UNIVERSIDADE ESTADUAL PAULISTA – UNESP

CÂMPUS DE JABOTICABAL

SILÍCIO NA MITIGAÇÃO DOS EFEITOS DO DÉFICIT HÍDRICO EM PLANTAS FORRAGEIRAS

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Engenheiro Agrônomo

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Tese apresentada à Faculdade de Ciências Agrárias e Veterinárias – Unesp, Campus de Jaboticabal, como parte das exigências para a obtenção do título de Doutor em Agronomia (Produção Vegetal).

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TÍTULO DA TESE: SILÍCIO NA MITIGAÇÃO DOS EFEITOS DO DÉFICIT HÍDRICO EM PLANTAS FORRAGEIRAS

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JUAN RICARDO ROCHA – Nascido na cidade de Ji-Paraná/RO em 04 de julho de 1993 e formado em engenharia agronômica no Instituto Federal de Educação Ciência e Tecnologia de Rondônia (IFRO) – Campus Colorado do Oeste em julho de 2016. Durante a graduação desenvolveu diversas atividades de pesquisa voltadas a ciência do solo e nutrição de plantas, realizou estágio obrigatório na Entidade Autárquica de Assistência Técnica e Extensão Rural do Estado de Rondônia – EMATER-RO, escritório local de Ji-Paraná e no laboratório de química do IFRO, Campus Colorado do Oeste. Possui mestrado em agricultura tropical pelo Programa de Pós-Graduação em Agricultura Tropical – PPGAT do Centro Universitário Norte do Espírito Santo (CEUNES), da Universidade Federal do Espírito Santo (UFES), onde trabalhou com projetos voltados a fertilidade do solo, conservação e manejo do solo e física do solo. Durante o doutorado fez estágio docência na disciplina de nutrição de plantas forrageiras, atuou como docente do Programa de Aperfeiçoamento à Docência no Ensino Superior (PAADES) na modalidade B na disciplina de fisiologia vegetal para a turma de Agronomia, em que ganhou o prêmio “Destaques do PAADES” e na disciplina de fisiologia vegetal para a turma de engenharia de biossistemas da Unesp, Campus de Tupã. Atualmente é membro do Grupo de Pesquisa em Nutrição de Plantas da Unesp – GENPLANT, onde desenvolve projetos com elementos benéficos e atenuação de estresses vegetais.

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“Se a educação sozinha não transforma a sociedade, sem ela tampouco a sociedade muda.”

Paulo Freire

Dedico,

Aos que sempre acreditaram nesse sonho comigo;

e a minha amada “Vó Detinha” (*in memoriam*).

SUMÁRIO

SILÍCIO NA MITIGAÇÃO DOS EFEITOS DO DÉFICIT HÍDRICO EM PLANTAS FORRAGEIRAS

RESUMO – A pastagem é a principal fonte de alimento para o rebanho bovino brasileiro, contudo, restrições ambientais podem reduzir severamente a produção de forragem. O silício (Si) pode aumentar a tolerância das plantas a condições estressantes por interferir em processos morfo-fisiológicos. O objetivo desse trabalho foi caracterizar os efeitos da utilização de silício sob o crescimento e produção de duas espécies de plantas forrageiras, submetidas ao déficit hídrico. Foram conduzidos seis experimentos, sendo dois utilizando *Brachiaria* e os outros quatro utilizando *Panicum maximum*, sendo estes, divididos em primeira e segunda brotação, respectivamente. Nos experimentos foram aplicados os mesmos tratamentos arranjados em esquema fatorial 2x2, sendo a aplicação de Si via fertirrigação aplicado no solo e o controle (omissão de Si) combinados com dois regimes hídrico do solo (70 e 40% da capacidade de retenção de água no solo). Foi avaliado a resposta da aplicação de Si via fertirrigação, avaliando se a presença de Si melhora o desenvolvimento das plantas, a partir de análises morfológicas e fisiológicas. As duas espécies forrageiras que receberam Si via fertirrigação especialmente cultivadas sob déficit hídrico tiveram maior acúmulo deste elemento na parte aérea. O déficit hídrico foi atenuado com aplicação do Si via fertirrigação ao favorecer o crescimento das forrageiras. O estudo evidencia a importância da função fisiológica do Si e seus efeitos na estequiometria do C e do N, negligenciado na maioria das pesquisas com pastagens cultivadas sob restrição hídrica.

Palavras-chave: elemento benéfico, estresse abiótico, nutrição de plantas.

SILICON IN MITIGATION OF THE EFFECTS OF WATER DEFICIT IN FORAGE PLANTS

ABSTRACT - Pasture is the main source of food for Brazilian cattle, however, environmental restrictions can severely reduce forage production. Silicon (Si) can increase plant tolerance to stressful conditions by interfering with morpho-physiological processes. The objective of this work was to characterize the effects of the use of silicon on the growth and production of two species of forage plants, submitted to water deficit. Six experiments were carried out, two using *Brachiaria* and the other four using *Panicum maximum*, which were divided into first and second sprouting, respectively. In the experiments, the same treatments arranged in a 2x2 factorial scheme were applied, with the application of Si via fertigation applied to the soil and the control (Si omission) combined with two soil water regimes (70 and 40% of the water retention capacity in the soil). ground). The response to the application of Si via fertigation was evaluated, evaluating whether the presence of Si improves plant development, based on morphological and physiological analyses. The two forage species that received silicon via fertigation, especially cultivated under water deficit, had greater accumulation of this element in the shoot. The water deficit was attenuated with the application of Si via fertigation, favoring the growth of forages. The study highlights the importance of the physiological function of Si and its effects on the stoichiometry of C and N, neglected in most studies with pastures cultivated under water restriction.

Keywords: beneficial element, abiotic stress, plant nutrition.

CAPÍTULO 1 – Considerações gerais

1. INTRODUÇÃO

Os impactos das mudanças climáticas no planeta vêm aumentando e um dos principais problemas é a ocorrência de eventos climáticos extremos como secas e enchentes. O cultivo deve ser aumentado em áreas com menos recursos disponíveis de água doce e com maiores períodos de limitação do estresse hídrico devido aos efeitos das mudanças climáticas (Oki e Kanae 2006). São 112 milhões de hectares de pastagens cultivadas, um equivalente a 13% da extensão territorial nacional (EMBRAPA 2018). Nessa extensa faixa territorial as plantas são submetidas a diferentes condições de estresses (Santos et al., 2008; Silva et al., 2011).

A deficiência hídrica se destaca por ser comum nos ecossistemas tropicais (Monteiro et al. 2014) e afeta diretamente as pastagens que ocupam vasta área cultivada no mundo, com predomínio das *Poaceae,* esse fato é preocupante porque quase a totalidade da produção de carne bovina provém de animais alimentados diretamente das pastagens, devido ao baixo custo de produção (Gomes et al. 2015).

O estresse por deficiência hídrica diminui as taxas de germinação, causa inibição da fotossíntese, perda de integridade da membrana e geração aumentada de espécies reativas de oxigênio (ERO) (Borjas-Ventura et al. 2018; dos Santos et al. 2020). O estresse hídrico prolongado causa declínio no potencial hídrico da folha e abertura estomática, reduz o tamanho da folha, suprime o crescimento da raiz, reduz o número, o tamanho e a viabilidade das sementes, atrasa a floração e a frutificação e limita o crescimento e a produtividade da planta.

Uma estratégia para atenuar os efeitos do estresse por deficiência hídrica em plantas forrageiras seria a aplicação de fertilizantes contendo silício (Si). Isto ocorre porque as plantas *Poáceas* são consideradas acumuladoras deste elemento (Cocker; Evans; Hodson, 1998). Soma-se a isto, o fato que em áreas de pastagens dada sua degradação em diferentes níveis a disponibilidade de Si do solo diminui (Yang et al. 2019b) especialmente os Neossolos Quartzarênicos, que predomina a fração granulométrica areia (Korndorfer et al., 1999). O Si é eficaz no alívio desses estresses,

incluindo seca, altas temperaturas, geada, salinidade, toxicidade de metais pesados e desequilíbrio de nutrientes (Ma and Yamaji 2008).

A maioria dos estudos com Si mostram seu efeito benéfico em atenuar os efeitos deletérios do déficit hídrico diminuindo a taxa transpiratória e aumentando a eficiência do uso da água (Abd El-Mageed et al. 2020; Jinger et al. 2020). Esse efeito pode ser conferido também em plantas sob altas temperaturas, comum em períodos de estiagem, outras pesquisas indicam benefícios na atenuação do estresse oxidativo em plantas sob estresse hídrico (Moro et al. 2018; Zhang et al. 2017a). A diminuição deste estresse oxidativo pode ocorrer pelo envolvimento do Si no aumento de compostos antioxidantes (Ashfaque et al. 2017; Kim et al. 2017).

Outro benefício do Si, seria a troca estequiométrica, que pode melhorar o metabolismo dos nutrientes, uma vez que o Si poderia substituir parte do C na parede celular da epiderme, pois se liga a compostos de celulose ou hemicelulose, favorecendo a estruturação celular, diminuindo a demanda por compostos estruturais como como lignina (que tem um alto custo energético para sua síntese), favorecendo assim a economia de energia da planta (de Oliveira Filho et al. 2021; Teixeira et al. 2020).

A compreensão de como as plantas respondem aos danos provocados pelo estresse hídrico é um importante ponto para que estratégias de manejo sejam desenvolvidas, tendo em vista o favorecimento da constância e produtividade das plantas forrageiras em condições adversas ao seu cultivo.

Diante disso surge a hipótese que o Si via fertirrigação em plantas forrageiras submetidas ao estresse ocasionado por restrição hídrica poderá mitigar os efeitos deste estresse por mecanismos fisiológicos e nutricionais incrementando a produção da planta. Este trabalho teve como objetivo geral avaliar os efeitos da utilização de silício sob o crescimento e produção de forragem, com plantas submetidas ao déficit hídrico e caracterizar como o Si influencia na produtividade de matéria seca e na fisiologia dessas plantas em condição de estresse hídrico.

Os objetivos específicos, são: (i) avaliar se o fornecimento de Si via fertirrigação promove incremento na sua absorção, modificação estequiométrica e melhoria em variáveis fisiológicas e no crescimento de *Brachiaria* spp. cultivadas sob dois regimes hídricos do solo (70 e 40% da capacidade de retenção de água no solo); (ii) avaliar se

o fornecimento de Si via fertirrigação melhora o sistema de defesa antioxidante e modifica a estequiometria C/N/Si e o crescimento de duas cultivares de *P. maximum* cultivadas sob dois níveis de umidade do; (iii) e avaliar se o fornecimento de Si via fertirrigação melhora os aspectos fisiológicos e conteúdo de água na planta envolvendo sistema de defesa antioxidante e modificação da estequiometria C/N/Si e o desempenho da rebrota de duas cultivares de *P. maximum* cultivadas sob dois regimes hídricos do solo.

2. REVISÃO DE LITERATURA

2.1. A importância das pastagens tropicais

A importância global das pastagens é indicada por sua extensão; eles compreendem cerca de 26% da área total de terras e 80% das terras agrícolas produtivas. A maioria das pastagens está em países tropicais em desenvolvimento, onde são particularmente importantes para a subsistência de cerca de um bilhão de pessoas pobres. As pastagens fornecem claramente a base alimentar para o gado pastando e, portanto, vários alimentos de alta qualidade, mas esse gado também fornece produtos como fertilizantes, transporte, tração, fibra e couro (Boval e Dixon 2012).

A intensificação das pastagens tropicais é uma importante estratégia de utilização da terra nos países em desenvolvimento (da Silva Cardoso et al. 2020). Na literatura científica, isso significa “aumento da produção” e “minimização do impacto ambiental” por meio da “melhor gestão de insumos, produtos, serviços ambientais e recursos naturais/capital” (Wezel et al. 2015).

A adoção de estratégias de intensificação da produção pecuária em áreas de pastagens tropicais depende do conhecimento dos agricultores sobre solo, recursos hídricos, manejo de plantas e animais e mercado de carne bovina. Consequentemente, às vezes tem se mostrado difícil quantificar a eficácia geral de intensificação particulares porque várias estratégias são implementadas em uma ampla gama de condições e são avaliadas de acordo com série de critérios (Boval et al. 2017). Além disso, as pastagens fornecem serviços e funções importantes, inclusive servindo como captadores de água, para preservação da biodiversidade, para necessidades culturais e recreativas e como potenciais sumidouros de carbono para aliviar as emissões de gases de efeito estufa (Boval e Dixon 2012).

No entanto, estresses abióticos como o estresse por deficiência hídrica (Kemesyte et al. 2017) e alta temperatura (Ahammed et al. 2019) ameaçam a persistência e a capacidade da pastagem para produção de biomassa (Latef et al. 2016), principalmente nas rebrotas. Portanto, a água é o principal limitante na produção agrícola (Sinclair e Rufty 2012) que pode ser agravada com os impactos das

mudanças climáticas, devido aos eventos extremos que induz irregularidade da precipitação pluvial causando a seca (Monteiro et al. 2014; Oki e Kanae 2006).

As mudanças climáticas promovem alterações na distribuição da precipitação pluvial em diferentes regiões do mundo podendo aumentar a vulnerabilidade agrícola (Karimi et al. 2018). O déficit hídrico tem aumentado sua ocorrência (Aryal et al., 2020), prejudicando aspectos fisiológicos da planta (Wang et al. 2018), especialmente nos ecossistemas tropicais (Monteiro et al., 2014) destacando-se as pastagens que são cultivadas nesta região.

A maioria das pastagens brasileiras está degradada, representando uma oportunidade considerável para a mitigação e aumento da produção de bovinos de corte e, consequentemente, aumentando a oferta global de proteína. Além disso, no Brasil, A produção de forragem é necessária para estratégias de alimentação sazonal que mantenham o desempenho animal durante os períodos de escassez de forragem (da Silva Cardoso et al. 2020).

Apesar da vasta área do país, a exploração de forragem no Brasil é baseada principalmente em *Brachiaria* spp*.* na maioria das regiões, mas também *Panicum maximum* spp. (de Moraes et al. 2014). A produção brasileira de carne bovina depende fortemente de pastagens cultivadas, das quais cerca de 80% são plantadas principalmente de *Brachiaria* (Borges Do Valle et al. 2017).

Cultivares comerciais de espécies de *Brachiaria* são importantes para a pecuária latino-americana, principal atividade econômica da região. O Centro Internacional de Agricultura Tropical (CIAT) mantém um banco de genes de forrageiras contendo 601 acessos de *Brachiaria* spp, com importantes características agronômicas que têm sido exploradas e exploradas por meio de programas de melhoramento de plantas (Nuñez et al. 2018).

A espécie *Panicum maximum* se destaca pela alta capacidade de produção de matéria seca, qualidade de forragem, facilidade de estabelecimento e aceitabilidade pelos animais (Torres et al. 2013). As pastagens produzem forragem em grandes áreas que podem ser pouco adequadas para cultivo ou outras atividades, o que permite a produção de ruminantes, sustentando a produção global de carne, um recurso crítico para milhões de pessoas dependentes da proteína animal para segurança alimentar (Sloat et al. 2018).

2.2. Efeitos do déficit hídrico em pastagens

O desempenho e a produtividade das culturas são resultados da expressão genotípica modulada pela interação contínua com o ambiente. Entre os aspectos ambientais, o estresse por deficiência hídrica e a salinidade são os fatores mais importantes, que limitam as forrageiras, incluindo gramíneas, em escala global (Ghafar et al. 2021). O primeiro fator que limita o rendimento das plantas em muitos ecossistemas de cultivo é a falta de água, e a produtividade das plantas nessas condições depende da distribuição da matéria seca entre os órgãos da planta e da distribuição espacial das raízes no solo (Afshoon et al. 2022).

As mudanças climáticas promovem alterações na distribuição da precipitação pluvial em diferentes regiões do mundo podendo aumentar a vulnerabilidade agrícola (Karimi et al. 2018). A seca, um fenômeno recorrente com grandes impactos tanto para os seres humanos quanto para os ecossistemas naturais, é o extremo climático mais difundido que dificulta principalmente o crescimento e a produtividade das culturas (Wang et al. 2021). O déficit hídrico tem aumentado sua ocorrência (Aryal et al., 2020), prejudicando aspectos fisiológicos da planta (Wang et al. 2018), especialmente nos ecossistemas tropicais (Monteiro et al., 2014) destacando-se as pastagens que são cultivadas nestas regiões.

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O estresse por deficiência hídrica tem efeitos marcantes nas plantas em níveis morfológicos, fisiológicos, bioquímicos e moleculares (Hsiao 1973). Esse estresse pode interromper o equilíbrio dinâmico de ERO, alterar solutos compatíveis com

células, suprimir a fotossíntese e diminuir a produtividade da água, o que resulta na supressão do crescimento das plantas, mudanças na morfologia e reduções no rendimento (Zhang et al. 2018).

A eficiência quântica do fotossistema II mostra considerável sensibilidade ao estresse hídrico, uma vez que o transporte de elétrons fotossintéticos através do fotossistema II é inibido e oxigênio envolvendo seus complexos e centros de reação são danificados. Uma das reações mais conhecidas do estresse hídrico é o fechamento dos estômatos para evitar a perda de água pelo processo de transpiração.

As plantas desenvolvem adaptações fenológicas para tolerância ao estresse, por exemplo, quando a disponibilidade de água não é suficiente para completar seu ciclo de vida em curtas durações (semanas a meses) (Kosar et al. 2021). As gramíneas perenes apresentam dormência temporária de gemas e meristemas sob estresse hídrico prolongado (Hanslin et al. 2019). A maioria das gramíneas forrageiras podem ser consideradas tolerantes à seca por terem adaptado vários mecanismos fisiológicos para sobrevivência em condições de baixa disponibilidade água (Moore et al. 2019). Além disso, sob estresse hídrico, as gramíneas acumulam vários osmólitos para ajuste osmótico e osmoproteção. Esses osmoprotetores se acumulam em células com estresse hídrico e estimulam o funcionamento de metabólitos normais (Razzaq et al. 2017). Esses osmoprotetores incluem prolina, glicinebetaína, açúcares e compostos fenólicos (Ghafar et al. 2021).

Ao considerar a planta, o déficit hídrico causa fome de carbono, que é um desequilíbrio entre a captação e a perda de carbono que resulta em um balanço negativo de carbono. A falta de carbono é, portanto, uma consequência da prevenção de falhas hidráulicas através do fechamento estomático (Sevanto et al. 2014). Rocha et al. (2021) observaram que o déficit hídrico diminuiu a absorção de Si, o teor de C e a eficiência de uso do C em plantas forrageiras. Essas alterações na estequiometria do C provocadas pelo déficit hídrico pode ser uma estratégia da planta para obter nova homeostase na tentativa de diminuir prejuízos no seu metabolismo.

O déficit hídrico prejudica o crescimento de *P. maximum* por diminuir a área foliar, altura, número de perfilhos e a massa seca indicando que as plantas forrageiras são sensíveis o estresse por deficiência hídrica. Portanto, a diminuição do potencial da água na folha inibe a expansão foliar das plantas (Rocha; Prado; Piccolo, 2022).

Os resultados dos estudos de Pecetti et al. (2017) sugeriram que os efeitos ambientais, como o estresse por deficiência hídrica, podem ter um impacto maior na qualidade do que os efeitos genéticos da forragem, mesmo para um conjunto populacional incluindo material selecionado para morfologia orientada para a qualidade. Diferentes espécies de forrageiras submetidas ao estresse hídrico tiveram redução da produção de biomassa (Komainda et al. 2019).

2.3. O silício no sistema solo-planta

O Si é o segundo elemento mais abundante da crosta terrestre com um conteúdo médio de 28,8% (Hans Wedepohl 1995). Ocorre em mais de 370 minerais formadores de rocha e é um componente básico da maioria dos solos (Haynes 2014). No entanto, nem todo Si no solo está disponível para as plantas, a maior parte dele está ligado a minerais de silicato recalcitrantes e apenas uma fração muito menor está disponível para as plantas (Struyf et al. 2010).

O principal determinante das concentrações de Si na solução do solo é a solubilidade de minerais primários e secundários (Karatha-nasis, 2002; Sommer et al., 2006). O Si está presente na solução do solo, principalmente como ácido silícico monomérico (H_4SiO_4) (Drees et al., 1989; Dove, 1995; Dietzel, 2000). A fração solúvel do Si é redox e dependente do pH (Ma and Takahashi 2002). Uma vez absorvido pelas plantas, o Si forma fitólitos, que são reciclados na solução do solo com a decomposição do material vegetal morto e podem novamente ser absorvidos pelas plantas (Greger et al. 2018).

As plantas absorvem Si na forma de molécula não dissociada de ácido ortossilícico, que é a única forma do elemento com probabilidade de cruzar a membrana plasmática da raiz da planta em faixas de pH fisiológico (Epstein 1994; Raven 2003). Para Laane (2018), para que haja uma adequada absorção do Si pela planta é importante que este esteja na solução na forma H_4SiO_4 que é a forma química absorvida pelas plantas. Assim, segundo Birchall (1995), para que o Si esteja nesta forma monomérica é necessário que a concentração do elemento em solução não seja superior a 3 mmol L^{-1} de Si, pois se isso ocorrer tem-se a polimerização formando-se ácido polisilícico e partículas coloidais não absorvidas pelas plantas.

Há diferença significativa na capacidade da planta de acumular Si. Que pode ser acumulado pelas plantas após a absorção mediada por transportador ativo ou por absorção passiva dentro do fluxo de transpiração, ou podem excluir Si e evitar o acúmulo (Ma e Yamaji 2008; Mitani e Jian 2005; Stefels et al. 2007). Os mecanismos de absorção de Si pela raiz diferem entre as espécies de plantas. Takahashi et al. (1990) propõem três possíveis tipos de absorção de Si por plantas superiores em relação a absorção de água: ativo (mais rápido / maior do que a absorção de água), passivo (velocidade semelhante à captação de água) e rejeitado (mais lento / menor do que a absorção de água).

Plantas com sistema ativo de captação de Si poderiam causar depleção significativa de Si, portanto, redução da concentração de Si na solução nutritiva; enquanto para plantas que absorvem Si passivamente, a concentração de Si na solução permaneceria inalterada. Em contraste, as plantas com o tipo rejeitado de absorção de Si tendem a aumentar a concentração de Si no meio externo (Yan et al. 2018).

As plantas apresentam formas diferentes de absorverem o Si, sendo classificadas em forma ativa, passiva ou exclusiva que irão determinar a qualificação das plantas quanto ao poder acumulativo em diferentes categorias: plantas acumuladoras (> 10 g kg^{-1} de Si), acumuladoras intermediárias (5 – 10 g kg^{-1} de Si) e exclusoras (ou não-acumuladora) (< 5 g kg^{-1} de Si) (Hodson et al. 2005; Trembath-Reichert et al. 2015). Segundo Yan et al. (2018), os impactos benéficos são ativamente associados às taxas de acumulação de Si em plantas que diferem significativamente entre e dentro das espécies de plantas. Em plantas acumuladoras de Si, o seu efeito benéfico se torna mais evidente (Campos et al. 2020).

Após a absorção do Si pelas raízes, na forma de H_4SiO_4, é translocado pelo xilema à parte aérea e se deposita na parede celular das células da epiderme das folhas (tecido com função de transpiração), na camada subcuticular e nos espaços intercelulares, à medida que a água evapora ou é transportada para outro tecido. (Ma e Takahashi 2002; Ma et al. 2006; Schaller et al. 2013). Os transportadores envolvidos no acúmulo de Si em plantas, são responsáveis pela absorção de Si nas raízes, pela descarga de Si no xilema e pela transferência vascular de Si. Mitani et al. (2011),

afirmam que se é necessário o aporte inicial, ou seja, o acúmulo de Si no broto para que haja o efeito benéfico do Si.

