; r = -0,89**, respectivamente), enquanto a relação entre teor de Si e índice de cor verde foi fortemente positiva em ambos solos (Fig 6 e, f). A diminuição da senescência foliar implica em menor proporção de material morto da forragem, o que pode melhorar o valor nutritivo da mesma (Melo et al., 2023c), indicando a necessidade de analisar em próximos estudos os aspetos nutricionais da forragem produzida sob desordens de N e aplicação de Si em diferentes solos.

5 Conclusões e perspectivas futuras

Este estudo permitiu compreender que a homeostase de N é primordial para a eficiência nutricional e produção de biomassa de *M. maximus*, em vista das alterações causadas pelas desordens de N na estequiometria C:N:P:S e na eficiência de uso do C dessa gramínea.

Ao constatar danos mais severos do excesso de ureia aplicada em solo arenoso em comparação com o solo argiloso tropical, ressalta-se a necessidade de pesquisa detalhada para confirmar se essa sensibilidade se deve de fato a toxicidade de amônio devido à inibição da nitrificação pelo biureto presente na ureia. Assim, reforça-se a necessidade de manejo racional da fertilização nitrogenada em pastagens para atingir uma nutrição adequada das plantas em diferentes tipos de solo.

A fertirrigação com nanosílica confirmou-se como uma alternativa para melhorar a tolerância do capim Zuri, sensível ao excesso de N em solo arenoso. O Si apresentou benefícios também às plantas cultivadas em subdosagem e em suficiência de N, tanto em Latossolo Vermelho quanto em Neossolo Quartzarênico, a partir da homeostase e eficiência de uso de nutrientes, podendo contribuir para maior sustentabilidade na produção de forragem.