O transporte de Si da solução do solo para a raiz e da raiz para a parte aérea é diferente nas várias espécies de plantas existentes. Assim, as espécies têm diferentes níveis de acumulação de Si, podendo ser explicada pelas diferenças na existência, densidade e localização do sistema complexo de proteínas transportadoras de Si (Yan et al. 2018). O transporte de Si no xilema é impulsionado pelo fluxo transpiratório da planta, porém, alguns tecidos com baixas taxas de transpiração podem acumular Si em níveis extremamente altos (por exemplo, casca de arroz). A disparidade entre a taxa de transpiração e o acúmulo de Si em tecidos específicos indicam a existência de distribuição controlada pelo metabolismo do Si absorvido pela raiz.

Os transportadores envolvidos no acúmulo de Si em plantas, são responsáveis pela absorção de Si nas raízes, pela descarga de Si no xilema e pela transferência vascular de Si. Mitani et al. (2011), afirmam que se é necessário o aporte inicial, ou seja, o acúmulo de Si no broto para que haja o efeito benéfico do Si.

Em estudos moleculares sobre captação e transporte de Si Ma and Yamaji (2015), consideraram um grande grupo de proteínas e genes com caracteres distintos como responsáveis para o transporte de Si da solução do solo para a raiz e da raiz para a parte aérea em várias espécies de plantas. E as espécies e tecidos que têm diferentes níveis de acumulação de Si pode ser, pelo menos parcialmente, explicada pelas diferenças na existência, densidade e localização do sistema complexo de proteínas de transporte de Si (Yan et al. 2018).

O arroz é uma planta considerada hiper acumuladora de Si, pois possui um modo ativo de absorção de Si (Chiba et al. 2009). Ma and Yamaji, (2006) identificaram os genes Lsi1 e Lsi2 como os transportadores responsáveis pelo influxo e efluxo de Si, respectivamente. Esses transportadores são responsáveis pela absorção eficiente de Si pelas raízes do arroz. Posteriormente, o transportador Lsi6 responsável pela descarga de Si no xilema foi identificado por Yamaji et al. (2008).

Uma vez absorvido, o Si é então translocado para a parte aérea por fluxo de transpiração através do xilema. Mais de 90% do Si absorvido pela raiz é translocado (Ma e Takahashi 2002), embora alguma quantidade de Si pode ser depositada na

parede celular da raiz e vasos do xilema (Balasta et al. 1989), o que pode impedir os vasos de compressão quando as taxas de transpiração são altas (Raven 1983).

Nas plantas, o Si é armazenado em tecidos vegetais intra ou extracelularmente como dióxido de silício não cristalino em diferentes estados de condensação, na forma de fitólitos ou outras formas amorfas em uma chamada camada dupla de Si na epiderme das folhas (Piperno 2006; Schaller et al. 2013; Stefels et al. 2007). Podendo ser acumulado nas folhas abaixo da cutícula aumentando a rigidez dos tecidos, contribuindo na substituição de parte do carbono das paredes celulares (Raven 1983), pois forma ligações de hidrogênio às moléculas de celulose (Schoelynck et al. 2010).

O alto acúmulo de Si é especialmente importante para aumentar a produção e torná-la sustentável em culturas como arroz (Yang et al. 2019a), milho (Kochanová et al. 2014), cana-de-açúcar (Oliveira et al. 2021), entre outras gramíneas e forrageiras (Buchelt et al. 2020; Rocha et al. 2022a), tipicamente acumuladoras de Si e de interesse comercial. As espécies de plantas de gramínea apresentam alto acúmulo de Si, mas a extensão do acúmulo difere entre as espécies de plantas (Chiba et al. 2009).

2.4. Efeitos fisiológicos, bioquímicos e na estequiometria do C:N:Si nas plantas submetidas ao déficit hídrico

Embora o Si não seja considerado um elemento essencial para as plantas, sabe-se que é benéfico para o crescimento e desenvolvimento das mesmas, principalmente sob condições de estresse (Wang et al. 2021). Sendo assim, conhecido como um protetor contra estresses e tem papel defensor contra uma ampla gama de estresses ambientais, incluindo deficiência hídrica. O Si aumenta a produtividade e melhora a qualidade da colheita, enquanto a falta deste elemento reduz a capacidade biológica da planta de resistir às condições de estresses por restrições hídricas (Epstein 2001; Malhotra e Kapoor 2019; Prado 2008). Estudos sob condições altamente controladas em vasos permitem uma avaliação detalhada da reação fisiológica das plantas à seca (Fariaszewska et al. 2017).

Aumentar a absorção de água pela raiz, regulando a superfície e a anatomia da raiz, é importante para a tolerância da planta ao estresse (Javot e Maurel 2002). O Si é essencial para o desenvolvimento radicular e absorção de água sob condições de estresse hídrico (Hattori et al. 2003). O estudo feito por Wang et al. (2021) indica

que tais mudanças mediadas por Si no desenvolvimento radicular também aumentam a silicificação endodérmica radicular e a suberização aumentando assim a capacidade de retenção de água para superar os efeitos do estresse hídrico.

O ajuste osmótico e o acúmulo de solutos celulares compatíveis são considerados processos fisiológicos vegetais que ocorrem em resposta ao estresse hídrico (Blum 2017; Sharp et al. 1988). Segundo Wang et al. (2021), um número crescente de estudos tem indicado que a aplicação de Si promove acúmulo de osmólitos em muitas espécies de plantas, especialmente acumuladores de Si, sob estresse hídrico, melhorando assim a força motriz osmótica para a absorção de água. Em consonância com este ponto, foi relatado que o Si regula as atividades de enzimas envolvidas no metabolismo de carboidratos e afeta a lignificação das paredes celulares, consequentemente regulando a síntese de assimilados e a eficiência do transporte.

A estratégia das plantas para atenuação do estresse por deficiência hídrica é reduzir a perda de água diminuindo, por exemplo, o número de folhas e a área foliar (Perlikowski et al. 2019). Portanto, a diminuição do potencial da água na folha inibe a expansão foliar visto em diversos cultivos (Boyer 1970). O aumento do conteúdo de Si nas plantas afeta as trocas gasosas, promovendo aumento do conteúdo de água em diferentes espécies de forrageiras como sorgo (Hattori et al. 2005), trigo (Ma et al. 2016) e cana-de-açúcar (Oliveira Filho et al. 2021). Wang et al. (2021) relatam que a aplicação de Si regula as trocas gasosas, o que por sua vez contribui para a tolerância à seca, em espécies como milho, soja, pepino e alfafa, resultando em um aumento da eficiência do uso da água e no alívio do estresse hídrico (Gao et al. 2004).

Nos estudos de Camargo et al. (2021), a aplicação de Si em cana-de-açúcar aumentou a taxa líquida de assimilação de CO_2, a transpiração da planta, condutância estomática e taxa de transporte de elétrons de folhas além da biomassa fresca e comprimento de colmos. As melhorias nas respostas das trocas gasosas em cana-de-açúcar com fornecimento de Si podem estar associadas à deposição de Si nos tecidos vegetais, como por exemplo, na cutícula, devido ao aumento da resistência desses tecidos, especialmente nas folhas, e, consequentemente, à estrutura da planta melhorada. O Si nas plantas reduz a concentração interna de CO_2 e aumenta a eficiência do uso da água e a eficiência da carboxilação instantânea (Sarto et al. 2016).

O fornecimento de Si diminui a transpiração foliar para reduzir a perda de água, bloqueando fisicamente a transpiração cuticular ou o movimento estomático. Em contraste, o Si aumenta o fluxo de seiva do xilema foliar e as taxas de transpiração sob estresse hídrico, correspondendo ao aumento das taxas de fotossíntese. O impacto diferencial do Si nas taxas de transpiração pode estar relacionado ao grau de estresse. Sob condições de estresse moderado, o Si poderia aumentar a absorção de água pelas raízes, correspondendo a taxas de transpiração aumentadas e, consequentemente, aumentar o crescimento das plantas sob estresse hídrico. Quando a absorção de água pela raiz é limitada sob forte estresse, as folhas da planta fecham seus estômatos para reduzir a perda de água, o que ocorre provavelmente por meio de um evento de sinalização sistêmica (Wang et al. 2021).

Em seu estudo Amin et al. (2016) afirmam que a aplicação de Si em plantas de milho em condição de deficiência hídrica, melhorou o crescimento da planta e o rendimento de grãos, e atribuíram isso à melhora na taxa fotossintética e à redução da transpiração, corroborando com o encontrado por Verma et al. (2020). De Oliveira et al. (2019) observaram aumento no crescimento de plantas de sorgo que tiveram aplicação foliar de Si, e atribuíram isso a menor perda de água por transpiração refletindo em um impacto positivo nas trocas gasosas. Estes estudos mostram que ganhos de crescimento podem ser alcançados pela disponibilização de Si para as plantas, resultando em crescimento da planta devido à transpiração reduzida.

Plantas sob déficit hídrico tem tecidos desidratados, promovendo a superprodução de ERO, o que pode causar o estresse oxidativo (Borjas-Ventura et al. 2020). As ERO promovem peroxidação lipídica danificando muitos compostos orgânicos celulares, como as membranas plasmáticas (Borjas-Ventura et al. 2018) aumentando o efluxo de eletrólitos para o espaço livre celular (Perera et al. 2019).

O aumento do estresse oxidativo causado pela deficiência hídrica, pode induzir interferência na eficiência quântica potencial do fotossistema II e inativação da cadeia transportadora de elétrons que formará ATP e NADPH (Krause e Weis 1991), assim a fluorescência permite avaliar o efeito do estresse hídrico sobre a fotossíntese (Ganieva et al. 1998). A razão Fv/Fm avaliada por Fariaszewska et al. (2020) em estudo com gramíneas forrageiras, indica que a fluorescência aumenta com o déficit hídrico mais severo pois o transporte fotossintético de elétrons através do PSII foi

inibido e o oxigênio envolvendo o complexo dos centros de reação foi danificado, o que acarretou redução da eficiência fotossintética.

A superprodução de espécies reativas de oxigênio (ERO) pode ser causada por diversos fatores abióticos (Hu et al. 2015), esse estresse oxidativo afeta a integridade da membrana, podendo diminuir o conteúdo de clorofila (Kochanová et al. 2014) e a produção de biomassa da planta (Chen et al. 2016; Mendoza-Villarreal et al. 2015), uma vez que a produção de sacarose foi desbalanceada na etapa fotossintética.

O efeito benéfico da aplicação de Si em plantas sob condições de estresse é devido à estimulação de sistemas antioxidantes vegetais, o que melhora a integridade física da membrana (Barreto et al. 2018; Kochanová et al. 2014), para proteger o aparato fotossintético vegetal (Vaculíková et al. 2014), e para aumentar a absorção de nutrientes (Chen et al. 2016; Ferreira Barreto et al. 2017; Mantovani et al. 2018). A diminuição do estresse oxidativo se deve a diminuição de ERO responsável pela degradação das membranas celulares (Ashfaque et al. 2017).

A aplicação de Si em plantas promove incremento de compostos antioxidantes não enzimáticos, como os compostos fenólicos. Qureshi et al. (2018) relataram que esses compostos afetaram os fenômenos de aumento celular e mitose retardando a senescência e até morte celular pela regulação e produção de antioxidantes não enzimáticos eliminadores de ERO mantendo altas taxas de fotossíntese. O efeito do Si no incremento dos compostos fenólicos foi verificado em outras culturas sob estresse abiótico, como por exemplo deficiência hídrica (Aninbon et al. 2016; Petridis et al. 2012; Silva et al. 2018).

A maioria dos estudos com Si para atenuar déficit hídrico indica a diminuição da taxa transpiratória aumentando a eficiência do uso da água (Abd El-Mageed et al. 2020; Jinger et al. 2020) e outras pesquisas indicam benefícios na atenuação do estresse oxidativo que é alto em plantas sob estresse hídrico (Moro et al. 2018; Zhang et al. 2017). A diminuição deste estresse oxidativo pode ocorrer pelo envolvimento do Si no aumento de compostos antioxidantes (Ashfaque et al. 2017; Kim et al. 2017). Há um aumento do conteúdo de clorofila em plantas sob estresse abiótico com a aplicação de Si amplamente relatado na literatura (Hussain et al. 2021; Ramírez-Olvera et al. 2019; Teixeira et al. 2020).

Outros estudos acrescentaram que o Si pode substituir parte do carbono em estruturas orgânicas da parede celular com baixo custo energético, aumentando a absorção de nutrientes e a eficiência do uso de nutrientes (Araújo et al. 2022). O efeito benéfico do Si é demonstrado pela sua capacidade de modificação estequiométrica em plantas mesmo sob condições de estresses abióticos, como por exemplo o incremento da relação C/N, promovido possivelmente por uma diminuição da concentração de N em plantas com aplicação de Si e pela diminuição da relação C/Si havendo assim, diminuição da concentração de C e aumento da concentração de Si.

De acordo com Yan et al. (2018), esse efeito se deve ao fato de que a diminuição da concentração de C ocorreu devido a substituição por Si em sítios de ligação entre os componentes da parede celular poupando o mesmo para ser utilizado em outras sínteses orgânicas vitais (Neu et al. 2017). Então, o uso de Si pode contribuir para um aumento na eficiência de uso do C em plantas, fato também visto na cultura do milho (Lavinsky et al. 2015). Frazão et al. (2020) em estudo com a cultura da cana-de-açúcar observaram que a aplicação de Si alterou a estequiometria do C favorecendo o crescimento da planta sob restrição hídrica.

Acompanhando as atuais pesquisas envolvendo as mudanças climáticas, será de suma importância para a produção agrícola sustentável e rentável economicamente, respostas quanto ao melhor aproveitamento por exemplo, da luz solar e difusão de CO_2, comumente aumentados com o passar dos anos. Visto sua capacidade de regulação estomática, devido ao aumento do conteúdo de água foliar, o Si, vem sendo alternativa na otimização de trocas gasosas, além de sua importância contribuição na proteção do aparato fotossintético, conferir melhor aproveitamento de energia luminosa. Faltando assim, pesquisar mais específicas quanto a modificação fisiológica da planta, para melhorar aproveitar o potencial benéfico do Si como fertilizante.

Os principais mecanismos que influenciam a capacidade do Si de mitigar os efeitos do estresse hídrico, segundo Wang et al. (2021), incluem o aumento da absorção e transporte de água, regulando o comportamento estomático e a perda de água por transpiração, acumulando solutos e substâncias osmorreguladoras e induzindo a defesa da planta associada a eventos de sinalização, consequentemente

mantendo a integridade total e balanço hídrico da planta. Os autores sugerem que futuras pesquisas ainda são necessárias para implementar o uso do Si na agricultura.

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CAPÍTULO 2 – Fertirrigação com silício atenua o estresse por deficiência hídrica por modificar a estequiometria do carbono, favorecendo os aspectos fisiológicos

Si fertigation attenuates water stress in forages by modifying carbon stoichiometry, favouring physiological aspects[1]

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Abstract

Climate change has aggravated the occurrence of drought periods, affecting pasturelands in different regions of the world. Silicon attenuates water deficiency in several species, but there is a lack of research to verify whether Si can modify C stoichiometry and its effects in mitigating water deficit in forage plants. To this end, this research was carried out with the aim of evaluating whether Si supply via fertigation causes an increase in its absorption, stoichiometric modification of C and improvement in physiological variables and in the growth of Brachiaria cultivated under two soil water regimes (70% and 40% of water holding capacity in the soil). Two experiments were carried out with the cultivars BRS RB331 Ipyporã and Mavuno grown in pots filled with Quartzipsamments. In the experiments, the same treatments arranged in a 2 × 2 factorial scheme were applied, with Si application via fertigation applied to the soil and control (Si omission) combined with two soil water regimes (70% and 40% of the water retention capacity in the soil, adequate and deficient water contents, respectively). The two forages that received silicon via fertigation specially cultivated under water deficit had a greater accumulation of Si in the shoot, decreased C content and C:Si ratio and increased C use efficiency, and decreased rate of electrolyte leakage with increased relative water content, leaf water potential, chlorophyll b content, quantum efficiency of photosystem II and, consequently, increased growth and dry matter production. The present research shows that the use of Si via fertigation promotes a new strategy to mitigate water deficit in forages, based on the improvement of the physiological

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aspects of the plant resulting from the modification of carbon stoichiometry, thereby increasing C use efficiency.

Keywords

carbon use efficiency, drought stress, grasslands, plant nutrition

1. INTRODUCTION

The impacts of climate change on the planet are increasing and one of the main problems is the occurrence of extreme weather events such as droughts and floods. The effects of climate change are expected to increase cultivation in areas with fewer freshwater resources available and longer periods of water stress limitation (Oki & Kanae, 2006).

Water deficiency stands out for being common in tropical ecosystems (Monteiro et al., 2014), and it directly affects pastures that occupy a vast cultivated area in the world. Water deficiency has a global impact on crop production and increases the seasonality of forage production (Sbrissia et al., 2020). This fact is worrying because almost all of the beef production comes from animals fed directly with pastures, because they have low cost of production. Olivera Viciedo et al. (2020) studied the impacts of water deficiency on *Megathyrsus maximus* and found a reduction in plant dry matter under such stress.

Water deficiency activates the defence system plants, inducing detoxifying processes (Borjas- Ventura et al., 2020). In addition, the diffusion of CO_2 decreases with stomatal closure, resulting in a lower rate of net assimilation of carbon (C), which is preferentially allocated to roots or stems over leaves (Hummel et al., 2010; Sharp & Davies, 1979). Plants can decrease C to deal with water deficit and minimize the damage to the growth of the shoot of the forage (Olivera Viciedo et al., 2021).

A strategy to mitigate the effects of water deficit in forages is the use of silicon. This is because *Poaceae* plants are considered to be accumulators of this element (Cocker et al., 1998). Moreover, availability of Si from the soil decreases in pasture areas as a result of degradation at different levels (Yang, Hao, et al., 2019; Yang, Howe, et al., 2019) especially in Quartzipsamments, in which the sand granulometric fraction is predominant (Korndörfer et al., 1999).

The absorbed Si is accumulated in the leaves below the cuticle, increasing tissue rigidity, and it may lead to the replacement of part of the C of the cell walls (Raven, 1983), since it forms hydrogen bonds to the cellulose molecules (Schoelynck et al., 2010). This can decrease the concentration of C in the cell wall, saving it to be used in other organic syntheses that are vital to plant growth, which may show greater efficiency in the use of C. However, there is not enough research to check whether or not Si can alter C stoichiometry in forage plants to attenuate the lower net carbon assimilation rate in plants under water deficit.

Current studies in different species have limited the benefits of Si to physiological aspects that induce attenuation of water deficit, for example, the maintenance of leaf water potential in corn plants (Amin et al., 2014), the preservation of photosynthetic pigments in sugarcane plants (Bokhtiar et al., 2012) as well as the reduction of effects caused by water stress due to increased photosynthetic rates, osmotic adjustment and the increase in water use efficiency for rice (Ming et al., 2012; Yang, Hao, et al., 2019; Yang, Howe, et al., 2019).

However, for forage species, there are few studies on water deficit and Si. In the study by Melo et al. (2003), relatively high doses of the element were used (up to 1,452 kg/ha of Si) in the soil in the form of calcium silicate. The authors concluded that Si application was not enough to increase dry matter production. As they did not evaluate physiological aspects of the plant, the biological effects of silicon in this species could not be clearly understood yet. Lack of response from the plants to Si may have occurred because the effect of this element is more evident in plants under stress (Epstein, 2001). In this latter study, water deficit was relatively very low (60% of soil water retention capacity) for fodder. In addition, this water deficit result does not reflect reality, as areas cultivated with pastures commonly experience severe water deficit (≤40% of soil water retention capacity).

The benefits of Si in pasturelands may be amplified by using fertigation to attenuate water stress, which is a common condition in drought periods in several regions worldwide, resulting in low forage production, regardless crop species. Si fertigation is performed by using the soluble source of the element, as potassium silicate. In order to guarantee Si absorption from plants, it is important to provide Si in its monomeric chemical form (H_4SiO_4) (Laane, 2018).

A requirement for supplying Si in its monomeric form is to maintain Si concentration lower than or equal to 3 mmol/L, because higher concentrations lead to polymerization, forming polysilicic acid and colloidal particles not absorbable by plants (Birchall, 1995). The use of Si fertigation in concentrations lower than 3 mmol/L is a promising strategy to guarantee adequate plant nutrition, without the need of higher Si contents. Additionally, Si fertigation may be carried out in pasturelands already grown without root impairment. However, when other sources of low- solubility Si is used (calcium silicate), it is necessary to incorporate it in the soil to induce it reactivity and solubilization. Moreover, in this case, the rates applied are relatively high (>1 t/ha), not enabling its use in pasturelands already grown. Thus, it is important to note the potential of using Si fertigation in pasturelands in relation to other Si applications.

It his noticeable that further studies about Si fertigation in pastureland are required, especially in understanding the reasons why it may mitigate severe water stress on forage species, as well as its mechanism, which may be beneficial to plant growth.

For this purpose, the following hypotheses should be tested: (a) The innovative use of Si supply via fertigation with a soluble source in relatively low concentration (2.5 mmol/L) during the growth cycle of the forage is sufficient to efficiently increase its absorption by the plant. (b) The Si absorbed by the plant modifies the stoichiometric C:Si ratio, increasing the efficiency of C use and, consequently, improving the physiological variables and the growth of forage under water deficit.

To this end, this experiment was carried out with the objective of evaluating whether Si supply via fertigation causes an increase in Si absorption, stoichiometric modification and improvement of physiological variables and in the growth of *Brachiaria* cultivated under two soil water regimes (70% and 40% of soil water retention capacity).

2. MATERIALS AND METHODS

Two experiments were carried out in a greenhouse at UNESP Câmpus Jaboticabal, from September to December 2019. A different forage cultivar was used in each experiment. The Brachiaria ‘BRS RB331 Ipyporã’, bred by Embrapa (Brazilian Agricultural Research Corporation) and the Brachiaria ‘Mavuno’ bred by Wolf Seeds,

are hybrids of bachiariagrass (B. ruziziensis x B. brizantha) registered in Brazil (MAPA [Ministry of Agriculture, Livestock and Food Supply] no. 30488 and no. 20160052, respectively). The difference between cultivars are related to different breeding programs, and thus different seed banks, in which a more detailed description about breeding steps is only public available for the cultivar bred by Embrapa, as stated by Borges do Valle et al. (2017). During the experimental period, the temperature and relative air humidity inside the greenhouse were recorded daily using a digital thermohygrometer (Figure 1).

In the two experiments, the treatments were arranged in a 2 × 2 factorial scheme, with the application of Si via nutritive solution (root) and the control (Si omission) combined with two water regimes at 70% and 40% of soil water retention capacity, arranged in randomized blocks with six replicates. The experimental unit consisted of a 7 dm^3 vessel filled with 6 dm^3 of samples of a Quartzipsamments.

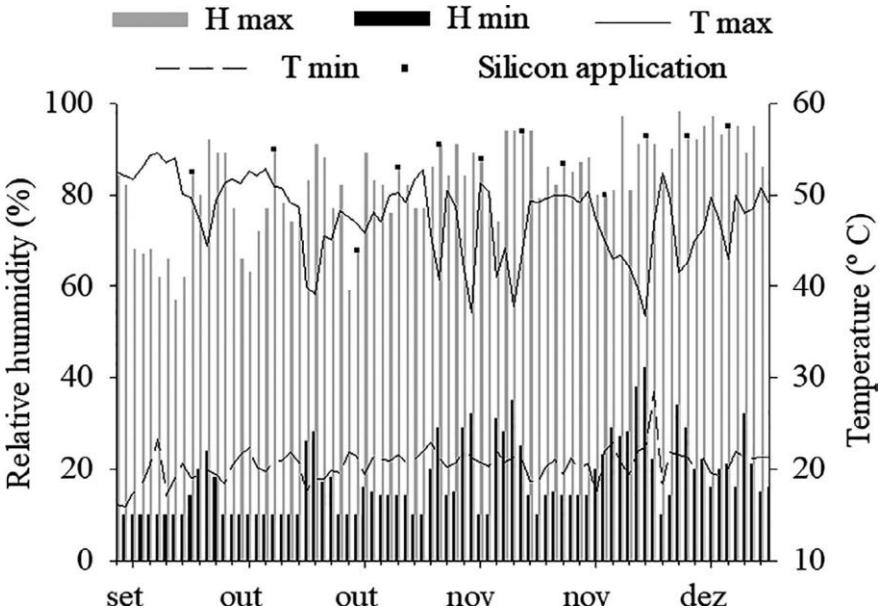

FIGURE 1 Maximum and minimum air temperature and humidity of the greenhouse and silicon application during the experimental period. H max, maximum humidity; H min, minimum humidity; T max, maximum temperature; T min, minimum temperature.

Before forage grass was planted, a chemical analysis of the soil was carried out for fertility purposes, according to the method described by Raij et al. (2001), and the following results were found: pH ($CaCl_2$): 4.3; organic matter: 9 g/dm^3, P resin: 2

mg/dm^3; Ca: 3 mmolc/dm^3; Mg: 1 mmolc/dm^3; K: 0.3 mmolc/dm^3; Al: 0 mmolc/ dm^3; H + Al: 16 mmolc/dm^3, sum of bases: 4 mmolc/dm^3; cation exchange capacity: 20 mmolc/dm^3; base saturation (K + Ca + Mg: K + Ca + Mg + H + Al): 21%. Si content (1 mg/dm^3) was determined using the method described by Korndörfer (2004). Soil granulometry was determined with 540 g/kg of sand, 380 g/kg of clay and 90 g/kg of silt.

Limestone was applied (Total neutralization power: 125%, CaO: 48%, MgO: 16%) in order to increase base saturation (BS: Ca^{2+} + Mg^{2+} + K^+/Ca^{2+} + Mg^{2+} + K^+ + H^+ + Al^{3+} × 100) at 60%, which corresponded to the dose of 0.285 g/dm^3 of soil being properly mixed in the soil (Raij et al., 2001). Thirty days after the application of limestone, fertilization was carried out by applying 150 mg/dm^3 of N, P and K, in the form of ammonium sulphate, triple superphosphate and potassium chloride, respectively, and 5 mg/dm^3 of Zn in the form of zinc sulphate, all mixed to the volume of the soil.

Then, the forage was sown with four plants per pot and, before applying the treatments, a uniform cut was made to the forage plants at 10 cm in height to standardize the plants and induce tillering.

Si was applied via fertigation using sodium silicate and potassium stabilized with sorbitol (113.4 g/L of Si and 18.9 g/L of K_2O), at a concentration of 2.5 mmol/L, simulating a 5 mm application depth every 5 days after cutting the plant uniformity for a period of 50 days. The pH value of the application solution was maintained at 5.5.

The water availability levels of the soil were determined on the basis of the microporosity values measured by the tension table method with a 60 cm high water column. This calculation took into account soil density, determined by the ratio of dry soil weight, after drying in an oven at 110°C for 24 hr, and the volume of unformed soil sample (Araújo Filho & Carvalho, 1997). Total microporosity was considered to be equivalent to 100% of soil water retention capacity; however, the water condition that was considered was 70% of this value, as it corresponds to the demand for most crops. The water deficit condition was achieved by maintaining the water level at 40% of soil water retention capacity. The control of water availability was performed daily by the method of weighing the vessels on the basis of replacement of evapotranspirated water.

The photosynthetic measurements of the quantum yield of PSII were carried out between 7 and 8 a.m., 50 days after the uniform cutting to ensure the adaptation of the leaf to the light. The first fully developed leaf of each plant was measured, and the following parameters were determined: (F0) = minimum fluorescence of the adapted leaf in the dark, (MF) = maximum fluorescence of the leaf adapted to the dark, (VF) = maximum variable fluorescence, (Fv/Fm) = maximum quantum efficiency of PSII, using a portable fluorometer (Opti- sciences— Os30P) (Lichtenthaler et al., 2005).

For the analysis of the pigments, two leaf discs of 6 mg were collected from the middle third of the leaf blade of the fully developed first leaf, according to the methodology proposed by Lichtenthaler (1987), with readings at 647 nm for chlorophyll *b* (Chl *b*) carried out in a Beckman DU 640 spectrophotometer. The levels were defined on the basis of fresh weight.

Assessment of damage to cell membrane integrity was based on the method of determining the electrolyte leakage rate, proposed by Dionisio- Sese and Tobita (1998). Three leaf discs (129 mm^2 each) were collected from the first fully developed leaf and emerged in a beaker containing 20 ml of deionized water, at ambient temperature for 2 hr. After this period, a reading of the electrical conductivity of the solution (EC1) was performed with the aid of a bench conductivity metre (TDS- 3 digital metre). Then, the samples were subjected to heating in an autoclave at 121°C for 20 min and, after cooling, a new final electrical conductivity reading (EC2) was performed. Electrolyte leakage was determined considering the following formula: EC1/EC2 × 100.

Leaf water potential (Ψw) was determined in the middle third of the leaf blade of the first fully developed leaf using a Scholander pressure chamber (Soil Moisture Equipment, USA). The pressure was applied until exudation occurred from the cut made in the leaf petiole, and the measurements were evaluated between 6 and 9 a.m. (Turner, 1981).

Relative water content in the leaf was determined by collecting three leaf discs (with approximately 129 mm^2) of the first fully developed leaf. They were immediately weighed to measure fresh tissue weight (Wf). After that, the samples were rehydrated in deionized water for 6 hr, to determine turgid weight (Wdt), using paper towels to extract the excess water. Dry weight (Wd) was determined after the discs remained in a forced air circulation oven at 80°C for 24 hr. The relative water content values were

determined by using the equation proposed by Barrs and Weatherley (1962): [(Wf − Wd)/ (Wdt − Wd)] × 100.

Plant height was measured considering the length from the base to the apex of the last leaf, and the number of tillers in the brachiaria was also counted. The leaf area was measured using a LICOR device, model 3100.

The plants were washed in running water, detergent solution (0.1% v/v), HCl solution (0.3% v/v), and deionized water. The samples were dried in an oven with forced air heating (65 ± 5°C) up to constant weight, and thereafter, plant dry matter was determined.

The Si content in the shoot was obtained by extracting the element according to the methodology described by Kraska and Breitenbeck (2010) and Si reading was performed by a spectrophotometer at 410 nm, as indicated by Korndörfer (2004). Based on Si content and dry weight, Si accumulation in the shoot of the plants was calculated.

Total concentration of C in the shoot was determined by dry combustion (1,000°C) using an elemental analyser (LECO Truspec CHNS) calibrated with the LECO 502– 278 wheat standard (C = 45.00% and *N* = 2, 68%).

The C:Si ratio was calculated as C content (g/kg of C)/Si content (g/kg of Si). Carbon efficiency was calculated using the equation: (dry weight)^2/C accumulation in the plant (g per pot) (Siddiqi & Glass, 1981).

The collected data underwent analysis of variance by the *F* test ($p \leq .05$) and the averages were compared by Tukey's test at 5% probability using the SAS® statistical software (SAS, 2008).

3. RESULTS

Water deficit in the presence or absence of Si decreased Si accumulation and Si content in the cultivar BRS RB331 Ipyporã (Figure 2a,c) and in Mavuno (Figure 2b,c). Si supply via fertigation increased its accumulation and its content in the two forages and in the two water regimes.

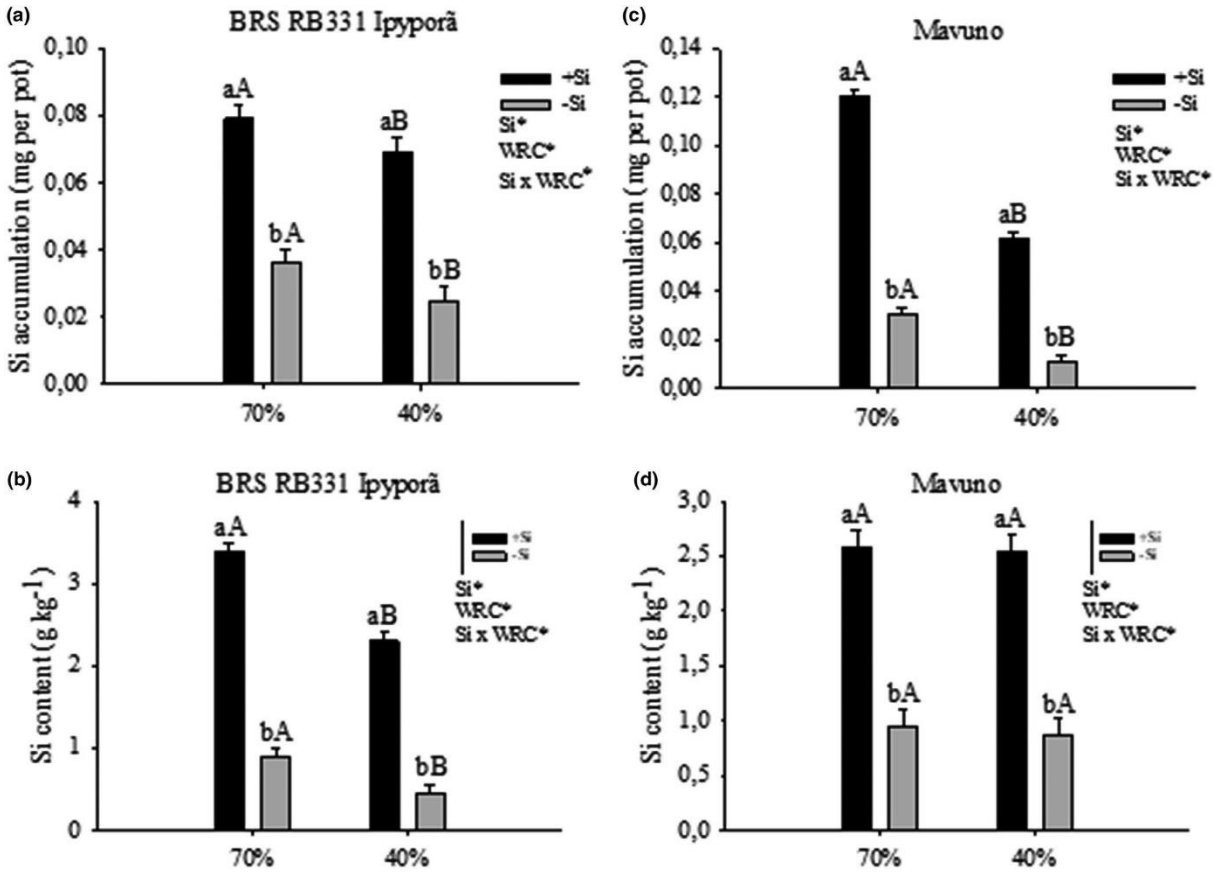

FIGURE 2 Accumulation of silicon (Si) (a, c) and silicon content (b, d) in the shoot of forage plants cultivated in soil with different soil water retention capacity (WRC) (70% and 40%) absence (−Si) and in the presence of fertigation with silicon (+Si). *Significant to 5% probability by the *F* test. Lowercase letters show differences in relation to Si and uppercase in relation to WRC. The bars represent the standard error of the mean, $n = 6$

Water deficit in the presence or absence of Si decreased C content in the shoot of the cultivar BRS RB331 Ipyporã (Figure 3a) and Mavuno (Figure 3b). The application of Si in the two water regimes decreased C content in the two forages, except in the cultivar BRS RB 331 Ipyporã cultivated without water restriction.

Water deficit in the absence or presence of Si did not affect the leaf C:Si ratio in the two forages. However, Si supply decreased the C:Si ratio in the two forages in the two water regimes (Figure 3b,e).

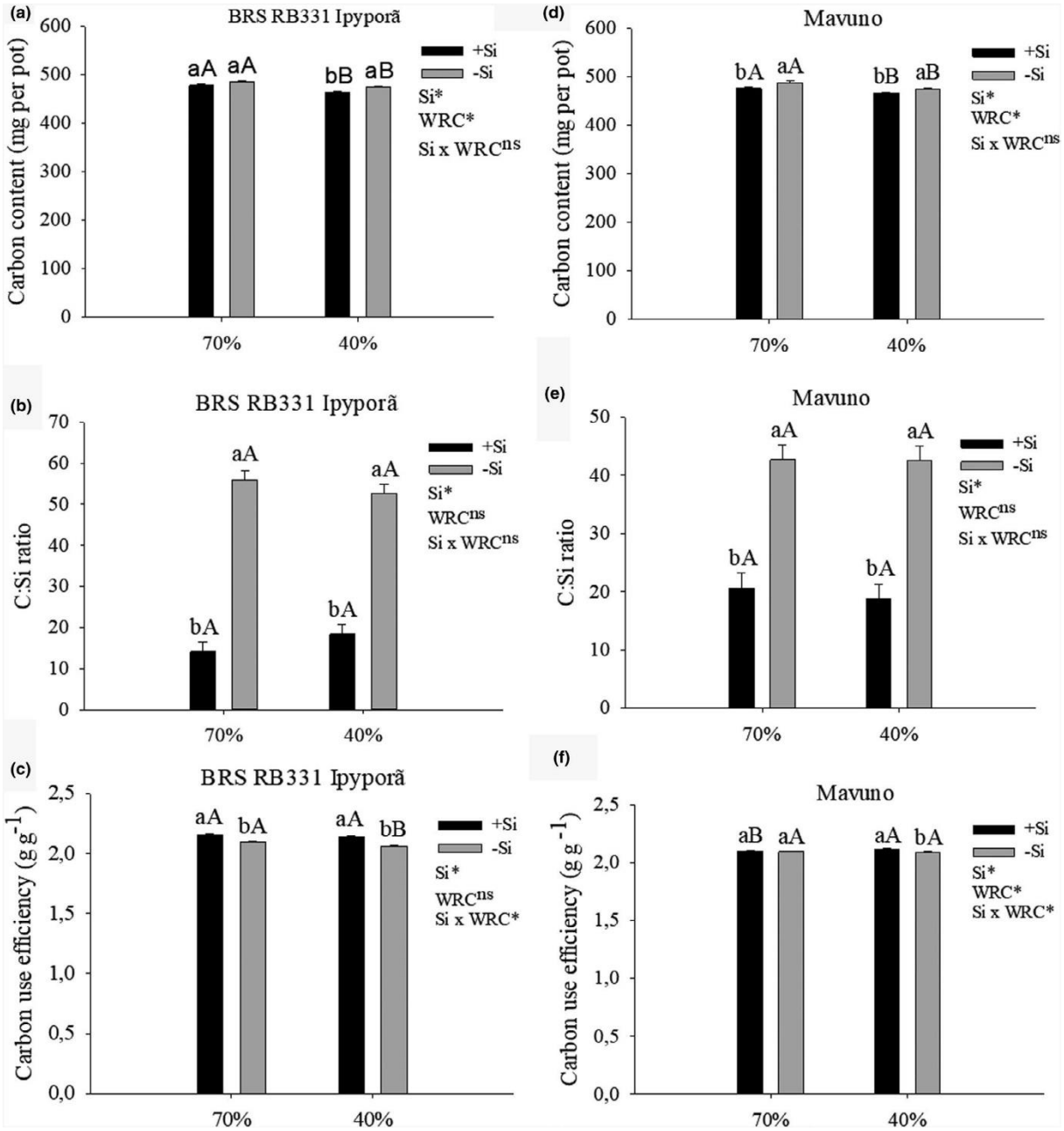

FIGURE 3 Carbon content (a, d), relation C:Si (b, e) and carbon use efficiency (c, e) in the shoot of forage plants cultivated in soil with different soil water retention capacities (WRC) (70% and 40%) absence (−Si) and in the presence of fertigation with silicon (+Si). *Significant at 5% probability. ns, not significant by the test *F*. Lowercase letters show differences in relation to Si and uppercase in relation to WRC. The bars represent the standard error of the mean, *n* = 6

The plants of the cultivar BRS RB331 Ipyporã in condition of water deficit, without addition of Si, had a decrease in carbon use efficiency, in comparison with plants with Si supply. The application of Si in this cultivar increased C use efficiency in

both conditions of water availability (Figure 3c). Water deficit in the cultivar Mavuno decreased C use efficiency when cultivated without Si application. With Si application in this cultivar, C use efficiency increased in both soil moisture conditions (Figure 3f).

Water deficit with Si omission increased the rate of electrolyte leakage in the two forages (Figure 4a,d). However, the application of Si, especially in plants under water deficit, reduced electrolyte leakage in the two forages.

The water deficit, especially in the Si omission, decreased relative leaf water content in the two forages (Figure 4b,e). Si fertigation increased relative water content of the two forages in the two water regimes, except for the cultivar Ipyporã without water restriction.

Water deficit, especially in the absence of Si, decreased the leaf water potential of the two cultivars. The application of Si in plants under water deficit increased the water potential, keeping it similar to the plant with adequate water availability. In plants without water restriction, the presence of Si in fertigation did not affect the water potential of the two forages (Figure 4c,f).

Water deficit decreased FSII quantum efficiency (Fv/Fm) only in forages that did not receive Si (Figure 5a,c). However, the application of Si in the two forages under water deficit increased the photochemical efficiency of PSII.

Water deficit decreased Chl *b* content only in the cultivar Mavuno grown in the absence of Si supply. In the two forages, the application of Si under water deficit increased Chl *b* content (Figure 5b,d).

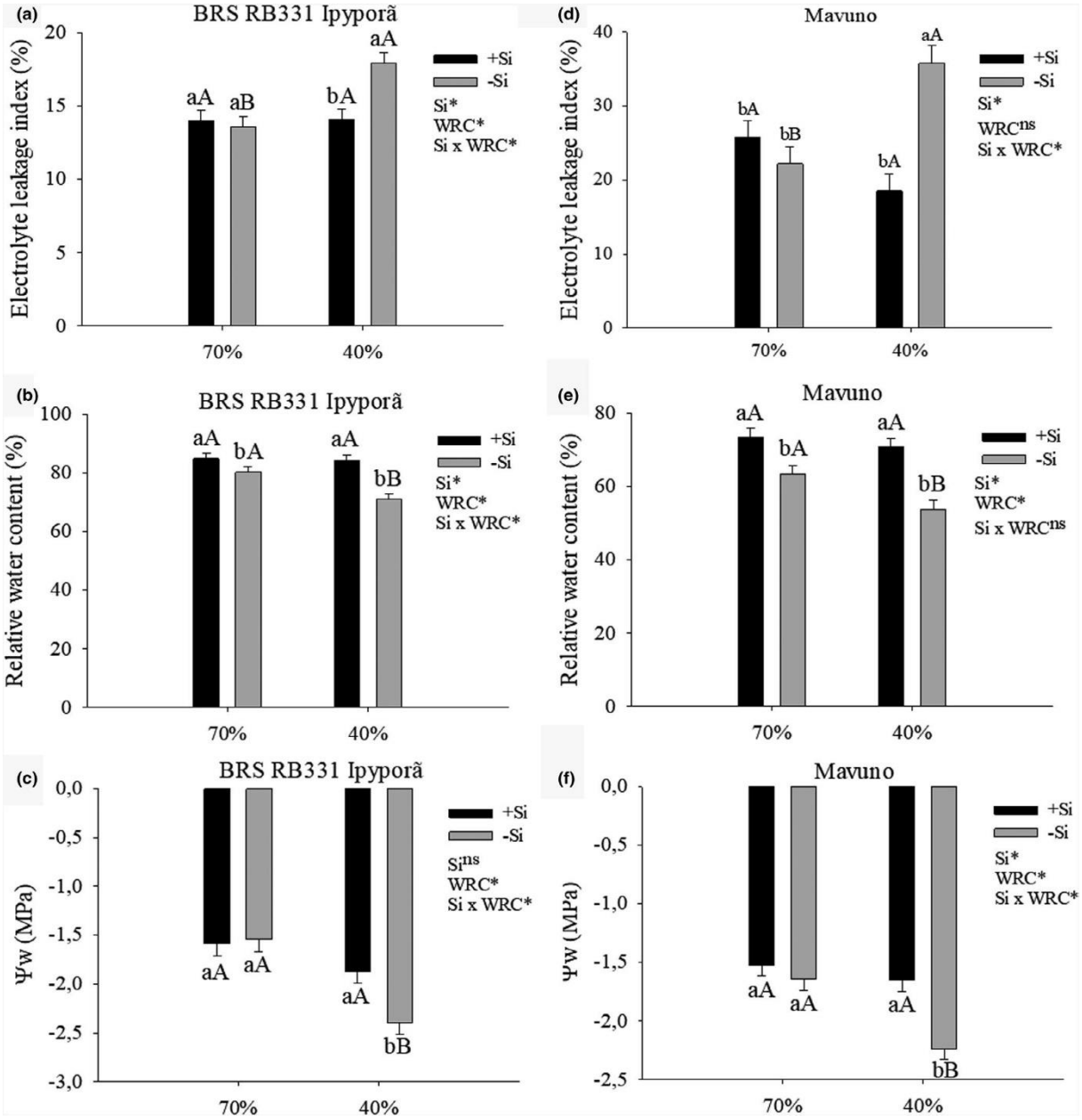

FIGURE 4 Electrolyte leakage index (a, d), relative water content (b, e), leaf water potential (Ψw) (c, f) of forage plants cultivated in soil with different soil water retention capacities (WRC) (70% and 40%) absence (−Si) and in the presence of fertigation with silicon (+Si). *Significant at 5% probability. ns, not significant by the test *F*. Lowercase letters show differences with respect to Si and uppercase in relation to WRC. The bars represent the standard error of the mean, *n* = 6

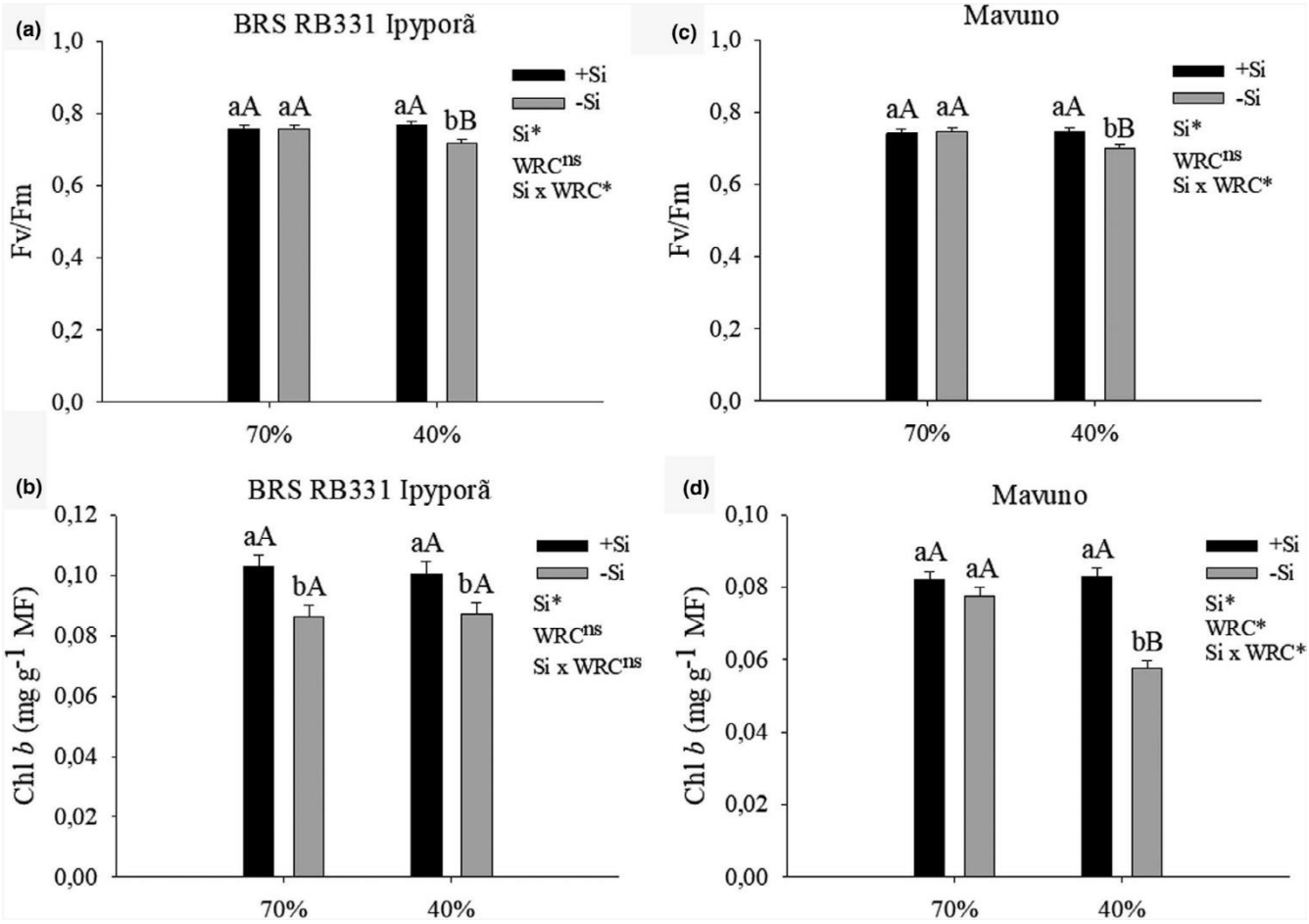

FIGURE 5 Quantum efficiency of photosystem II (Fv/Fm) (a, c) and chlorophyll *b* (Chl *b*) (b, d) of forage plants grown in soil with different soil water retention capacities (WRC) (70% and 40%) absence (−Si) and in the presence of fertigation with silicon (+Si). *Significant at 5% probability. ns, not significant by the test *F*. Lowercase letters show differences in relation to Si and uppercase in relation to WRC. The bars represent the standard error of the mean, *n* = 6

Water deficit without addition of Si decreased the number of tillers in the two cultivars. The application of Si, especially under water deficit, increased the number of tillers of the two forages (Figure 6a,d).