6 Material suplementar

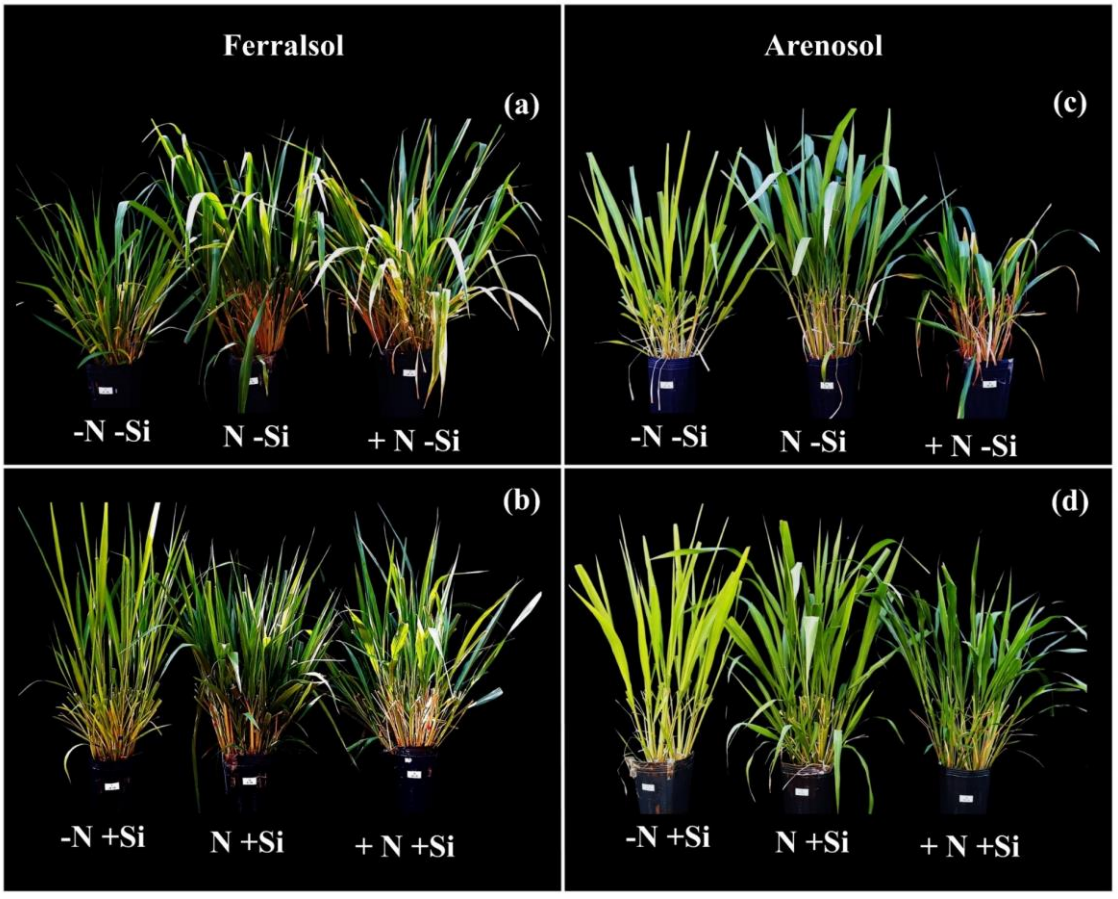


Fig. 1 Aspectos visuais da parte aérea de plantas de capim Zuri (*Megathyrsus maximus*) cultivadas sob níveis deficiente (-N), suficiente (N) e excessivo de nitrogênio (+N) com (+Si) ou sem fertirrigação de nanosílica (-Si), em Latossolo Vermelho distroférrico (a, b) e em Neossolo Quartzarênico distrófico (c, d) ao final do quinto ciclo de rebrotação (Foto: Melo CCF; Amaral DS).

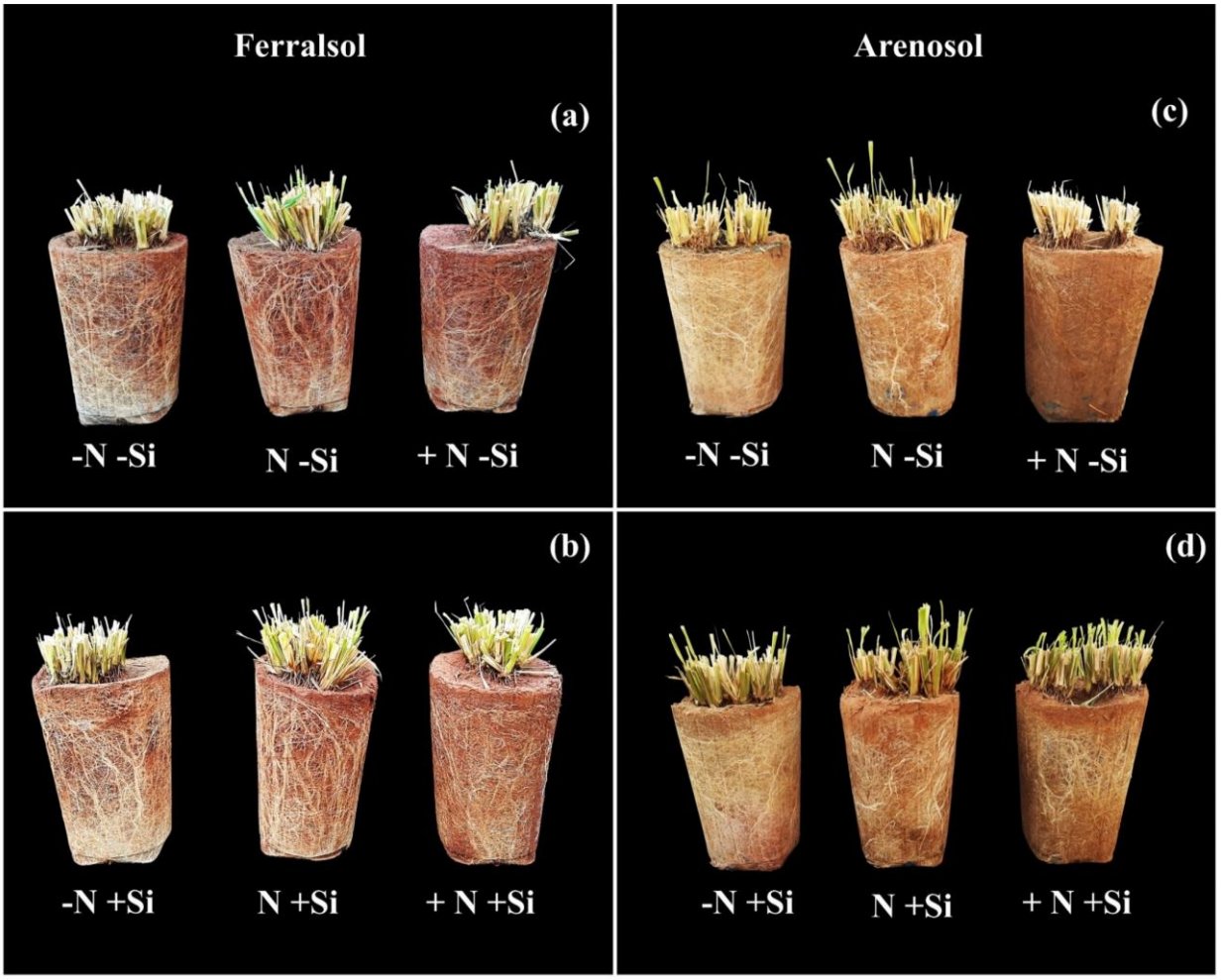


Fig. 2 Aspectos visuais do sistema radicular em plantas de capim Zuri (*Megathyrsus maximus*) cultivadas sob níveis deficiente (-N), suficiente (N) e excessivo de nitrogênio (+N), com (+Si) ou sem fertirrigação de nanosílica (-Si), em Latossolo Vermelho distroférrico (a, b) e em Neossolo Quartzarênico distrófico (c, d) ao final do quinto ciclo de rebrotação (Foto: Melo CCF; Amaral DS).