In the two forages under water deficit in the absence and presence of Si, leaf area (Figure 6b,e) and dry weight (Figure 6c,f) decreased. However, the Si application increased the leaf area and dry weight of the two cultivars in the two water regimes.

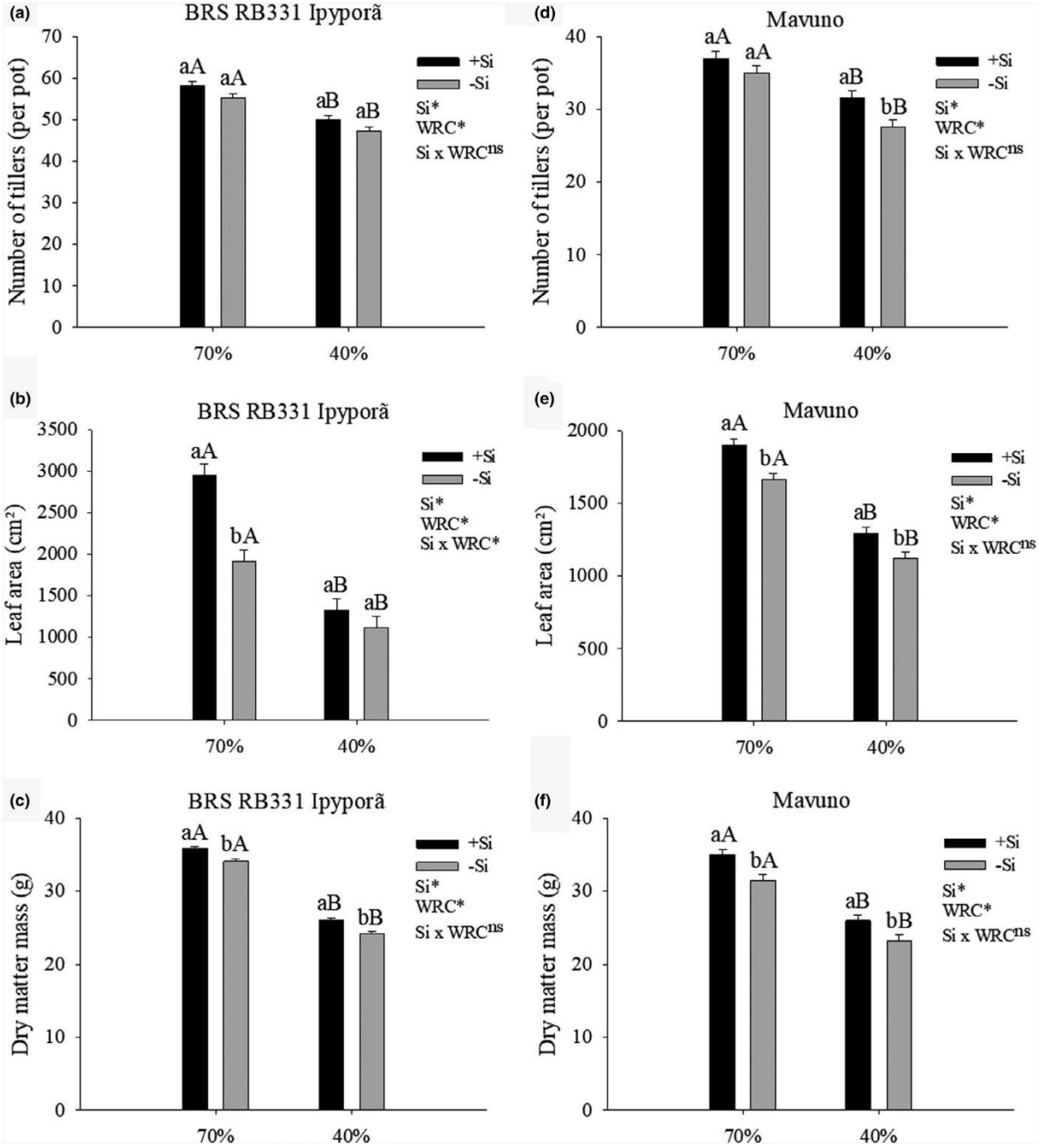

FIGURE 6 Plant height (a, e), number of tillers (b, f), leaf area (c, g) and dry matter mass (d, h) of forage plants grown in soil with different soil water retention capacity (WRC) (70% and 40%) absence (−Si) and in the presence of fertigation with silicon (+Si). ns, not significant by the test *F*. Lowercase letters show differences in relation to Si and uppercase in relation to WRC. The bars represent the standard error of the mean, *n* = 6

4. DISCUSSION

Climate change has aggravated water deficit; it is the biggest cause of losses in pasture growth and production (Kunrath et al., 2018; Sadras et al., 2016; Sinclair &

Rufty, 2012). Thus, the drastic reduction in freshwater resources owing to agricultural activities currently remains as one of the most challenging problems. Although freshwater is necessary for human life, food production is also essential for a population that is growing at a rapid pace (Besharat et al., 2020). In this context, that is, the cultivation of forages that provide greater production and supply of animal protein in different water regimes, one needs to ensure the future sustainable development of humanity, especially in semiarid regions.

As far as plants are concerned, water deficit causes hunger for carbon, which is an imbalance between C inputs and outputs, which results in a negative carbon balance. The lack of carbon is, therefore, a consequence of the prevention of hydraulic failures through stomatal closure (Sevanto et al., 2014).

In this research, the biological damage in the study two forages was clear, especially in BRS RB331 Ipyporã plants without the application of Si. These changes in C stoichiometry caused by water deficit may be a strategy of the plant to obtain new homeostasis in an attempt to decrease losses in its metabolism. However, this event caused by the water deficit is little discussed.

The physiological losses of water deficit were very evident because they caused a decrease in water content in the plant and in water potential in the two forages. This occurs after a decrease in the water levels and the water potential of the soil, and increased pressure gradient in the xylemic vessels, which may cavitate and lose their hydraulic conductivity (Hasanuzzaman et al., 2019; McDowell et al., 2008).

In addition, water deficit caused oxidative stress owing to the increased rate of cell electrolyte leakage in forage leaves. This is because water deficit induces the production of reactive oxygen species, which promote oxidation of lipids and proteins in the membranes causing their rupture and increase the rate of cell leakage (Nachimuthu et al., 2017). These reactive oxygen species can degrade photosynthetic pigments because of chloroplast disturbances (Parida et al., 2002). The consequence is a decrease in the quantum efficiency of photosystem II, which impairs photosynthesis (Pospíšil, 2016), given the increased resistance to CO_2 diffusion (Galmés et al., 2011), a fact that occurred in the study with forages grown under water deficit in the absence of Si application.

Water deficit decreases leaf size, interrupting the growth of the shoot (Chaves et al., 2010). This may or may not be due to a decrease in the length and/or the number of leaves produced, depending on stress intensity (Wery, 2005; Zhang et al., 2019). Foliage expansion processes are more affected by drought than carbon assimilation, leading to higher concentrations of carbohydrates per unit weight in plants with water stress compared to well- watered plants (Dosio et al., 2011). This effect of water deficit of hindering the growth of the two forages occurred in the present research because it decreased the number of tillers, leaf area and, consequently, shoot dry weight.

Biological damage was very evident in the two forages because water deficit was severe (40% of soil water retention capacity). Similar results have been reported by other authors in similar forages (*Brachiaria* spp.) (de Gaspari Pezzopane et al., 2015; Moro et al., 2018; Santos et al., 2008).

The forages were clearly sensitive to water deficit, since their production was limited by the damage caused to the physiology of the plants (Sinclair & Rufty, 2012), indicating the importance of sustainable strategies to reduce such loss through the use of Si. It is vital to gain further insights into the mechanisms of action of this beneficial element in forages cultivated under water deficit, which occur in different regions of the world.

For this purpose, initially, the forage's ability to absorb Si should be better understood. The forages had a great capacity to absorb Si under water deficit, as its application increased Si accumulation in the shoot by 335% and 143% for the BRS RB331 Ipyporã and Mavuno cultivars, respectively. Silicon, when absorbed by the plant, is deposited mainly on the wall of the cells of the leaf epidermis (Savant et al., 1997).

Fertigation with silicon was efficient in the nutrition of these forages because the amount of this element applied during cultivation was relatively low (139.4 mg per pot containing 6 dm^3 of soil); considering the area of 1 ha (2,000 m^3 of soil in layer 0– 20 cm), it corresponds to 46.5 kg/ha of Si. In previous studies, Si application in the soil in a total area in the form of calcium silicate of restricted solubility (0.095 g/L of Si at 17°C) (Alcarde et al., 2003) also resulted in an increase in Si in *Brachiaria* plants, but using 2 t/ha (Korndörfer et al., 2010) and 6 t/ha (Sarto et al., 2016).

The high efficiency of Si fertigation can be attributed to the use of totally soluble sources with a stabilizer and in element concentrations (2.5 mmol/L) without risk of polymerization. Therefore, the findings of the present research indicate the viability of using Si via fertigation; therefore, the first hypothesis can be accepted. It indicates that this form of application of the element is efficient to increase its absorption. This study will offer new ideas to provide efficient Si nutrition especially in forages grown in a semiarid climate.

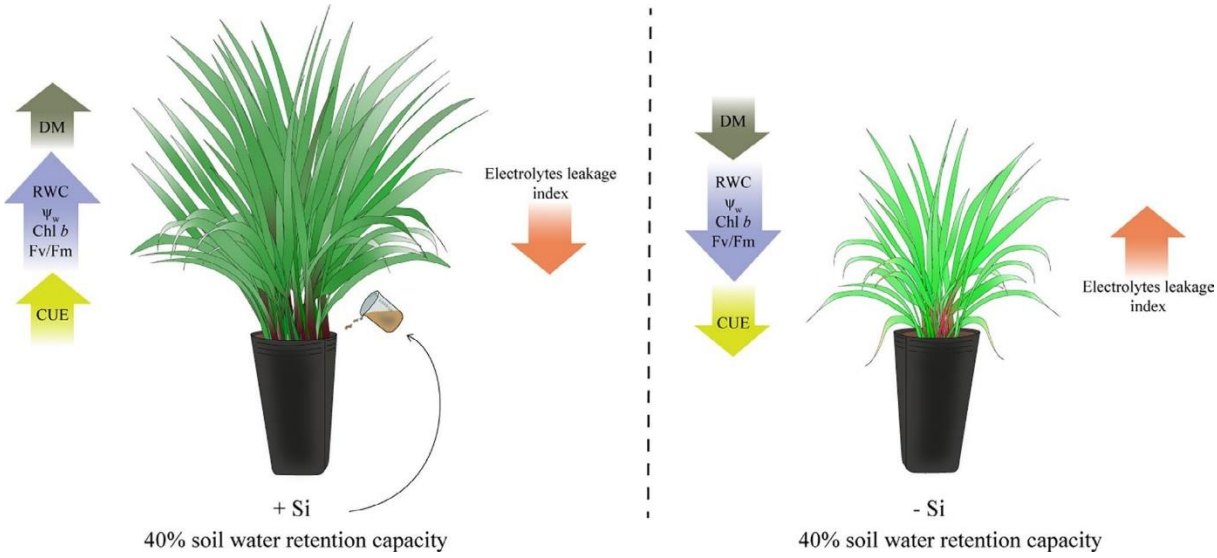

FIGURE 7 Representation of a forage plant in the condition of water deficit in the absence (−Si) and in the presence of fertigation with silicon (+Si) and a summary of its beneficial in the effects of the carbon use efficiency (CUE), relative water content (RWC), leaf water potential (Ψw), chlorophyll *b* (Chl *b*) and quantum efficiency of photosystem II (Fv/Fm) and dry matter (DM)

The increase in Si absorption in the plant promoted stoichiometric modification of C, decreasing its content and increasing the C:Si ratio in the leaves of the two forages, especially when they were grown under water deficit. Si can contribute by replacing part of the carbon in cell walls (Raven, 1983), increasing cellulose content (Schaller et al., 2012). This is because Si forms hydrogen bonds to cellulose molecules in the cell wall (Schoelynck et al., 2010), and this compound has an energy cost 10 to 20 times lower than the production of lignin (Raven, 1983).

Therefore, Si has the effect of decreasing the concentration of C in the cell wall of leaves; therefore, it can be used in other organic syntheses that are vital for plants under water deficit. This is important because plants under water deficit face competition for energy for the synthesis of defence compounds (which incur high

metabolic costs for synthesis and storage) or for the use of their energy in other functions such as growth, maintenance and reproduction (Lavinsky et al., 2015).

This benefit of Si possibly occurred, as it was evidenced in the present research that C use efficiency increased in the two forages grown under water deficit. This effect of Si in increasing C use efficiency attenuated the competition for energy that is common in plants under water deficit. Therefore, this finding that indicates yet another role for Si in attenuating water deficit is unprecedented in forages and, consequently, it must be supported by important physiological responses of the plant to withstand water stress.

The beneficial physiological responses of plants under water deficit promoted by Si were clear in this study. This is because it is a plant strategy for survival in periods of water deficit whose aim is to preserve the integrity of its proteins, enzymes and cell membranes, based on osmotic adjustment with increased water potential and relative water content (Bezerra et al., 2019). This effect occurred in the present study because there was a decrease in oxidative stress promoted by Si in forages under water deficit as a result of a decrease in the leaf electrolyte leakage rate, possibly owing to the increase in antioxidant activity (Kim et al., 2017) and the increase in water content in the plants. Si can contribute to greater resistance of xylemic vessels (Ma et al., 2004), which transports water to the plant (McElrone et al., 2004), thereby increasing the volume of water assimilated by plants (Sperry et al., 2002). It also decreases water losses by decreasing the leaf transpiration rate (Galmés et al., 2011).

These benefits of Si in the two forages under water deficit favoured the increase in quantum efficiency of photosystem II, in comparison with non- stressed plants. The greater efficiency in the use of radiation is due to the greater efficiency in the use of water by plants (Sadras et al., 2016) and the effect of Si in increasing the content of photosynthetic pigments such as chlorophyll *b*. These biological effects of Si in forages under water deficit favoured the increase of tillering and, consequently, of leaf area and dry matter of the two forages.

In plants without water deficit, it is also evident that the use of Si increased the dry matter of the two forages owing to the increase in leaf area. Therefore, the indications that Si would benefit only plants under stress (Epstein, 2001) have been discussed, since effects have been observed in plants without stress, in different

species such as corn (Besharat et al., 2020); therefore, it is considered an almost essential element (Liang et al., 2015).

Our findings evince that Si fertigation can attenuate water stress, as previously hypothesizes, as it indicated that the Si absorbed by the plant modifies the stoichiometric C:Si ratio, increasing C use efficiency. Consequently, there were benefits in the physiological variables and growth of forage under water deficit (Figure 7).

The present finding proposes the use of Si fertigation at a concentration of 2.5 mmol/L in forages with or without water deficit so that it can increase the sustainability of these production systems, especially in soils with a sandy texture with low available Si content.

5. CONCLUSION

The decrease in freshwater resources resulting from climate change is one of the most challenging problems, as severe water deficit causes disturbance in the carbon stoichiometry with important physiological damage to forage plants.

The two forages that received silicon via fertigation, especially those cultivated under water deficit, had a greater accumulation of Si in the shoot, decreased C content and the C:Si ratio, increased carbon use efficiency and decreased the electrolyte leakage rate, and increased relative water content, leaf water potential, chlorophyll *b* content, quantum efficiency of photosystem II and, consequently, growth and dry matter production.

The present research has shown that the use of Si via fertigation provides a new strategy to mitigate water deficit in forages, based on the improvement of the physiological aspects of the plant owing to the modification of carbon stoichiometry, thereby increasing C use efficiency.

ACKNOWLEDGEMENTS

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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CAPÍTULO 3 – Mitigação dos efeitos da deficiência hídrica em duas cultivares de *Panicum maximum* spp. pela aplicação de Silício

Mitigation of Water Deficit in Two Cultivars of *Panicum maximum* by the Application of Silicon[1]

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Abstract

Silicon (Si) is known as an attenuator for water deficit through increasing water status. The mechanisms involved in Si to mitigate this stress may be linked to decreasing oxidative stress and increasing phenolic compounds, associated with stoichiometric homeostasis of carbon (C), nitrogen (N), and Si, although there is a lack of research especially in forage crops. This research aimed to evaluate whether the supply of Si via fertigation improves the antioxidant defense system and modifies the C/N/Si stoichiometry and the growth of two cultivars of *Panicum maximum* cultivated under two soil water regimes (70 and 40% water retention capacity). Two experiments were developed, and the same treatments were applied using a 2 × 2 factorial arrangement, with Si applied via fertigation (2.5 mmol L^{-1}) to the soil, while the control (without Si) was combined with two levels of soil moisture (70 and 40% of the soil water retention capacity). The two cultivars showed high accumulation of silicon in the shoot, low C content, low C/Si and C/N ratios, and high nutritional efficiency for the use of C in both water conditions. This is related to the potential of the Si to provide the greater antioxidant defense owing to higher production of phenolic compounds and decreased electrolyte leakage index. There was an increase in relative water content, leaf water potential, total chlorophyll content, and quantum efficiency of photosystem II, as shown by greater growth and dry mass production. Si application is a promising strategy to mitigate water deficit, ensuring new physiological and nutritional homeostasis, contributing to a more sustainable agriculture by means of feeding the herds that depend on pasturelands.

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1 Introduction

Climate change promotes alterations in rainfall distribution in different regions of the world that may cause vulnerability to agriculture (Karimi et al., 2018). Occurrence of water deficit has increased (Prakash Aryal et al., 2020), harming physiological aspects of plants (Wang et al., 2018), especially in tropical ecosystems (Monteiro et al., 2014) particularly pasture fields (*Poaceae*) that are grown in this region.

The species *Panicum maximum* stands out for its high dry matter production capacity, forage quality, ease of establishment, and acceptability by animals (Torres et al., 2013). There are different cultivars of this group, two of which were launched in 2001; the Massai cultivar is a spontaneous hybrid between *Panicum maximum* x *Panicum infestum*, characterized by high forage production and high leaf/stem ratio, tillering capacity and leaf emission (Emerenciano Neto et al., 2018). The other cultivar is BRS Zuri (*Panicum maximum*) launched in 2013 with caespitose growth, tall, and erect; it is characterized by having high forage production; wide, long, and arched leaves; and thick stem (EMBRAPA, 2015).

Pasture lands produce fodder in large areas that may be unsuitable for cultivation or other activities; this allows the production of ruminants, sustaining global meat production, a critical resource for millions of people who depend on animal protein for food security (Sloat et al., 2018).

Water deficit causes adverse effects on plant development due to increased production of reactive oxygen species (ROS) promoting oxidative stress seen in rice plants (Liu et al., 2019). This ROS promotes lipid peroxidation, damaging the organic molecules that make up membranes, photosynthetic pigments, DNA, and RNA, thus possibly leading to cell death (Borjas-Ventura et al., 2018). Moreover, the fact that water deficit causes disturbance in the photosynthetic electron transport through the PSII has some consequences: decreased photosynthetic efficiency (Fariaszewska et al., 2020), which causes stress to plants, and decreased plant growth.

Silicon (Si) has been identified as a beneficial element due to its characteristic of attenuate abiotic stress in a sustainable manner without damaging the environment, and it can have global applications (Imtiaz et al., 2016). Therefore, the use of Si can mitigate water deficit in forages in sub-irrigated systems reducing water use and electricity costs. The expectation of response of forage plants to the application of

silicon is due to two factors; one is the fact that the available content of this element in the soil is usually low in the main growing regions (Yang et al., 2019), especially in Entisols with sandy texture (Korndörfer et al., 1999); the other reason is the fact that Poaceous forages are considered to be Si accumulators (Cocker et al., 1998), indicating their high Si absorption capacity. In this scenario, if there is a water deficit, the expectation of an increase in the production of biomass by the forage may be high, the application of Si especially using a soluble source via fertigation that is available on the market, although such information is yet despised.

Most studies that used Si to attenuate water deficit in different crops have similarly reported the fact that a decrease in the transpiration rate promotes an increase in water use efficiency and, consequently, it can favor the plant growth (Abd El-Mageed et al., 2020; Jinger et al., 2020). Being able to increase the water content and root system in corn crop (Besharat et al., 2020).

More recent research has indicated benefits of Si in mitigating oxidative stress, which is high in plants under water deficit (Moro et al., 2018; Teixeira et al., 2021). To mitigate and repair this damage, plants developed a complex Si-mediated antioxidant system responsible for increasing the plant content of enzymatic antioxidants by increasing the activity of enzymes such as catalase and superoxide, dismutase (SOD), and in addition decreasing activity of malondialdehyde (MDA) (Abdelaal et al., 2020; de Oliveira et al., 2019). Another strategy of the plant is to increase the content of non-enzymatic antioxidant compounds, such as carotenoids, tocopherols, ascorbate, and glutathione (Kim et al., 2017) as well as other promising phenols found in rice plants (Qureshi et al., 2018).

The phenolic compounds are a vast class of secondary metabolites performing several roles for the defense and survival of plants (Tsimogiannis & Oreopoulou, 2019). These antioxidant compounds eliminate ROS from cells, forming an important first line of defense to deal with stress in different species (Das & Roychoudhury, 2014), but studies on *P. maximum* are limited.

The antioxidant benefit of Si can favor nutritional gains, inducing another effect of Si, which is to ensure greater homeostasis in plants, maintaining an almost constant balance of nutrients, regardless of the changes that occur in the external environment, can also occur through the stoichiometric modification of C/N/Si, a fact that is not widely

considered in studies with plants under water restriction. There are reports indicating that Si has the ability to form hydrogen bonds with organic compounds, such as cell wall molecules (Schoelynck et al., 2010). A part of the C of the cell wall could be exchanged for Si, reducing the need or demand for structural compounds and the concentration of cellular C that is found in the leaves of *Saccharum officinarum* (Frazão et al., 2020), *Chenopodium quinoa* (Lata-Tenesaca et al., 2021), and *Arachis hypogaea* (Fernandes et al., 2021). Consequently, there would be a change in the stoichiometry of C with other elements, especially those that have a structural biological function (Rocha et al., 2021; Oliveira Filho et al., 2021), that is, those that compose the structure of the organic compounds of the plant, particularly N, which is the nutrient most required by *Poaceae*. The benefit of Si in stoichiometric ratios such as C/N may allow plants to have a strategy to govern the balance of nutrients against possible nutritional disorders in the culture medium, as it is known that Si attenuates N deficiency (Silva et al., 2021).

This increase in Si content and decrease in C in the cell wall would save energy for plants because the energy cost for including Si in the carbon skeleton is low in comparison to the assimilation and insertion of a new C in this structure (Calero Hurtado et al., 2020; Raven, 1983). This energy saving promoted by Si may be important especially in plants under water restriction that normally have an energy deficit (Bechtold & Field, 2018). This can increase the nutritional efficiency of using C, that is, plants' capacity to convert the assimilated C into biomass, but this has not yet been addressed for forage plants.

To identify novel mechanisms governing the mitigation of water deficit in forages by silicon, we hypothesized that silicon (1) increases antioxidant defense by the production of phenolic compounds and (2) favors the physiological aspects associated with the stoichiometric modification of C/N and C/Si, which can increase nutritional efficiency for the use of C with a direct consequence in the growth of *P. maximum*, regardless of cultivar.

In order to test the hypothesis, this research was carried out with the objective of evaluating whether the supply of Si via fertigation improves the antioxidant defense system and modifies the C:N:Si stoichiometry and the growth of two cultivars of *P.*

maximum grown under two levels of soil humidity (70 and 40% of the soil water retention capacity).

2 Material and Methods

2.1 Plant Material and Growth Conditions

Two experiments were carried out at the São Paulo State University, in Jaboticabal, Brazil, in 2020, with *Panicum maximum* cultivars Massai (experiment 1) and BRS Zuri (experiment 2).

Seeds of *Panicum maximum* were obtained from the Brazilian Agricultural Research Corporation of the Ministry of Agriculture, Livestock and Food Supply, Brazil (registered and protected by the Ministry of Agriculture, Livestock and Supply). This research was not conducted with endangered species and was conducted in accordance with the Declaration of IUCN Policy on Research Involving Endangered Species.

Meteorological data (air temperature and relative humidity) were collected daily using a thermohygrometer (Fig. 1).

2.2 Experimental Design and Treatments

In both experiments, the treatments were arranged in a 2 × 2 factorial scheme, with the application of Si via fertigation (root) and the treatment without application of Si, combined with two water regimes at 70 and 40% (water stress condition) of the soil water retention capacity, arranged in randomized blocks with six repetitions. The experimental unit consisted of a 7 dm^3 vessel filled with 6 dm^3 of samples from an Entisol (Quartzipsamments) (USDA, 2014).

Chemical analysis of the soil for fertility purposes was carried out according to the method described by Raij et al. (2001), with the following results: pH $CaCl_2$ = 4.3, O.M. (organic matter) = 9 g dm^{-3}, P in resin extractor = 2, S = 18 mg dm^{-3}, Ca = 3, Mg = 1, K = 0.3, Al = 0, H + Al = 16, SB (sum of bases) = 4, T (cation exchange capacity) = 20 $mmol_c$ dm^{-3}, and V (base saturation) = 21%. Si content (3.0 mg dm^{-3}) was determined using the method described by Korndörfer (2004). Soil granulometry was determined using the method described by Gee and Or (2018), with the following results: 540 g kg^{-1} of sand, 380 g kg^{-1} of clay, and 90 g kg^{-1} of silt.

Limestone was applied (total neutralization power: 125%, CaO: 48%, MgO: 16%) to the soil as recommended by Raij et al, (2001) aiming to increase base saturation to 60%, which corresponded to the dose of 0.285 g dm^3 of soil being properly mixed in the soil volume. Thirty days after limestone application, fertilization was carried out by applying 150 mg dm^{-3} of N, P, and K, in the form of ammonium sulfate, triple superphosphate, and potassium chloride, respectively, and 5 mg dm^{-3} of Zn in the form of zinc sulfate, all mixed to the volume of the soil.

Then, the forage was sown, and after seedling emergence, thinning was carried out keeping four plants per pot. Five days afterwards, the forage was cut at a height of 10 cm to standardize the plants and induce tillering, and 10 days later, the treatments were applied.

Si was applied via fertigation in the form of sodium silicate and potassium stabilized with sorbitol (113.4 g L^{-1} of Si and 18.9 g L^{-1} of K_2O), at a concentration of 2.5 mmol L^{-1}, as found by Birchall (1995), simulating a 5-mm irrigation depth every 5 days, following the study by Teixeira et al. (2020) as a reference. The beneficial element was applied for a period of 50 days right after the uniform cut of forages.

Soil water availability levels were determined on the basis of the microporosity values obtained by the tension table method with a 60-cm high water column, considering the soil density determined by the ratio of dry soil mass in an oven at 110 °C, for 24 h, to the volume of undisturbed soil sample (EMBRAPA, 2017). Total microporosity was considered to be equivalent to 100% of the soil water retention capacity; however, the water condition taken into consideration was 70% of this value as it corresponds to the demand for most crops. The water deficit condition was achieved by maintaining the water level at 40% of the soil water retention capacity, determined on study of Rocha et al. (2021). Previous studies suggest that the best benefit of Si occurs in plants with a water level close to 40% and at a water level close to 70%; it is sufficient to achieve maximum forage dry mass production. Water availability was controlled daily by the method of weighing the vessels, based on the replacement of evapotranspirated water.

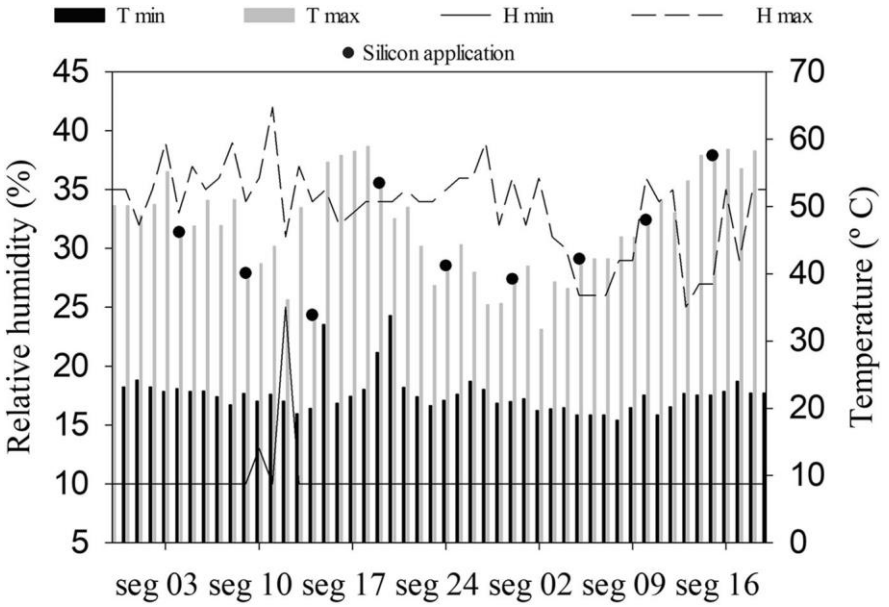

Fig. 1 Maximum and minimum air temperature and humidity of the greenhouse and silicon application during the experimental period. H min, minimum humidity; H max, maximum humidity; T min, minimum temperature; T max, maximum temperature

2.3 Performed Analyses

2.3.1 Phenolic Compounds

At 45 days after the application of the treatments, biological evaluations were carried out. Leaf + 1 (first fully developed leaf) was collected from a tiller chosen at random to determine the content of total phenolic compounds, following the method described by Singleton and Rossi (1965).

2.3.2 Quantum Efficiency of PSII (Fv/Fm)

Measurements of quantum yield of PSII were carried out between 7 and 9 h, to ensure the adaptation of the leaf to light, which was measured on the first fully developed leaf of each plant. Maximum variable fluorescence (Fv:Fm), which would be the maximum quantum efficiency of PSII, was determined using a portable fluorometer (Opti-sciences – Os30P) (H. K. Lichtenthaler et al., 2005).

2.3.3 Quantification of Chlorophyll

For the analysis of the pigments, two 6-mg leaf discs were collected from the middle third of the leaf blade of the first fully developed leaf, using as a solvent a

solution containing 80% acetone, for the extraction of photosynthetic pigments, and 20% deionized water for the extraction of water-soluble pigments, and left to rest in the Eppendorf until the complete extraction of the pigments. According to the methodology proposed by Lichtenthaler (1987) with readings at 663 nm for chlorophyll *a* (Chl *a*), 647 nm for chlorophyll *b* (Chl *b*), performed on a Beckman DU 640 spectrophotometer, the levels being defined based on fresh mass.

2.3.4 Electrolyte Leakage Index

Damage to cell membrane integrity was assessed using the method of determining the electrolyte leakage index (EL), proposed by Dionisio-Sese and Tobita (1998). Ten leaf discs (129 mm^2) were collected from the first fully developed leaf and submerged in a beaker containing 20 ml of deionized water, at room temperature for 2 h. After this period, a reading of the electrical conductivity of the solution (EC1) was performed with the aid of a bench conductivity meter (TDS-3 digital meter). Then, the samples were heated in an autoclave at 121 °C for 20 min, and after cooling, a new final electrical conductivity reading (EC2) was performed. Electrolyte leakage was determined considering the following formula: EC1:EC2 × 100.

2.3.5 Relative Water Content

Leaf water potential (Ψw) was determined in the middle third of the leaf blade of the first fully developed leaf with the aid of a Scholander pressure chamber (Soil Moisture Equipment, USA). The pressure was applied until exudation occurred from the cut made in the leaf petiole, and the measurements were evaluated between 6 and 9 am (Turner, 1981).

Relative water content in the leaf (RWC) was determined by collecting three leaf discs with approximately 129 mm^2 of the first fully developed leaf. They were immediately weighed to measure fresh tissue mass (Pf). After that, the samples were rehydrated in deionized water for 6 h to determine turgid mass (Pst), using paper towels to extract the excess water. Dry mass (Ps) was determined after the discs remained in a forced air circulation oven at 80 °C for 24 h. Relative water content values were determined by the equation proposed by Barrs and Weatherley (1962): [(Pf – Ps):(Pst − Ps)] × 100.

2.3.6 Plant Height, Number of Tillers, and Leaf Area

Plant height was measured considering the length from the base to the apex of the last leaf, and the number of tillers was counted. Leaf area was measured using a LICOR device, model 3100.

2.3.7 Dry Matter Production

The plants were washed in running water, detergent solution (0.1% v:v), HCl solution (0.3% v:v), and deionized water. The plant material was dried in a forced air circulation oven (65 ± 5 °C) to constant mass, and plant dry mass (aerial part) was determined.

2.3.8 Silicon Analysis

Si content in the shoot was determined by extracting the element according to the methodology described by Kraska and Breitenbeck (2010), and Si reading was performed by a spectrophotometer at 410 nm as indicated by Korndörfer (2004). Based on Si content and dry mass, Si accumulation in the shoot of the plants was calculated.

2.3.9 Carbon Analysis

Total C concentration in the shoot was determined by dry combustion (1000 °C) using an elemental analyzer (LECO Truspec CHNS) calibrated with the LECO 502–278 wheat standard (C = 45.00% and N = 2.68%). The accumulation of total C was calculated as a result of the total concentration of C multiplied by the dry mass (DW), and the results expressed as g of C, adapted as described by Rosales et al. (2020); thus, the carbon use efficiency (CUE) was calculated from the equation: $(DW)^2$ / accumulation of C in the plant (g per pot) (Siddiqi & Glass, 1981). The C/Si ratio was calculated as C content (g kg^{-1} of C)/Si content (g kg^{-1} of Si).

2.3.10 Nitrogen Analysis

The total nitrogen (N) content was determined from acid digestion, according to the method described by Bataglia et al. (1983).

2.3.11 Statistical Analysis

The data were submitted to a bidirectional analysis of variance by the F test ($p \leq 0.05$) after verifying the homogeneity of the variances (Shapiro–Wilk W test). The means of the procedures with water restriction (without and with Si) were compared with the adequate soil moisture condition (without and with Si) by the Tukey test, with a 5% probability, using the SAS® statistical software (SAS, 2008).

3 Results

Regardless of Si application, water deficiency reduced Si accumulation by 38% in the Massai cultivar, and no changes were found for the BRS Zuri. Si supply via fertigation increased its accumulation in the two forages under water deficit and only in BRZ Zuri under adequate soil moisture condition (Fig. 2a, d).

The water deficit in the absence of Si reduced the C content only in BRS Zuri (Fig. 2b, e) but increased the N content in both forages (Fig. 2c, f). The application of Si in fertigation reduced the C content in plants with water deficit in the BRS Zuri cultivar and for the two water regimes and in the Massai cultivar (Fig. 2b, e) and decreased the N content in both cultivars in the two water regimes (Fig. 2c, f).

The water deficit without the application of Si decreased the relative water content (Fig. 3a, c) and decreased the Ψw in the two cultivars (Fig. 3b, d). The Si solution applied via Si fertigation increased the relative amount of water of the two forages with water deficit and in adequate water condition for the BRS Zuri cultivar (Fig. 3a, c) and increased the Ψw in both cultivars in both water regimes (Fig. 3b, d).

The phenolic compound content of the plant was low in the absence of Si in both cultivars and in both water regimes (Fig. 4a, e), but under water deficit, the EL increased in both forages, except in an adequate condition of water availability in the cultivar Massai with Si application (Fig. 4b, f). The application of Si via fertigation promoted an increase in the levels of phenolic compounds in the two cultivars and in the two water regimes (Fig. 4a, e) and decreased the EL in both cultivars and in the study water regimes, except for the cultivar Massai cultivated without restriction water (Fig. 4b, f).

The water deficit without Si application decreased the total chlorophyll content (Chl a + b) (Fig. 4c, g) and the PSII quantum efficiency (Fv: Fm) in the two forages (Fig. 4d, h). The application of Si increased the total chlorophyll content in the two forages and in the two water regimes, except for the cultivar BRS Zuri without water restriction (Fig. 4c, g) and increased the quantum efficiency of PSII in the two forages under water restriction (Fig. 4d, H).

The water deficit in the absence or presence of Si decreased the C:N ratio in both cultivars, except for the Massai cultivar that did not receive Si (Fig. 5a, d) increased the C:S ratio in the Masai cultivar and decreased in the BRS Zuri cultivar (Fig. 5b, e). The application of Si increased the C:N ratio in both cultivars and in the two water regimes (Fig. 5a, d) and decreased the C:Si ratio in the two cultivars grown in the two water regimes (Fig. 5b, e).

Water deficit, regardless of Si, did not alter carbon use efficiency (CUE) in either cultivar, except for the Zuri cultivar that received Si. However, the application of Si increased carbon use efficiency in both cultivars and in both water regimes, except for BRS Zuri without water restriction (Fig. 5c, f).

Water deficit, regardless of silicon, decreased leaf area, 58% for Massai and 35% for BRS Zuri (Fig. 6a, e); height, 26% for Massai and 19% for BRS Zuri (Fig. 6b, f); tillers numbers, 24% for Massai and 22% for BRS Zuri (Fig. 6c, g); and dry mass, 32% for Massai and 28% for BRS Zuri (Fig. 6d, h). However, Si application increased leaf area, 30% in 70% WRC and 27% in 40% WRC for Massai and 14% in 70% WRC and 23% in 40% WRC for BRS Zuri; height, 3% in 70% WRC and 3% in 70% WRC and 24% in 40% WRC for Massai and 8% in 70% WRC and 21% in 40% WRC for BRS Zuri; and dry mass, 4% in 70% WRC and 12% in 40% WRC for Massai and 9% in 70% WRC and 10% in 40% WRC for BRS Zuri; therefore, the changes were found in the two cultivars in the two water regimes, except for the Massai cultivar without water restriction.

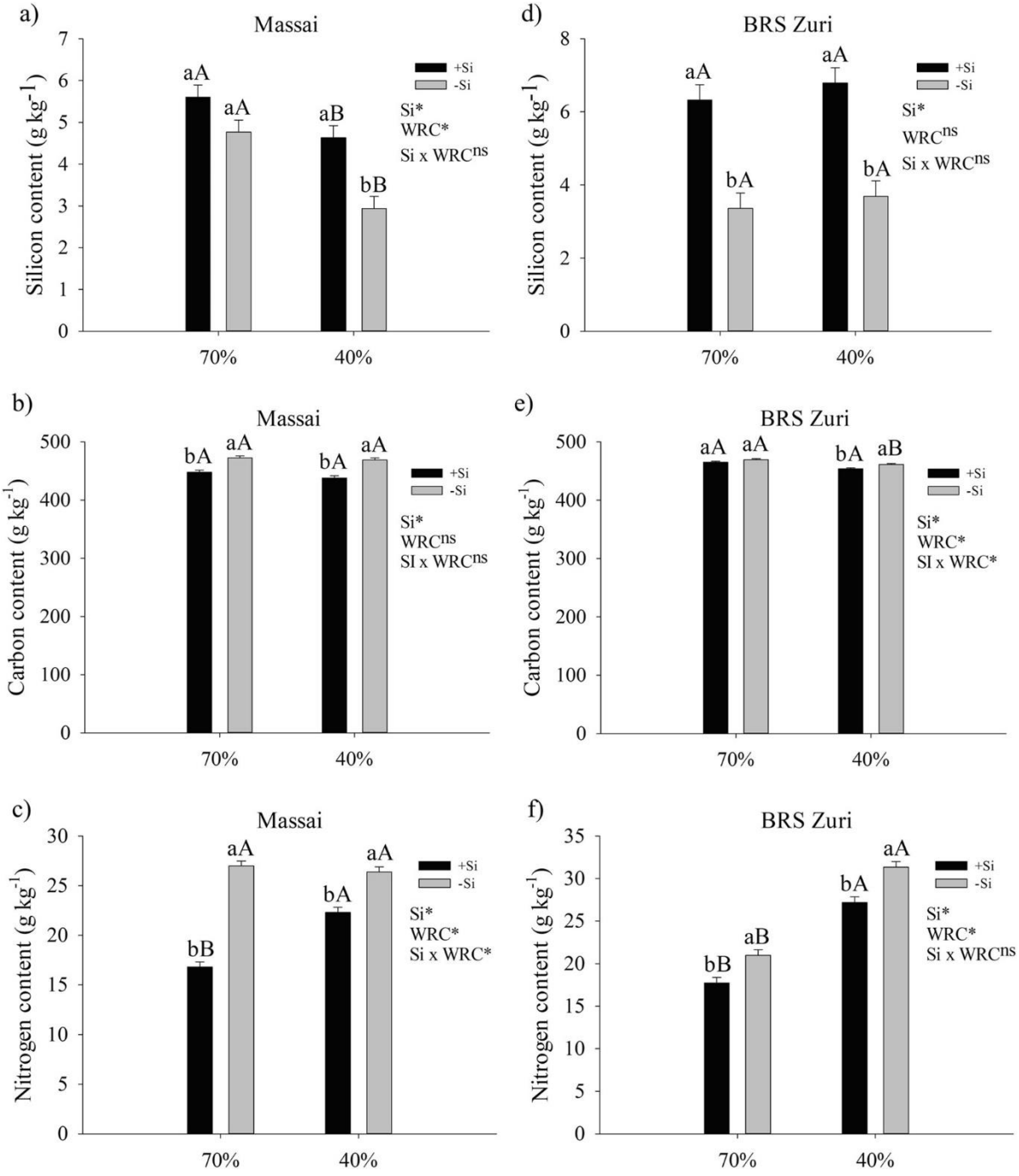

Fig. 2 Silicon content (**a**, **d**), carbon content (**b**, **e**), and nitrogen content (**c**, **f**) in the aerial part of forage plants cultivated in soil with different soil water retention capacities (WRC) (70 and 40%) absence (-Si) and in the presence of fertigation with silicon (+ Si). Single asterisk: significant at 5% probability. ns, not significant by the F test. Lowercase letters indicate differences in relation to Si within each water condition and uppercase letters in relation to WRC within each Si condition. The bars represent the standard error of the mean, n = 6

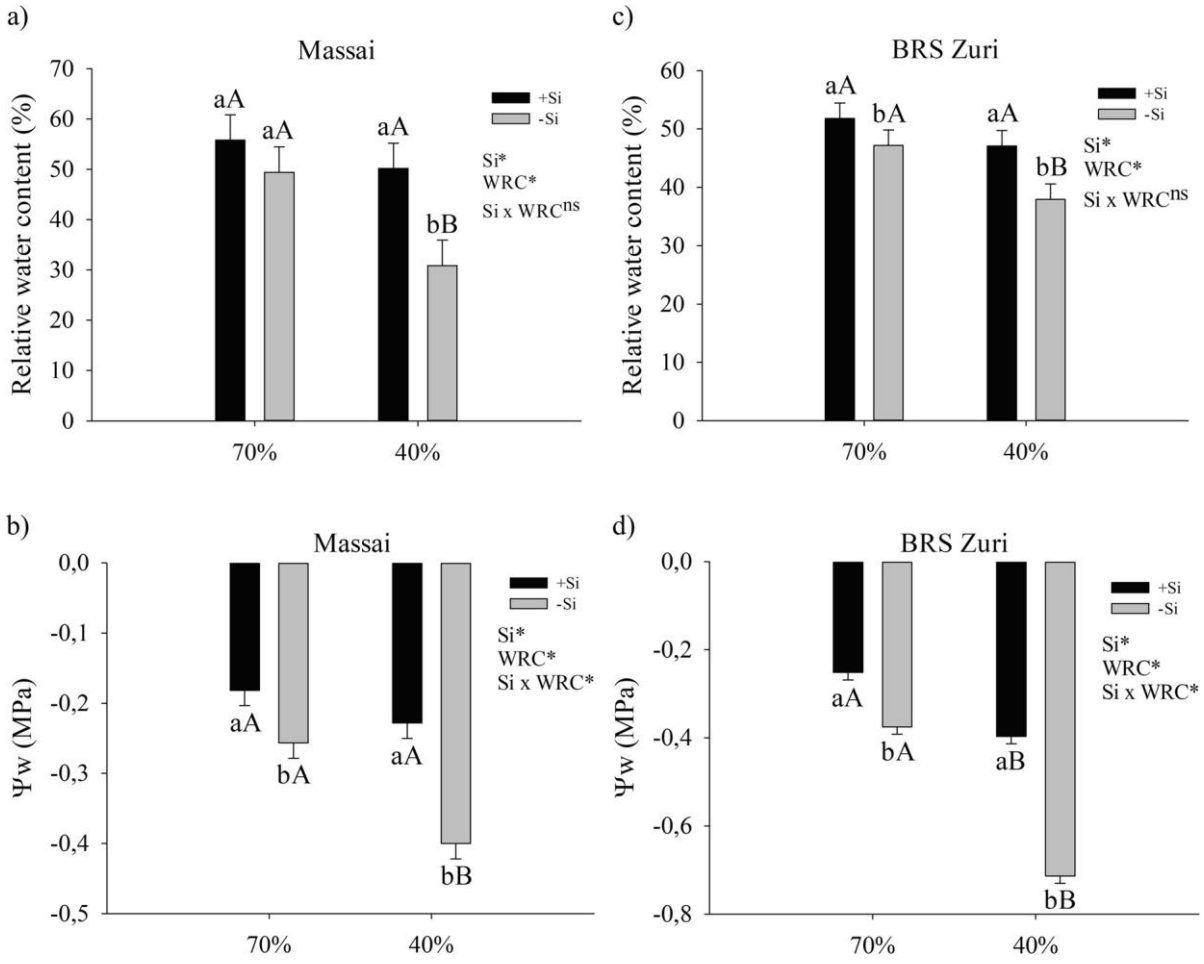

Fig. 3 Relative water content (**a**, **c**) and leaf water potential (Ψw) (**b**, **d**) of forage plants cultivated in soil with different soil water retention capacities (WRC) (70 and 40%) absence (-Si) and in the presence of fertigation with silicon (+ Si). Single asterisk: significant at 5% probability. ns, not significant by the F test. Lowercase letters indicate differences in relation to Si within each water condition and uppercase letters in relation to WRC within each Si condition. The bars represent the standard error of the mean, *n* = 6

4 Discussion

The plant's strategy to mitigate drought damage is to reduce water loss by decreasing the number of leaves and leaf area (Perlikowski et al., 2019). We found that the water deficit used to maintain 40% of the soil water retention capacity in the absence of Si impaired the growth of the two cultivars of *P. maximum* by decreasing leaf area, height, number of tillers, and dry mass (Fig. 6). This result indicates the sensitivity of these genotypes to drought. Our study showed that this loss from water deficit in the growth of the study forages is due to a decrease in the relative water

content and water potential of the leaf (Fig. 3). Therefore, the decrease in leaf water potential inhibits leaf expansion of plants (Boyer, 1970).