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CAPÍTULO 5 - Considerações finais e perspectivas futuras

Os sistemas de produção animal a pasto presentes em todo o mundo são diversos e complexos, tendo como um pilar importante a nutrição das plantas forrageiras para atingir altas produtividades e a sustentabilidade. Essa pesquisa evidenciou que os primeiros resultados sobre os benefícios do Si em gramínea forrageira cultivada sob desordens de N ou de P propiciando otimizar o manejo desses nutrientes para o cultivo de pastos em diferentes solos de regiões tropicais.

Em relação às desordens por deficiência de P ou de N em *M. maximus* cv. Zuri, a fertirrigação com Si foi benéfica à homeostase C:N:P e à morfogênese, mas não houve mitigação do prejuízo à produção de massa seca, pois, o perfilhamento e a eficiência de uso de C foram muito limitados sob restrição desses nutrientes. No entanto, foi revelado um potencial de uso do Si nas condições de deficiência de N ou de P que deverá ser alvo de próximos estudos, pois, pode constituir uma estratégia para aumentar a eficiência nutricional do N nas pastagens sob restrição moderada ou leve de P ou de N, e é importante analisar seu potencial em outras espécies forrageiras.

O capim Zuri apresentou alta sensibilidade ao excesso de P ou de N quando cultivado em Neossolo Quartzarênico distrófico, devido à alta disponibilidade do fosfato nesse solo em relação ao Latossolo Vermelho distroférrico e, aos possíveis efeitos deletérios do biureto presente na ureia à nitrificação, respectivamente. Ficou claro que a fertirrigação com nanosílica foi eficiente em mitigar os prejuízos causados pelos excessos nutricionais em capim Zuri, com atenuação das alterações na homeostase elementar, melhora na eficiência de uso de nutrientes, inclusive do C, diminuindo a perda na produção de forragem.

Foi evidenciado de forma inédita que o Si pode melhorar processos morfogênicos da gramínea (aparecimento, alongamento e senescência foliar) tanto sob desordens de P ou de N quanto no capim sob suficiência nutricional. Além disso, alguns efeitos na composição morfológica e bromatológica da forragem se destacaram como a diminuição do percentual de material morto e do teor de lignina

nas plantas, bem como incrementos importantes no teor de proteína, sem diminuir a digestibilidade da massa seca.

Ficou evidente que a influência dos solos nos estresses nutricionais de P e de N, devido ao fato de que os atributos químicos e físicos dos solos apresentam íntima relação com a capacidade que um solo tem de fornecer nutrientes às plantas. Por isso, a suscetibilidade de uma cultura às desordens nutricionais (inclusive das gramíneas forrageiras) podem ser influenciadas pelo tipo de solo cultivado, bem como sua resposta à aplicação de tecnologias como a fertirrigação com Si. É importante destacar que a aplicação de 4 mg dm^{-3} de P solúvel em Neossolo Quartzarênico teve alta liberação do nutriente devido à baixa adsorção do P neste solo o suficiente para um crescimento significativo do capim Zuri (Material suplementar).

Uma outra implicação do fator solo na forrageira estudada foi a expressiva suscetibilidade de *M. maximus* ao excesso de P ou de N, devido especialmente à textura do solo. O solo arenoso (Neossolo Quartzarênico) com menor capacidade de adsorção de fosfato que o solo argiloso (Latossolo Vermelho) favoreceu a elevação do teor de P ou de N na parte área das plantas sob excesso desses nutrientes, causando severa desordem nutricional que prejudicou a morfogênese da gramínea. Por outro lado, em Latossolo o excesso de P prejudicou a produção de massa seca apenas no primeiro ciclo de crescimento das plantas, mas alguns parâmetros morfológicos e bromatológicos foram afetados em ambos solos sob excesso de P ou de N.

A atenuação da deficiência de P ou de N pela fertirrigação com Si não aconteceu de maneira plena em nenhum dos solos analisados, pois, não houve incremento na produção de MS nessa condição. Esses resultados são contrários aos observados em muitos estudos dessas deficiências em gramíneas como arroz, trigo e até mesmo em forrageiras cultivadas em solução nutritiva. Portanto, mais pesquisas com diferentes espécies e solos são pertinentes (inclusive com solos de diferentes mineralogias da fração argila como predominância de argilas 2:1 ou gibbsíticos) para gerar um pacote tecnológico robusto da fertirrigação com Si em pastagens.