Plants under water deficit have dehydrated tissues, promoting the overproduction of reactive oxygen species (ROS) (Borjas-Ventura et al., 2020) which induce lipid peroxidation in membranes (Borjas-Ventura et al., 2018) and increase the efflux of electrolytes to apparent cell free space. This effect of water deficit in the absence of Si was very clear in this study, given the high level of extravasation of cellular electrolytes in the two cultivars of *P. maximum* (Fig. 4b, f). This result reinforces the occurrence of oxidative stress and, consequently, the degradation of total chlorophyll in both forages grown under water restriction (Fig. 4c, g).

In this context, the increase in oxidative stress caused by water deficit decrease the potential quantum efficiency of PSII (Fv:Fm) and the inactivation of the electron transport chain that will form ATP and NADPH (Krause & Weis, 1991), thus decreasing photosynthesis efficiency (Ganieva et al., 1998). Therefore, this damage resulting from water deficit in the Fv:Fm ratio is well documented in forages (Fariaszewska et al., 2020), a fact that has also been found in the present work for the two cultivars under water restriction without addition of Si (Fig. 4d, h).

In stressful conditions, plants maintain a balance between the metabolism of C and N with physiological processes (Calero Hurtado et al., 2020). Thus, the stoichiometric analysis of C and N can be useful to assess the variation of these nutrients in plant tissues under abiotic stresses, notably water deficit (Wang et al., 2019). We evidenced that stoichiometric homeostasis varies with cultivar, because in Masai, there was a mechanism to maintain C and N homeostasis even when the cultivar was under water deficit, unlike cultivar BRS Zuri, whose homeostasis was disturbed when the C/N ratio was decreased, probably owing to the decrease in C in this cultivar.

In our study, we showed that the two forages, even when under water deficit, are considered to be Si accumulators, given the high foliar content of this element in these plants, owing to the presence of efficient transporters in the membranes that favored the absorption process, which was optimized by the method of application via fertigation. Therefore, for the first time, it has been reported that the way of supplying Si using a soluble source and applying it via fertigation at a concentration of 2.5 mmol

L^{-1} supplied every 5 days during the growth of forages proved to be an efficient application method for the nutrition of these plants. This beneficial effect is due to the concentration of the element used (2.5 mmol L^{-1}), which did not induce polymerization that according to Birchall, (1995) occurs only in Si concentrations above 3 mmol L^{-1}.

The increase in Si in the plants, when affecting gas exchange, has promoted an increase in water content in different species such as sorghum (Hattori et al., 2005) and wheat (Ma et al., 2016). This fact was evidenced in our study, given the increase in water content and leaf water potential of the two forages under water restriction (Fig. 3). In addition, the best water status in the plant that received Si favors the stomatal osmoregulation capacity (Moro et al., 2018).

Maintaining the water status of plants that received Si under water restriction reduces oxidative stress (Biju et al., 2017; Hasanuzzaman et al., 2018) and cell membrane degradation (Ashfaque et al., 2017) as there was decreased cell electrolyte leakage in the two forages (Fig. 4b, f) and also in sugar cane (Teixeira et al., 2020). This can be explained by the effect of Si in increasing the content of the non-enzymatic antioxidant compound phenols in the two cultivars under water deficit (Fig. 4a, e). The increase in nonenzymatic antioxidants promoted by Si is involved in the attenuation of stress by removing ROS indirectly through the regeneration of the two main redox molecules (ascorbate and glutathione) in cells (Kim et al., 2017).

The antioxidant effect of phenolic compounds was described by Qureshi et al. (2018) for delaying senescence and cell death by regulating and eliminating ROS while maintaining the plant's physiological process. However, this effect of Si on the increase of phenolic compounds occurred only in some non-forage species under water deficiency, such as peanuts (Arachis hypogaea L.) (Aninbon et al., 2016), olive trees (Olea europaea L.) (Petridis et al., 2012), and tobacco plants (Nicotiana tabacum) (Silva et al., 2018).

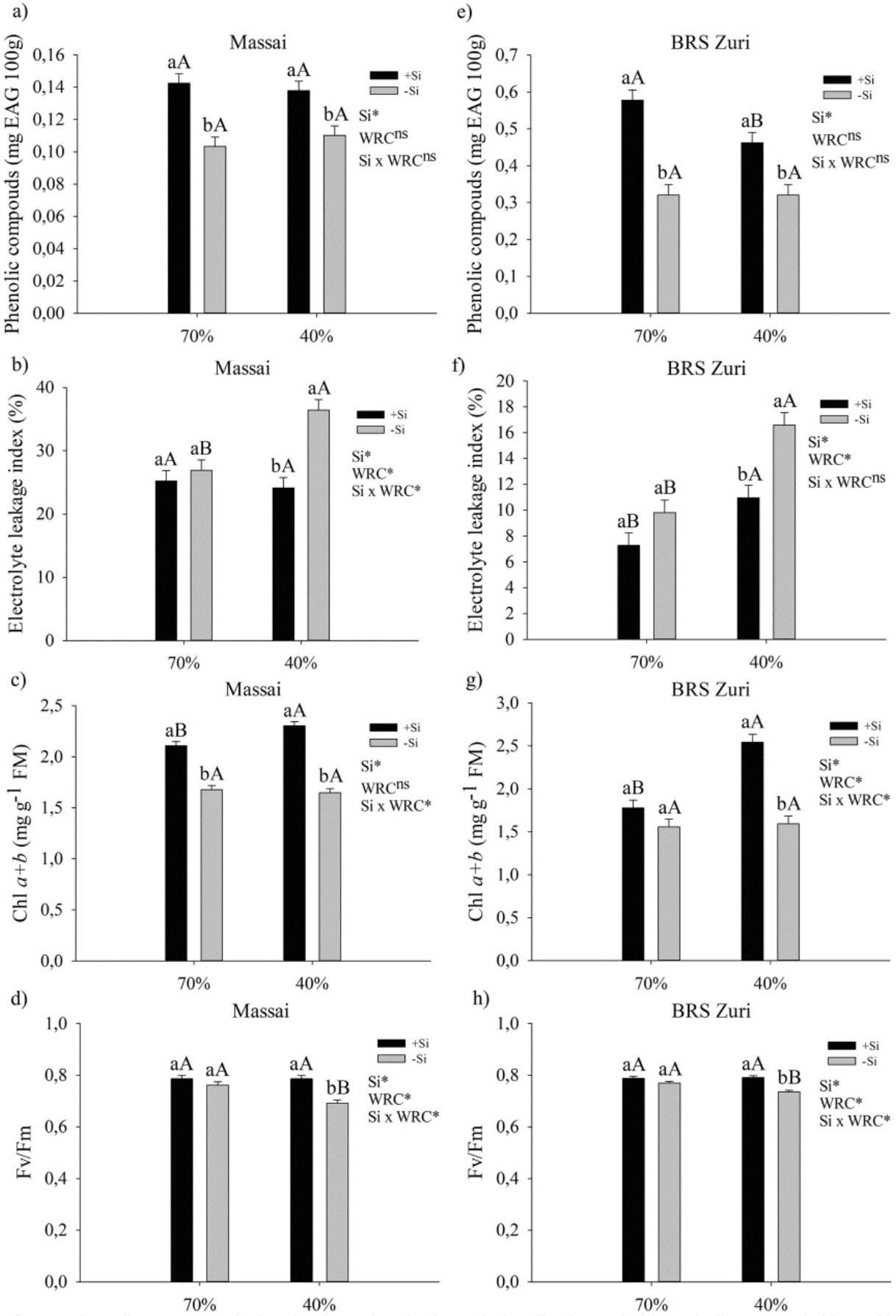

Fig. 4 Phenolic compounds (**a**, **e**), electrolyte leakage index (**b**, **f**), total chlorophyll content (Chl *a* + *b*)

(**c**, **g**), and quantum efficiency of photosystem II (Fv/Fm) (**d**, **h**) of forage plants grown in soil with different soil water retention capacities (WRC) (70 and 40%) absence (-Si) and in the presence of fertigation with silicon (+ Si). Single asterisk: significant at 5% probability. ns, not significant by the F test. Lowercase letters indicate differences in relation to Si within each water condition and uppercase letters in relation to WRC within each Si condition. The bars represent the standard error of the mean, *n* = 6

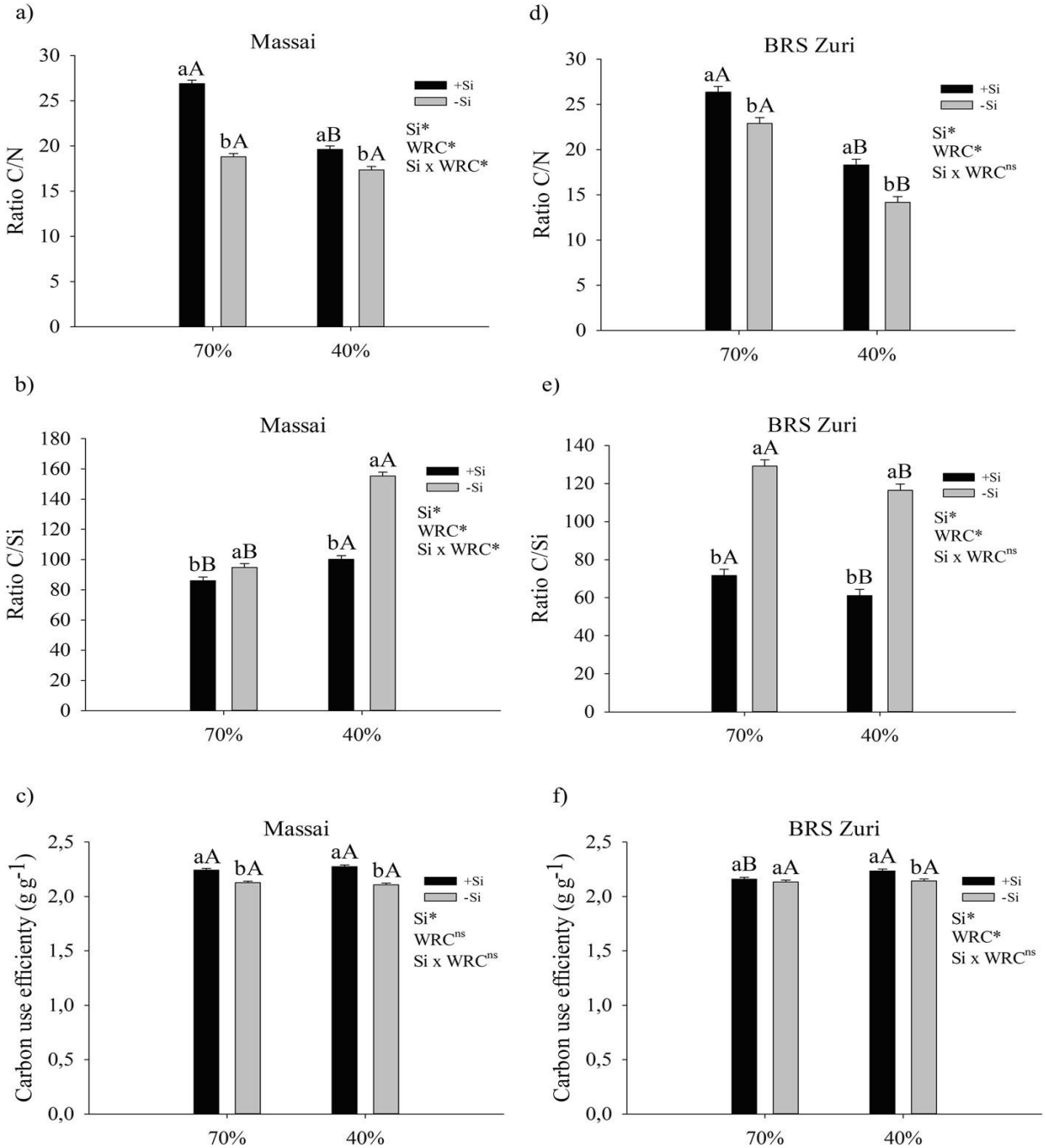

Fig. 5 Ratio C/N (**a**, **d**), ratio C/Si (**b**, **e**), and carbon use efficiency (**c**, **f**) in the aerial part of forage plants cultivated in soil with different soil water retention capacities (WRC) (70 and 40%) %) absence (-Si) and in the presence of fertigation with silicon (+ Si). Single asterisk: significant at 5% probability. ns, not significant by the F test. Lowercase letters indicate differences in relation to Si within each water condition and uppercase letters in relation to WRC within each Si condition. The bars represent the standard error of the mean, *n* = 6

This antioxidant benefit of Si in the attenuation of water deficit was evidenced by the increase in total chlorophyll content in the two forages (Fig. 4c, g), a fact also reported in corn plants by Parveen et al. (2019). Since chlorophyll is sensitive to degradation by ROS (Bechtold & Field, 2018), it would act as a stress marker, reinforcing the importance of Si in increasing plants' antioxidant defense system (Borjas-Ventura et al., 2020) to ensure their physiological homeostasis even under water deficit.

Our study showed that there is not only one mechanism promoted by Si to mitigate water deficit in forages, as we also found a change in stoichiometric relationships, increasing the C/N ratio (Fig. 5a, d) and decreasing C/Si (Fig. 5b, e). It was clear that the change in these stoichiometric relationships was due to the fact that the use of Si in plants under water deficit promoted a decrease in the concentration of leaf C (Fig. 2b, e) in the two forages. This new stoichiometric homeostasis, promoted by the use of Si in the plant under water restriction, is noteworthy. According to Yan et al., (2018), such homeostasis is due to the fact that the decrease in C concentration occurred because of the substitution by Si restricted to the cell wall in its binding sites between its components, e.g., cellulose saving C, but which can be used in other metabolisms Therefore, this stoichiometric change showed that the use of Si effectively contributed to the greater homeostasis of its metabolism, as there was greater efficiency in the use of C in the two cultivars of forages grown under water deficit (Fig. 5c, f). This fact was also found only in the corn crop (Lavinsky et al., 2015), and, consequently, it favored the growth of the two forages (Fig. 6), which can be seen visually (Fig. 7).

In addition, the benefit of Si in stoichiometric homeostasis C/N and C/Si also occurred in forages without water deficit, but the improvement in growth of the cultivar BRS Zuri was more evident. This Si benefit in C stoichiometry was also found in sugarcane plants, favoring their growth even without water restriction (Frazão et al., 2020), although it can be influenced by the cultivar or cultivated species. Therefore, importantly, we found that the Si benefit is more evident in physiological aspects in plants under stress, although it can occur less intensely in plants without occurrence of stress, a fact also reported by Coskun et al. (2019).

Our finding allows us to accept the hypothesis indicating that the benefits of Si in mitigating water deficit are due to the action of two mechanisms that operate in an integrated manner, on the basis of an increase in antioxidant defense resulting from the synthesis of phenolic compounds. This favors physiological aspects associated with the modification of the stoichiometric analysis of C/N and C/Si, increasing the efficiency of C use and consequently its growth, regardless of forage cultivar. Therefore, this finding shows the effect of Si in inducing the mechanisms for greater tolerance to water restriction in Siaccumulating forages, but there is a need for further studies in other non-accumulating Si species, especially those cultivated in soils with low available Si content.

Our research proposes the use of fertigation with Si in forage plants of the group of *Poaceae* to favor their growth in crops, especially when under risk of water deficit. It may be possibly applied on a global scale because, according to Tenikecier and Ates (2018), this group of plants predominates in pasture lands cultivated in different regions of the world.

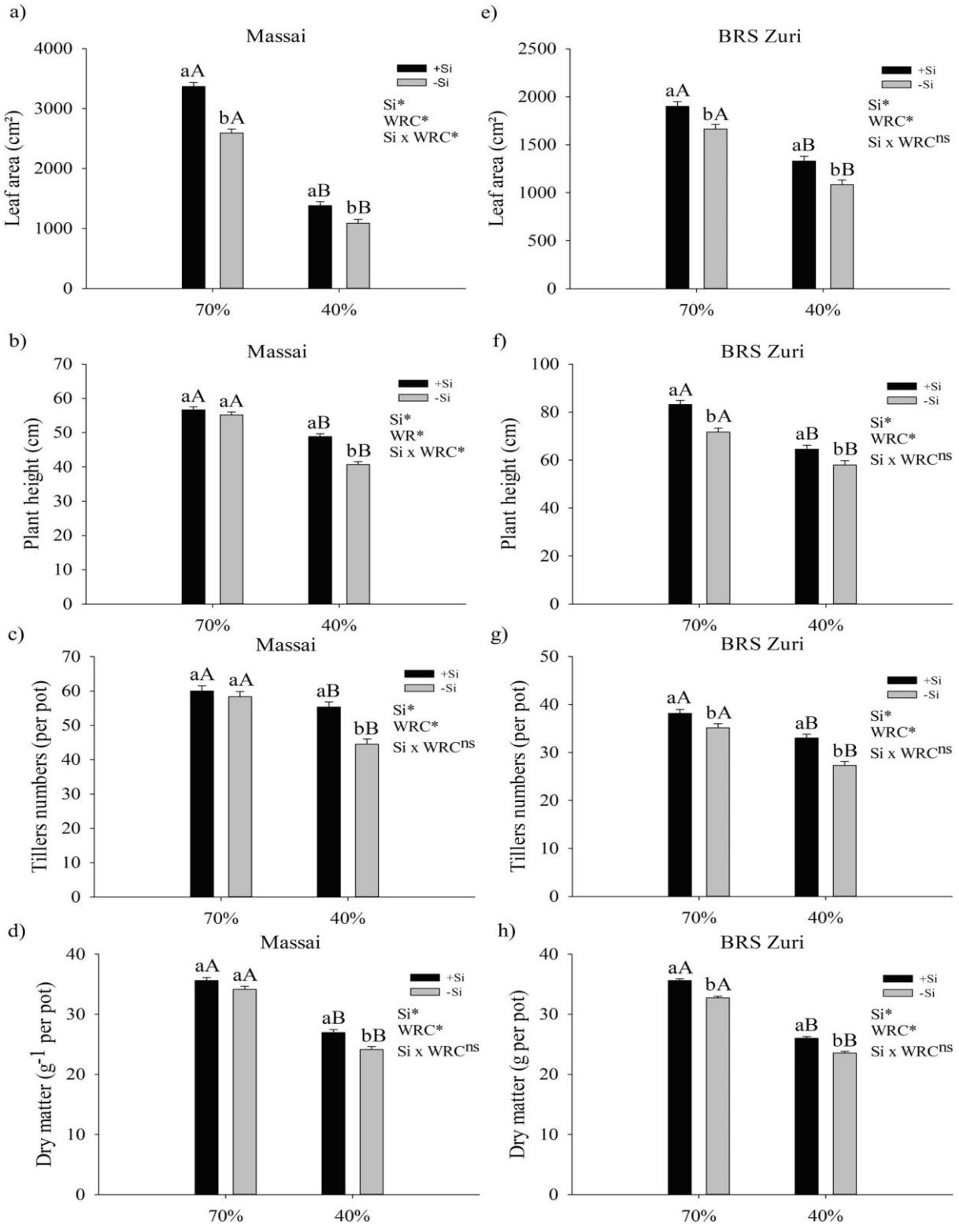

Fig. 6 Plant height (**a**, **e**), number of tillers (**b**, **f**), leaf area (**c**, **g**), and dry matter mass (**d**, **h**) of forage plants grown in soil with different soil water retention capacity (WRC) (70 and 40%) absence (-Si) and in the presence of fertigation with silicon (+ Si). ns, not significant by the F test. Lowercase letters indicate differences in relation to Si within each water condition and uppercase letters in relation to WRC within each Si condition. The bars represent the standard error of the mean, *n* = 6

Fig. 7 Figure of a forage plant in the condition of water deficit in the absence (-Si) (left pots) and in the presence of fertigation with silicon (+ Si) (right pots)

5 Conclusion

Water deficit causes biological damage in *P. maximum* cultivars Massai and BRS Zuri, but the supply of Si via fertigation has mitigated this stress by favoring the antioxidant defense system, associated with the stoichiometric alteration of C/N/Si, thus increasing efficiency in the use of C.

The study shows a promising strategy for *Poaceae* to use Si to mitigate water deficit, ensuring new physiological and nutritional homeostasis and more sustainable crops, an important fact for feeding herds that depend on pasture lands.

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Author Contribution

Juan Ricardo Rocha: Conceptualization, methodology, software, formal analysis, investigation, data curation, writing (original draft preparation), writing (review and editing), and visualization. Renato de Mello Prado: Term, methodology, validation, investigation, supervision, and project administration. Marisa de Cassia Piccolo: Resources and data curation.

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Ethics Approval Not applicable.

Consent to Participate Not applicable.

Consent for Publication Not applicable.

Conflict of Interest The authors declare no competing interests.

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CAPÍTULO 4 – Novos resultados sobre como o silício permite o cultivo de *Panicum maximum* spp. em solo submetido à deficiência hídrica

New outcomes on how silicon enables the cultivation of *Panicum maximum* in soil with water restriction[1]

Juan Ricardo Rocha[1*], Renato de Mello Prado[1] & Marisa de Cássia Piccolo[2]

Climate change increases the occurrence of droughts, decreasing the production of tropical forages through the induction of physiological stress. Si is expected to broaden the limit from physiological stress of forages grown under water restriction, which may come from an improvement in the stoichiometric homeostasis of Si with N and C, favoring physiological aspects. This study assessed whether Si supply via fertigation improves physiological aspects and the water content in the plant by means of an antioxidant defense system and changes in the C:N:Si stoichiometry during the regrowth of two cultivars of *Panicum maximum* grown under two soil water regimes (70 and 40% of the soil's water retention capacity). The forages studied are sensitive to water deficit without silicon supply. The application of Si via fertigation attenuated the water deficit, favoring plant growth by stabilizing the stoichiometric homeostasis C:N and C:Si, which are responsible for increasing the plant capacity of converting accumulated C in dry mass, favoring the water content of the plant tissue and the photosynthetic efficiency. This study highlights the importance of the physiological function of Si, and effects on the stoichiometry of C and N, which are neglected in most research on forages grown under water restriction.

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Introduction

Pasture (*Poaceae*) is the main food source for livestock in the tropical regions of the world[1,2] due to its high biomass production capacity and acceptability to a nimals[3], but it is sensitive to d rought[4]. Abiotic stresses such as drought[5] and the high temperature[6] threatens its biomass production capacity[7]. Water is, therefore, the main limiting factor for agricultural p roduction[8], and the impacts of climate change can aggravate s tress[9,10] promoting physiological disturbances in photosynthesis, loss of integrity of the membrane and generation of reactive oxygen species (ROS)[11,12]. It is noteworthy that stoichiometric homeostasis is useful to explain and predict the responses of different plants to stresses such as d rought[13].

Under drought, plants activate their defense system to minimize damage. This is even more evident in species that absorb silicon, that is, they have a high capacity to capture and transport Si to the l eaves[14,15]. Most studies so far on Si and water deficit in different species have discussed the effect of this element in reducing the transpiration rate, which increases the efficiency of water u se[16–18], the regulation of multiple defenses a ntioxidants[19], pigment levels[20] and photosynthetic p arameters[21,22]. Studies have suggested that Si reduces water stress due to less water loss by cuticular transpiration[23], but the cuticular transpiration rate is very low compared to stomatal transpiration[24], suggesting that Si also affects other mechanisms that need to be better investigated. Recent research has indicated that Si absorption improves its physiological aspects mainly by modifying elemental stoichiometry and could minimize damage from water deficit[25–27]. However, most studies on stoichiometric homeostasis focus mainly on N and P, studies on the Si are incipient[28,29].

These aspects are important because plants under water deficit have energy requirements for their metabolism, with a limitation in C O_2 assimilation rate accompanied by an increase in the activity of another sink of absorbed energy, for example, photorespiration[30]. In this scenario, nutrient uptake is also affected, impairing plant metabolism and disturbing the stoichiometric homeostasis of C, N, and Si in plant tissues under water deficit[31]. However, the use of Si can favor elementary stoichiometric homeostasis by interfering with the composition of the cell, especially the cell wall. Noteworthy, most of the Si absorbed (90%) by the plant is in the form of

amorphous silica, which is mostly used in Si-cellulose structures in the cell wall[32]. Complexation of Si with cell wall macromolecules is likely to occur by sugar stabilization, in a similar way to that of borate-mediated formose reaction[33]. Silicon thus binds, for example, to hemicellulose components via Si–OC bonds, forming an organosilicate compound[34].

Despite the lack of studies on Si, this nutrient requires less energy to be incorporated into leaf tissues than C. It can thus replace part of the C in cell wall organic compounds such as cellulose and hemicellulose, mainly due to its high permeability in lipid bilayers[35]. The effect of Si in improving C assimilation by plants is because a large part of it can be incorporated into photosynthetically active tissue cells at the expense of stabilizing c ompounds[36]. These energy benefits of Si favor plant metabolism, that is, the stoichiometric homeostasis of C and N. This in turn may increase C use efficiency and consequently C conversion into biomass, i.e., plant growth under water deficit.

According to literature reports, Si absorption varies depending on the genetic factor[37]; However, further investigations should clarify whether this benefit occurs in other pasture species such as *Panicum maximum*. This specie is widely cultivated worldwide, especially due to its regrowth capacity. Studies show that silicon reduces reducing oxidative stress by increasing the synthesis of antioxidant c ompounds[38,39], but these benefits may be due to the improvement of elementary stoichiometric (C:N) homeostasis. Therefore, further research is needed to prove this assumption.

In this context, the hypothesis should be tested whether Si can attenuate water deficit because plants can tolerate a higher level of physiological stress after stoichiometric homeostasis has been improved. This improvement would change the C:N and C:Si ratios, consequently affecting the capacity of plants to convert cumulative C into dry matter. These elements in turn would favor some physiological processes and the growth of two cultivars of *P. maximum*.

This information might help in the systematic assessment of the impacts of Si accumulation on the increase of the limit of physiological stress of plants due to its effect on the stoichiometry of C and N in pastures. Also, it provides may serve as a reference for the management of pastures under water restriction.

To test the hypothesis, this study assess whether Si supply via fertigation improves physiological aspects and water content in the plant by involving the antioxidant defense system. In addition, the study analyzes whether Si supply modifies the C:N:Si stoichiometry and the regrowth performance of two *P. maximum* cultivars grown under two soil water regimes (70 and 40% of soil water holding capacity).

Material and methods

Plant material and growth conditions.

Two trials were carried out at São Paulo State University (UNESP), in Jaboticabal, Brazil in the year 2020, concerning the second growth cycle or the regrowth of *P. maximum* cultivars Massai (experiment 1) and BRS Zuri (experiment 2).

Seeds of *P. maximum*, were obtained from the Brazilian Agricultural Research Corporation of the Ministry of Agriculture, Livestock and Food Supply, Brazil (registered and protected by the Ministry of Agriculture, Livestock and Supply—MAPA). This research was not conducted with endangered species and was the is accordance with the Declaration of IUCN Policy on Research Involving Endangered Species.

During the development of the study, meteorological data were collected daily, namely temperature (T) and relative air humidity (H) in the place of cultivation of the experiments, using a thermohygrometer (Fig. 1).

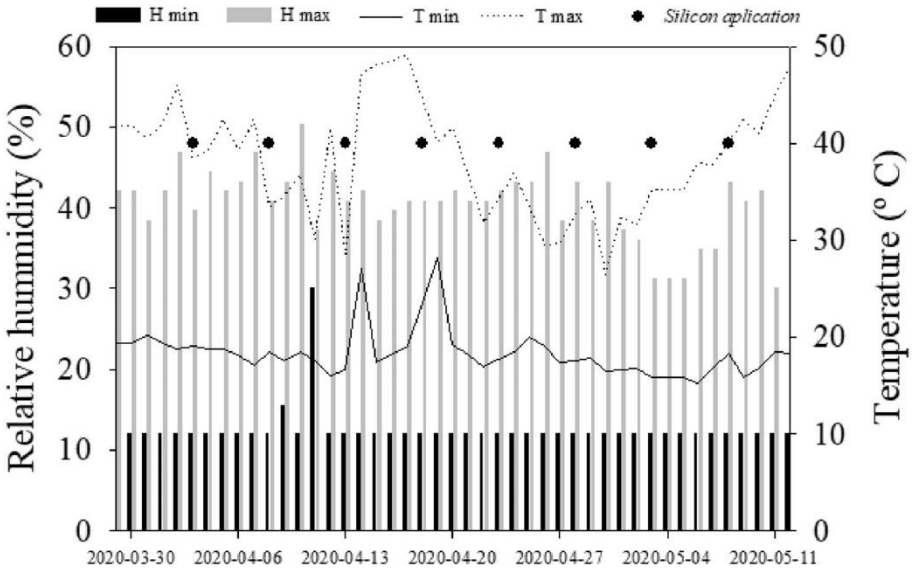

Figure 1. Maximum and minimum air temperature and humidity of the greenhouse and silicon application during the experimental period. *H min* minimum humidity, *H max* maximum humidity, *T min* minimum temperature, *T max* maximum temperature.

Experimental design and treatments.

In both experiments, the treatments were arranged in a 2 × 2 factorial scheme, with the application of Si via fertigation (root) and the control (without application of Si) combined with two water regimes at 70% and 40% of soil water retention capacity, arranged in randomized blocks with six repetitions. The experimental unit consisted of a 7 dm^3 vessel filled with 6 dm^3 of samples from an Entisol (Quartzipsamment).

Chemical analysis of the soil was carried out for fertility purposes according to the method described by Raij et al.[40]. The following results were found: pH C aCl_2 = 4.3; O.M. (organic matter) = 9 g dm^{-3}; P in resin extractor = 2 mg dm^{-3}; S = 18 mg dm^{-3}; Ca = 3 mmol dm^{-3}; Mg = 1 mmol dm^{-3}; K = 0.3 mmol dm^{-3}; Al = 0 mmol dm^{-3}; H + Al = 16 mmol dm^{-3}; SB (sum of bases) = 4; CEC (cation exchange capacity) = 20 $mmol_c$ dm^{-3}; V (base saturation) = 21%. The available Si content was determined (3.0 mg dm^{-3}) using the method described by Korndörfer[41]. Soil particle size distribution was determined using the method described by Gee and Or[42], and the following results were found: 540 g kg^{-1} of sand, 380 g kg^{-1} of clay and 90 g kg^{-1} of silt.

Thirty days later, lime was applied to the soil to correct acidity, and to increase base saturation (K + Ca + Mg/ K + Ca + Mg + H + Al) to 60%. Fertilization was carried out by applying 150 mg dm^{-3} of N, P and K, in the form of ammonium sulfate, triple superphosphate and potassium chloride, respectively, and 5 mg dm^{-3} of Zn in the form of zinc sulfate; they were all mixed to the volume of the soil.

The forage was first cut at 12 cm from the ground level at 45 days after uniform cut of the shoots. At 10 days after this cut, the second growth cycle of the forage started and the treatments were applied, using Si via fertigation and adapting the two study water availability regimes.

The source of Si was sodium silicate and potassium stabilized with sorbitol (113.4 g L^{-1} de Si and 18.9 g L^{-1} of K_2O), in the concentration of 2.5 mmol L^{-1}, as indicated by B irchall[43], simulating a 5 mm irrigation depth every five days. The study of Rocha et al.[25] on *Brachiaria* was used as a reference; Si was applied immediately after the first cycle of forage for a period of 40 days.

The levels of soil water availability were determined using the microporosity values found by the tension table method with a 60 cm high water column; this measurement was performed while considering soil density, which was determined by

the ratio of soil dry weight in the greenhouse at 110 °C, for 24 h, and the volume of undisturbed soil s ample[44]. Total microporosity was considered as equivalent to 100% of soil water retention capacity; however, the water condition was considered as 70% of this value, as it corresponds to the usual demand for most crops. The water deficit condition was achieved by maintaining the water level at 40% of the soil water retention capacity, determined on study of Rocha et al.[25]. Previous studies suggest that the best benefit of Si occurs in plants with a water level close to 40% and at a water level close to 70% it is sufficient to achieve maximum forage dry mass production. Water availability was controlled daily by the method of weighing the vessels after replacement of evapotranspiration water.

Performed analyses.

Phenolic compounds.

Biological evaluations were carried out at 45 days after the application of the treatments. Leaf + 1 (first fully developed leaf) was collected from a tiller chosen at random to determine the content of total phenolic compounds, following the method described by Singleton and Rossi[45].

Quantum efficiency of PSII (Fv/Fm).

To ensure the adaptation of the leaves to light, quantum yield of PSII was measured between 7 and 9 a.m., on the first fully developed leaf of each plant. Also, maximum variable fluorescence (Fv/Fm), which would be the maximum quantum efficiency of PSII, was determined using a portable fluorometer (Opti-sciences—Os30P)[46].

Quantification of chlorophyll.

Total chlorophyll index was determined using an indirect electronic chlorophyll meter (Clorofilog—Falker® brand). Reading was performed in the middle third of the leaf blade of the first fully developed leaf, which uses three light frequency ranges; thus, the optical measurement analyzes the absorption of light by the leaf by estimating the presence of chlorophyll.

Electrolyte leakage index.

Damage to cell membrane integrity was assessed using the method of determining the electrolyte leakage index (EL), proposed by Dionisio-Sese and T obita[47]. Ten leaf discs (129 mm^2) were collected from the first fully developed leaf and emerged in a beaker containing 20 ml of deionized water, at room temperature for 2 h. After this period, a reading of the electrical conductivity of the solution (EC1) was performed with the aid of a bench conductivity meter (TDS-3 digital meter). Then, the samples were subjected to heating in an autoclave at 121 °C for 20 min and, after cooling, a new final electrical conductivity reading (EC2) was performed. The electrolyte leakage index was determined considering the following formula: EC1/ EC2 × 100.

Relative water content.

Relative water content in the leaf (RWC) was determined by collecting three leaf discs (with approximately 129 mm^2) of the first fully developed leaf, which were immediately weighed to measure tissue fresh matter (Fm). After that, the samples were rehydrated in deionized water for 6 h, to determine turgid matter (Tm), using paper towels to extract the excess water. Dry matter (Dm) was calculated after the discs had remained in a forced air circulation oven at 80 °C for 24 h. The relative water content values were determined by the equation proposed by Barrs and Weatherley[48]: [(Fm − Dm)/(Tm − Dm)] × 100.

Plant height and number of tillers.

Plant height was measured considering the length from the base to the apex of the last leaf, and the number of tillers was counted.

Dry matter production.

The plants were washed in running water, detergent solution (0.1% v:v), HCl solution (0.3% v:v) and deionized water. The plant material was dried in a forced air circulation oven (65 ± 5 °C) to constant mass and plant dry mass weight was determined.

Silicon analysis.

The Si content in the shoot was measured by extracting the element according to the methodology described by Kraska and B reitenbeck[49], and Si reading was performed by a spectrophotometer at 410 nm, as indicated by Korndörfer[41]. Si accumulation the shoots of the plants was calculated based on Si content and dry matter.

Carbon analysis.

Total concentration of C in the shoots was determined by dry combustion (1000 °C), using an elemental analyzer (LECO Truspec CHNS) calibrated to the standard LECO 502–278 of wheat (C = 45.00% e N = 2.68%). Total N content was determined following the method of Bataglia et al.[50].

Carbon efficiency was calculated using the equation: (dry matter)^2/C accumulation in the plant[51].

Statistical analysis.

The collected data underwent analysis of variance by the F-test, and the averages were compared by Tukey's test, both at 1 and 5% probability, using the SAS® statistical software[52].

Results and discussion

Biological damage from water deficit in forages.

Reports on the tolerance to water deficit damage in the forage cultivars under study are scarce, especially in relation to N and C accumulation, Si effects, and physiological attributes.

Pastures grown under water restriction with and without silicon showed a decreased cumulative amount of the beneficial element. However, pastures grown with or without water restriction that had received silicon had an increase in the cumulative amount of silicon (Fig. 2a,d). Carbon content decreased in pastures that had received silicon, regardless of water availability (Fig. 2b,e). Water restriction increased N content in both treatments with and without Si for both forages. Silicon fertigation only

in plants with water restriction increased N content in cultivar Massai but decreased it in cultivar BRS Zuri (Fig. 2c,f).

The present study evidenced, especially with Si addition to the crop, that water deficit in the *P. maximum* pasture, regardless of cultivar, significantly impairs plant growth by changing homeostasis, i.e., decreasing the C:N ratio by reducing plant C content. This induces instability in the metabolism of the crop, especially in terms of physiological processes[31,53]. Thus, it was clear that water deficit aggravated physiological stress in the pastures due to an increase in electrolyte leakage, followed by a decrease in Fv/Fm. In other words, photosynthetic efficiency decreased in association with lower relative water content in the plant, which reduced the growth of both *P. maximum* cultivars.

Water deficit in both pastures with and without silicon supply decreased the C:N ratio, except in cultivar Massai, in which the omission of silicon increased this ratio. In an adequate condition of water availability, there was no difference between the absence and presence of Si in the pastures (Fig. 3a,d). Other authors report the same results for different forages, such as sugarcane[53]. Water deficit in the pastures did not change the C:Si ratio, regardless of Si. In pastures with or without water deficit, silicon fertigation decreased the C:Si ratio (Fig. 3b,e).

Although this species has a high capacity for dry matter accumulation because it has a high protein c ontent[54], it is sensitive to d rought[55]. Drought damage to plant growth, is due to the loss of stoichiometric stability of nutrients[56], which balances the mass of various elements between plants and their e nvironments[57].

A promising alternative to mitigate water deficit damage in the pasture is the use of Si. This element plays a vital role in the physiological, metabolic, and/or functional processes of p lants[58] when properly absorbed by the crop. The present study evidences the high capacity of the pastures under study to absorb Si when under water restriction. This is because *P. maximum* is a Si-accumulating species (leaf Si content > 10 g kg^{-1}), which means that these plants might have specific efficient carriers in the process of Si absorption (monosilicic acid)[37,59].

Biological benefits of silicon in mitigating water deficit in forage.

The high Si absorption by the pastures was important because it was enough to change C and N contents in the pastures under water deficit, and consequently the C:N ratio. However, Si absorption varied depending on the cultivar. In cultivar Massai, the absorption of this element decreased due to an increase in N content, while the opposite occurred in cultivar BRS Zuri. This may have occurred because cultivar Massai has higher N absorption efficiency than BRS Zuri. One cultivar or species may have greater absorption efficiency than another because it has a more efficient nitrogen transporter. In other words, it has better kinetic indexes, such as low KM and minimum concentration, which is governed by genetics[31].

The decrease in the C:Si ratio in plants grown under water restriction is a result of Si supply, which increased the absorption of this element and decreased C content in both pastures. Long et al.[28] also reported the importance of silicon in elementary stoichiometry in a study with banana trees under water deficit.

The benefit of stoichiometric homeostasis reflected the high metabolic efficiency of C, that is, Si significantly increased C use efficiency in *P. maximum* pastures under water restriction (Fig. 3b,e). Other authors report this effect in *Brachiaria* spp. pastures under drought[25] and in sugarcane plants without water s tress[60].

Carbon use efficiency (CUE) decreased in pastures with water restriction without silicon application. However, this variable increased in pastures where this element had been applied. In pastures under adequate water availability, silicon fertigation also increased CUE (Fig. 3c,f). Sugarcane plants under water deficit also showed decreased carbon use e fficiency[53]. This increase in C use efficiency (Fig. 3c,f) by Si may have occurred in both pastures because there was a clear decrease in C content in plants grown under water restriction (Fig. 2b,e).

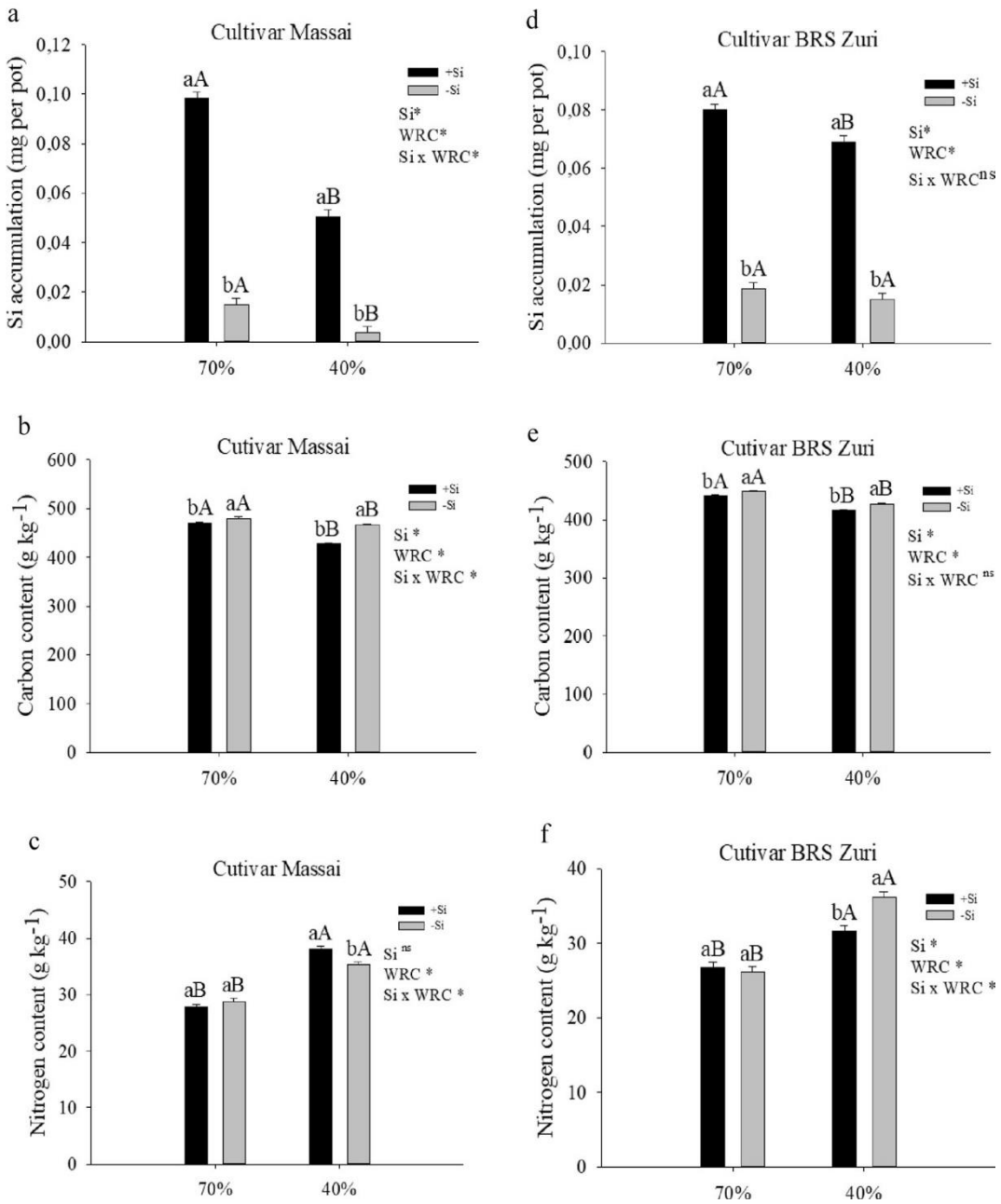

Figure 2. Silicon (Si) content (**a**, **d**), carbon (C) content (**b**, **e**) and nitrogen (N) content (**c**, **f**) in the aerial part of forage plants cultivated in soil with different soil water retention capacity (WRC) (70 and 40%) absence (− Si) and in the presence of silicon fertigation (+ Si). *Significant to 5% probability by the F test. Lowercase letters show differences in relation to Si and uppercase in relation to WRC. The bars represent the standard error of the mean, n = 6.

Hao et al.[29] reported similar results in native grass species, in which high Si content correlated with low levels of C. This decrease in C content may have occurred because when absorbing the beneficial element, the plant applies an “exchange strategy” to C, particularly in cell wall components such as cellulose. This is because the energy cost of including Si in the carbon chain is lower than that of including C itself[61]. This strategy thus improves the homeostasis of resistance to water deficiency in pastures. Reports indicate that the increase in Si in plant tissues may decrease lignin synthesis in the cell wall, which has a high energy c ost[62]; The plant uses a “low cost strategy” when occupying binding sites between cell wall components, providing similar structural resistance to that of l ignin[63].

These findings may support the promising role of Si in pasture management. This was evidenced from the effect of Si on elemental stoichiometry homeostasis in both forages grown under water restriction, which favored vital physiological processes by increasing the relative water content of the plant by approximately 14% (Fig. 4a,d). However, the effect of Si on the stoichiometric homeostasis of C might have induced energy savings in the plant, which is critical under water deficit conditions. Plants under water deficit have a limitation in the C O_2 assimilation rate accompanied by an increase in the activity of another sink of absorbed energy, for example, photorespiration[30]. Studies on other crops confirm this finding, indicating a benefit of Si on stoichiometric homeostasis in plants under water deficit. Some examples are the studies of Rocha et al.[25] on pasture, and Oliveira Filho et al.[26] and Teixeira et al.[64] on sugarcane.