O uso da nanosílica na fertirrigação de *M. maximus* cv. Zuri foi muito eficiente em favorecer a absorção do Si pelas plantas, tanto sob desordens quanto sob suficiência nutricional, elevando seu teor na parte aérea e sem nenhum efeito de fitotoxicidade.

Alguns efeitos da aplicação de Si durante o cultivo da gramínea forrageira foram pronunciados, como a diminuição da senescência foliar, que ocorreu independente do estado nutricional e do tipo de solo em que as plantas foram cultivadas. Além disso, mais estudos são necessários para avançar na compreensão da ação do Si sobre a morfogênese das gramíneas forrageiras, dado que este é o primeiro estudo nesse tema.

Espera-se que a fertirrigação com Si contribua com a melhoria da produção de gramíneas forrageiras em solos de regiões tropicais fortalecendo a pecuária. É importante enfatizar que a fonte SiO_2 nanoparticulado por apresentar partículas em dispersão, pode facilitar a aplicação de Si em sistemas de fertirrigação (seja por aspersão ou gotejamento), dispensando o uso de estabilizadores, o que constitui maior assertividade no fornecimento de Si.

Para produtores que não dispõem de sistema de irrigação, mas que realizam um manejo mais intensivo com adubações na época chuvosa, é importante que novos estudos busquem desenvolver tecnologias economicamente viáveis de aplicação da nanosílica via pulverizações estratégicas especialmente na fase de crescimento ativo da forrageira. Esse fornecimento de Si pode ser benéfico não só para a eficiência de uso dos nutrientes pelas plantas na época chuvosa, mas para a resiliência do pasto na época de restrição hídrica.

A aplicação da nanosílica em cultivo de gramíneas forrageiras aponta ainda para a utilização dessas plantas na remediação de solos que apresentam excesso de N ou de P. Isso é possível pois, foi demonstrado que o Si permite o pleno acúmulo de massa seca por essas plantas sob excessos nutricionais, permitindo a exportação desses nutrientes da área de forma rentável, pois, a forragem pode ser utilizada para pastejo, como forragem fresca picada no cocho ou para ensilagem. Essa remediação pode devolver a aptidão do solo para o cultivo de outras culturas, e ainda diminuir o

risco de contaminação de águas. Portanto, é necessário avançar nas pesquisas em campo em diferentes espécies de gramíneas forrageiras, solos e doses de Si para obter um programa pioneiro no manejo otimizado do Si em pastagem, o que será de alto impacto dada a relevância mundial e a diversidade de condições de cultivo dos pastos.

5.4 Material complementar

A seguir encontra-se imagens com alguns detalhes dos experimentos (Figuras de 1 a 8).



Fig 1. Plantas de capim Zuri em Neossolo Quartzarênico distrófico típico cultivada sem aplicação de P (à esquerda) e com aplicação de 4 mg dm^{-3} de P na ocasião da semeadura (à direita). Foto: Melo, CCF; Amaral DS.



Fig 2. Plantas de capim Zuri em Neossolo Quartzarênico distrófico típico cultivada em excesso de P sem Si (à esquerda) e com fornecimento de Si (à direita). Foto: Melo, CCF; Amaral DS. Foto: Melo, CCF; Amaral DS.



Fig 3. Plantas de capim Zuri antes do corte de uniformização cultivadas em solo em ambiente de casa de vegetação. Foto: Melo, CCF; Amaral DS



Fig 4. Plantas de capim Zuri após corte uniformização a 17 cm de altura do nível do solo, realizado aos 27 dias após a emergência. Foto: Melo, CCF; Amaral DS



Fig 5. Processo de marcação de perfilhos novos e contagem de perfilhos mortos logo após a coleta de biomassa do estrato pastejável, utilizando fios de cores distintas para cada geração de perfilhos. Foto: Melo, CCF; Amaral DS



Fig 6. Aferição do diâmetro de perfilho em perfilhos monitorados quanto a parâmetros morfogênicos e estruturais do capim Zuri. Foto: Melo, CCF; Amaral DS



Fig 7. Aspecto do sistema radicular de plantas de capim Zuri após seis ciclos de crescimento em Neossolo Quartzarênico sob excesso de P sem Si (à esquerda) e com fornecimento de Si (à direita). Foto: Melo, CCF; Amaral DS.



Fig 8. Amostragem do sistema radicular do capim Zuri cultivado por seis ciclos de crescimento em Latossolo Vermelho distroférrico. Foto: Melo, CCF; Amaral DS.