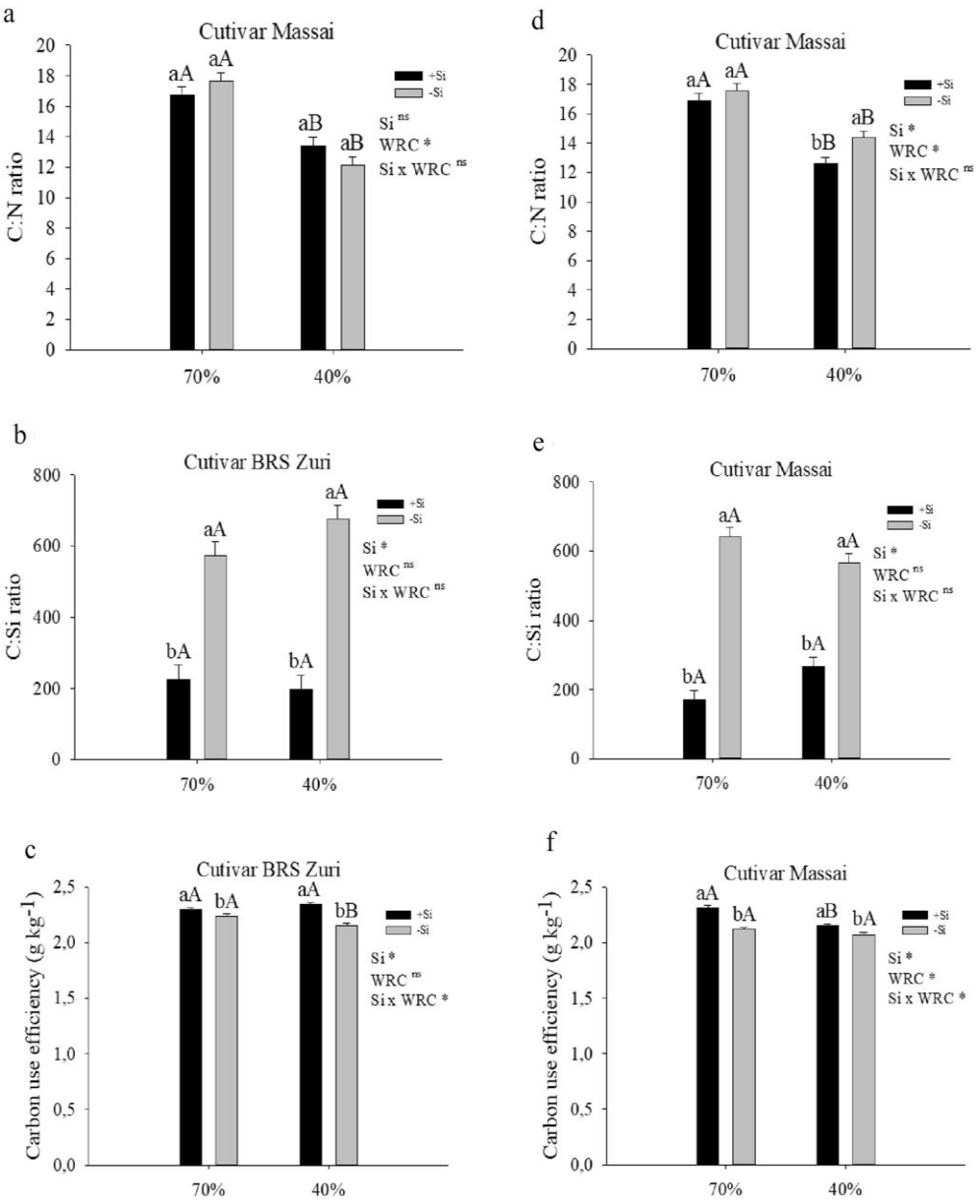

Figure 3. Ratio C:N (**a**, **d**), ratio C:Si (**b**, **e**) and carbon use efficiency (**c**, **f**) in the aerial part of forage plants cultivated in soil with different soil water retention capacities (WRC) (70 and 40%) %) absence (− Si) and in the presence of silicon fertigation (+ Si). *Significant at 5% probability. ns: not significant by the test F. Lowercase letters show differences in relation to Si and capitalization in relation to WRC. The bars represent the standard error of the mean, n = 6.

Pastures under water deficit without silicon fertigation showed decreased relative water content in the plants. On the other hand, silicon fertigation increased the relative water content of forages under water deficit

(Fig. 4a,d). Wang et al.[65] performed a review to elucidate the effect of silicon on plant water transport processes. The authors indicated that silica deposition on leaf cuticle and stomata decreases water loss from transpiration under water deficit stress. However, accumulating evidence suggest that silicon maintains leaf water content not by reducing water loss, but rather through osmotic adjustments, enhancing water transport and uptake. According to the same authors, enhancement of stem water transport efficiency by silicon is due to silica depositing in the cell wall of vessel tubes, avoiding collapse and embolism.

The physiological improvement promoted by Si in attenuating water deficit in pastures probably correlates with the reduction of oxidative stress. In this sense, cell electrolyte leakage decreased (Fig. 4b,e), from the increase of the non-enzymatic antioxidant compound in both forages (Fig. 4c,f) or from the activity of antioxidant enzymes[66]. This reduces reactive oxygen species, which are common in plants under water d eficit[67].

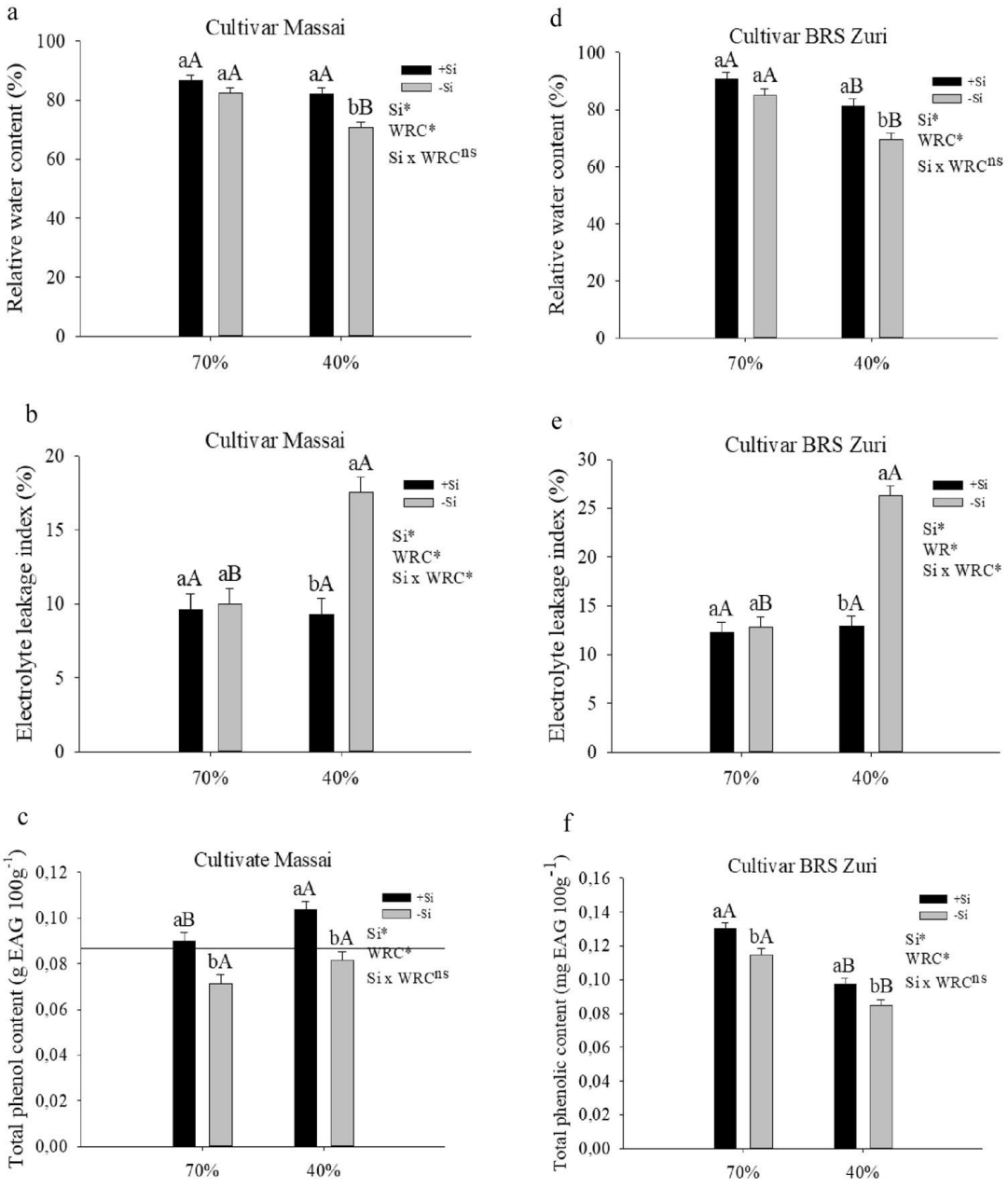

Figure 4. Relative water content (**a**, **d**), electrolyte leakage index (**b**, **e**) and Total phenolic content (**c**, **f**) of forage plants cultivated in soil with different soil water retention capacities (WRC) (70 and 40%) absence (− Si) and in the presence of silicon fertigation (+ Si). *Significant at 5% probability. ns: not significant by the test F. Lowercase letters show differences with respect to Si and uppercase in relation to WRC. The bars represent the standard error of the mean, n = 6.

Water deficiency affected the production of phenolic compounds depending on the cultivar. In Massai, this variable only increased with Si supply; in BRS Zuri, however, it decreased regardless of Si. Plants with silicon fertigation had increased phenolic compound content in pastures under both water availability conditions (Fig. 4c,f). Other authors have reported this effect of Si in increasing phenolic compounds in crops such as faba bean[68] and sugar b eet[69]. This supports the hypothesis that Si can attenuate the oxidative stress caused by water deficit by increasing the non-enzymatic antioxidant compound.

Exogenous application of Si protects the photosynthetic pigments from oxidative damage by reducing membrane lipid peroxidation. In peanut, this type of application either maintained or reduced H_2O_2[68]. Another effect of Si that demonstrates the attenuation of oxidative stress in pastures under water deficit was the increase in Fv/

Fm; in other words, it favored photosynthetic efficiency. In both pastures, the condition of water restriction without silicon supply decreased the quantum efficiency of PSII (Fv/Fm). However, the supply of silicon in pastures, regardless of water condition, increased the photochemical efficiency of PSII (Fig. 5a,c).

The protection of photosynthetic pigments by Si is also indicative of decreased oxidative stress[58]. The present study evidenced this situation, as the beneficial element increased the total chlorophyll index in both forages under water deficit (Fig. 5b,d). Wang et al.[69] reported that Si delays the degradation of chlorophyll–protein complexes, as the element alters the protein components of the thylakoid, thus optimizing the light collection and stability of PSI. Another benefit of Si would be an increase in osmoprotection as a result of the greater accumulation of metabolites, mainly sugars and sugar alcohols (talose, mannose, fructose, sucrose, cellobiose, trehalose, pinitol, and myo-inositol) and amino acids (glutamic acid, serine, histidine, threonine, tyrosine, valine, isoleucine, and leucine), as seen in peanut p lants[68].

Si benefit on forage productivity under water deficit.

Water restriction with or without silicon supply decreased the height of both pastures, and silicon application in both water regimes increased plant height (Fig. 6a,d). Water restriction with or without silicon supply decreased the number of tillers in both pastures, except for the cultivar BRS Zuri that had received Si. Silicon application

increased the number of tillers in both pastures in both water regimes, except for the cultivar Massai without water restriction (Fig. 6b,e). The dry weight of both pastures decreased under water deficit, regardless of silicon. However, the dry matter of the pastures increased after Si application, with or without water restriction (Fig. 6c,f).

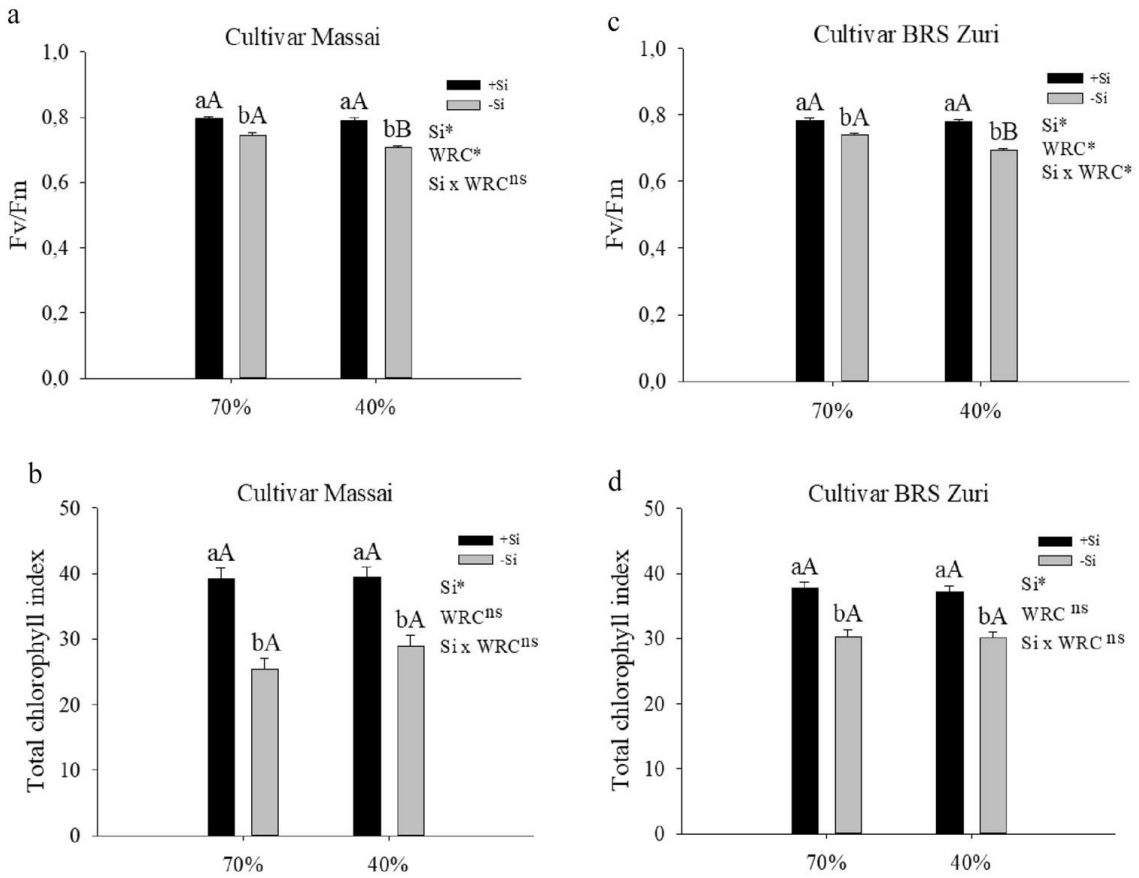

Figure 5. Quantum efficiency of photosystem II (Fv/Fm) (**a**, **c**) and total chlorophyll index (Chl a + b) (**b**, **d**) of forage plants grown in soil with different soil water retention capacities (WRC) (70 and 40%) absence (− Si) and in the presence of silicon fertigation (+ Si). *Significant at 5% probability. ns: not significant by the test F. Lowercase letters show differences in relation to Si and capitalization in relation to WRC. The bars represent the standard error of the mean, n = 6.

Thus, the mitigating effects of Si on the physiological processes of both pastures grown under water deficit were responsible for increasing forage growth by promoting an increase of 12% in plant height and 31% in the number of tillers, which is one of the main components of pasture production. This resulted in a 25% increase in dry matter accumulation in relation to the pasture without Si (Fig. 7). Other authors have also

reported the mitigating effect of Si on water deficit with a view to increasing plant growth in forage c rops[70] and other crops like wheat[71] and r ice[72].

The present study showed that the effect of Si on the attenuation of drought is not restricted only to physiological aspects involving increased plant water content and photosynthetic or biochemical efficiency. It also regulates elemental stoichiometric homeostasis as discussed above, confirming the biological strategy reported by Hao et al.[29] in other forage grasses. Our study indicates that the line of research on the relationship between water deficit and Si in elementary stoichiometry is promising and should advance towards a better understanding of the multiple effects of this beneficial element on the plant.

Animal production depends on the amount of biomass produced for grazing. The report of Habermann et al.[73] has indicated that climate changes, such as droughts, are threatening pasture production and have a negative impact on animal and protein production. To solve this, the present research serves as a reference for Si fertigation management during the growth of *P. maximum*. This management consists of a sustainable alternative to improve production with greater nutritional balance even under soil water restriction, favoring water use efficiency in cultivation (Fig. 8). Moreover, Si has long-term potential to reduce the occurrence of droughts, favoring the sustainability of ecosystems. This is because the use of the beneficial element in the soil does not produce greenhouse gases, without negative impacts on the production environment[74,75].

Future perspectives.

Peatlands and other terrestrial ecosystems represent large reservoirs and filters for Si, controlling Si transfer to the oceans. Land use change during the last 250 years has decreased soil Si availability by increasing export and decreasing Si storage due to higher erosion and a decrease in potentially Si-accumulating plants. Moreover, it has led to a twofold to threefold decrease of the base flow delivery of Si[76]. This raises concern over forage crops, reinforcing the need for silicate fertilization to explain the response of these species to the application of this element. Future perspectives would focuse on the benefits of Si in elementary stoichiometry and its relationship with physiological and biochemical aspects.

Studies should use, other forage species, especially dicotyledons sensitive to water deficit, which have different mechanisms for Si absorption. This will allow a better understanding of whether the Si mechanisms that attenuate drought in monocotyledons also occur in dicotyledons.

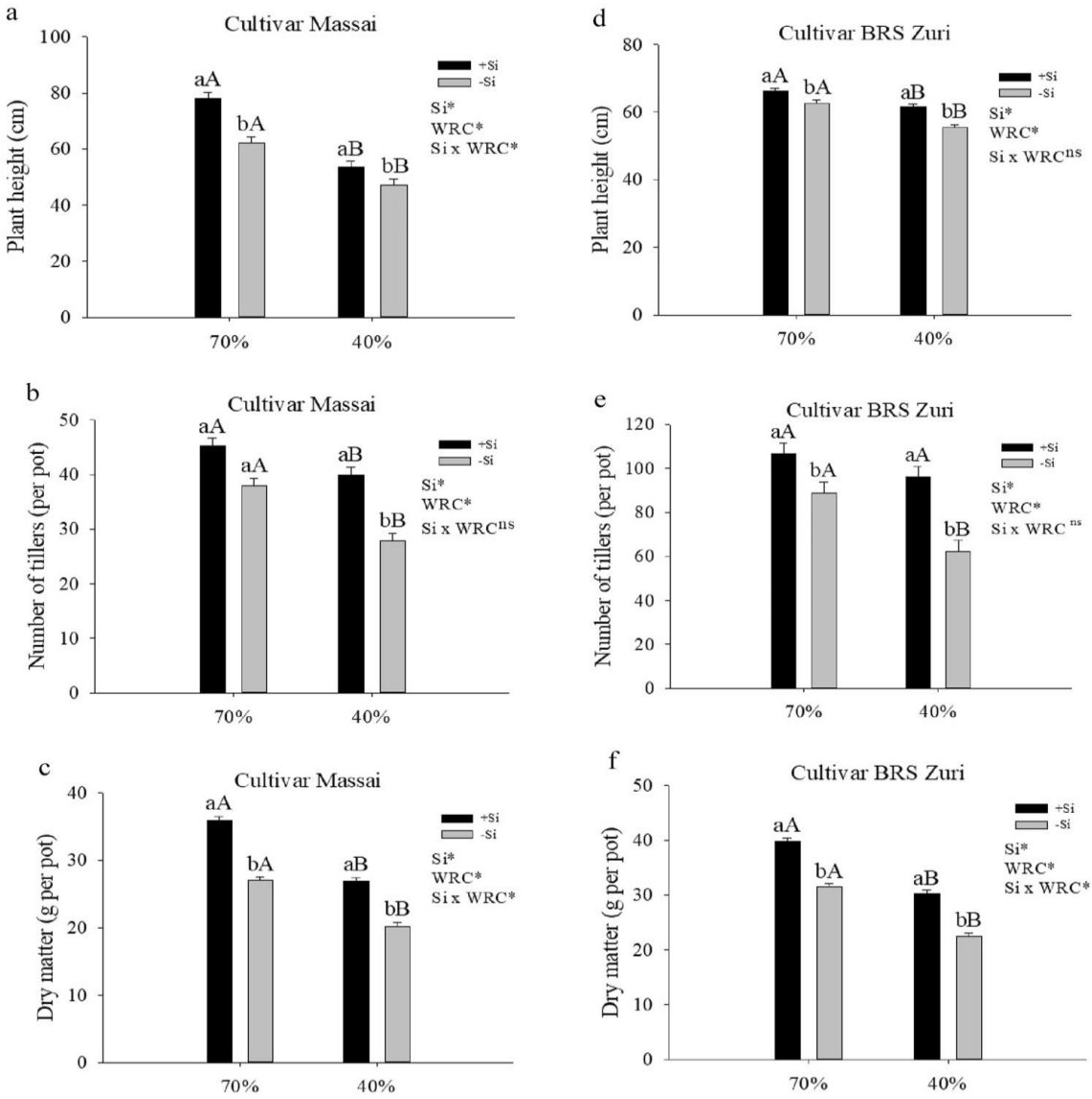

Figure 6. Plant height (**a**, **d**), number of tillers (**b**, **e**) and dry matter mass (**c**, **f**) of forage plants grown in soil with different soil water retention capacity (WRC) (70 and 40%) absence (− Si) and in the presence of silicon fertigation (+ Si). ns: not significant by the test F. Lowercase letters show differences in relation to Si and capitalization in relation to WRC. The bars represent the standard error of the mean, n = 6.

Conclusion

Panicum maximum cultivars Massai and BRS Zuri are sensitive to water deficit without silicon supply, which causes disturbance in stoichiometric homeostasis and consequently in physiological aspects of the crop.

Water deficit was attenuated by Si, which had been applied via fertigation to favor the growth of the two cultivars of *P. maximum*. It stabilized the stoichiometric homeostasis of C:N and C:Si, which is responsible for increasing the conversion capacity of cumulative C in the plant into dry matter, thus contributing to some physiological processes in the plant—for example, increasing both the water content of plant tissues and photosynthetic efficiency.

The present study highlights the importance of plant nutrition associated with the physiological function of Si but neglected its effects on the stoichiometry of C and N, addressed in most research on pastures usually grown under water restriction.

Figure 7. Figure of a forage plant in the condition of water deficit in the absence (− Si) and in the presence of silicon fertigation (+ Si) and a summary of its beneficial in the effects of the plant growth.

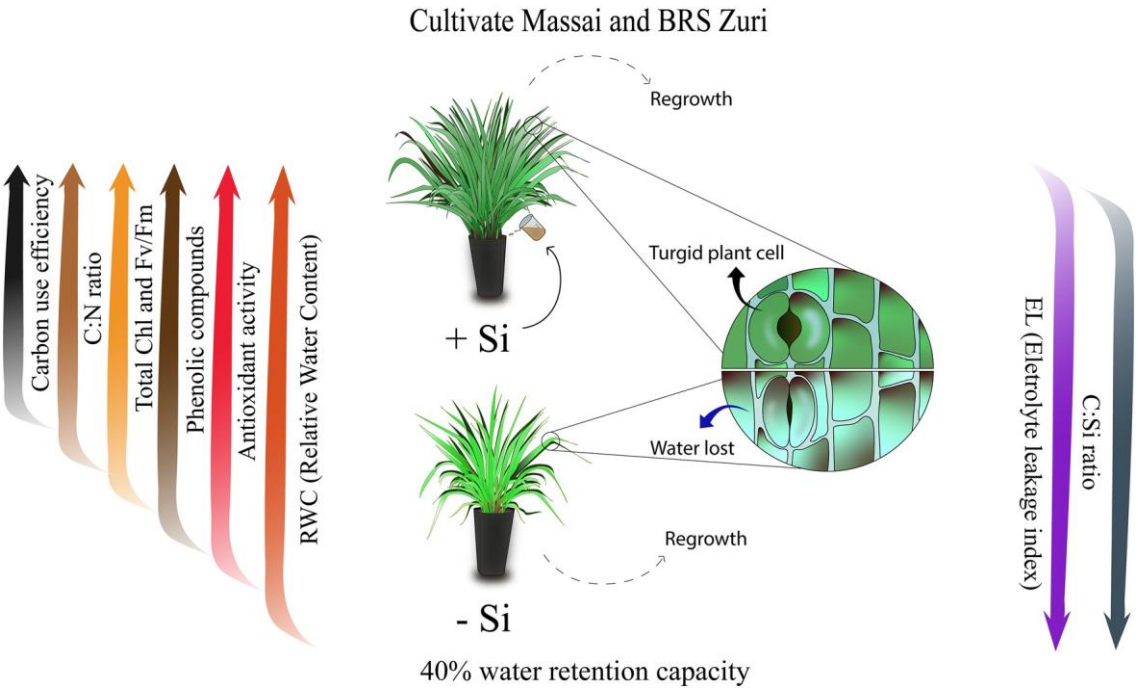

Figure 8. Benefits of Si in elementary stoichiometry and its relationship with physiological and biochemical aspects.

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J.R.R.: conceptualization, methodology, software, formal analysis, investigation, data curation, writing—original draft preparation, writing—review and editing, visualization. R.M.P.: term, methodology, validation, investigation, supervision, project administration. M.C.P.: resources, data curation.

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Competing interests

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