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Beneficial effects of silicon in plants under abiotic stress conditions: A new approach[1]

Efeitos benéficos do silício em plantas sob condições de estresse abiótico: Uma nova abordagem

Sâmia Paiva de Oliveira Moraes[2], João Fabrício Mota Rodrigues[3], Maria Eugenia Ortiz Escobar[4]*, Francisca Soares Araújo[2], Teogenes Senna de Oliveira[5]

ABSTRACT - Considering the importance of Silicon (Si) for plants, many studies have focused to evaluate the ability of the element to alleviate abiotic stress in different species, mainly of agricultural interest. For all species, Si offers a range of benefits in reducing the effects of biotic and abiotic stress, being especially associated with increases in plant biomass. However, after performed a systematic quantitative review of studies linking Si to the relief of abiotic stress in plants, it was demonstrated that there is a reduction in the effects of Si over time and that the effects of Si were smaller in recent studies. Furthermore, was found that plants under different types of stress had similar responses to Si, suggesting that abiotic stress relief mechanisms in plants may be common among conditions of water stress, salinity, and heavy metals – the main environmental stresses studied in the literature. This study can guide future research, which should not be limited to simply evaluating the existence of any Si stress-relieving effects, but also to understand the variation that exists in these mechanisms and considered that they depend on the type of stress and the factors involved in reducing these effects.

Key words: Relief mechanisms. Systematic review. Reduced effect. Biomass.

RESUMO - Considerando a importância do Silício (Si) para as plantas, nas últimas décadas muitos estudos avaliaram a capacidade do elemento em aliviar o estresse abiótico em diferentes espécies, a maioria delas de interesse agrícola. Para todas as espécies, o Si oferece uma gama de benefícios às plantas na redução dos efeitos do estresse biótico e abiótico, estando especialmente associado a aumentos na biomassa das plantas. No entanto, quando realizamos uma revisão quantitativa sistemática de estudos que relacionam o Si ao alívio do estresse abiótico em plantas, demonstramos que há uma redução dos efeitos do Si ao longo do tempo e que os efeitos do silício foram menores nos estudos mais recentes. Além disso, descobrimos que plantas sob diferentes tipos de estresse tiveram respostas semelhantes ao Si, sugerindo que os mecanismos de alívio do estresse abiótico nas plantas podem ser comuns entre as condições de estresse hídrico, salinidade e metais pesados – os principais estresses ambientais estudados na literatura. Nosso estudo pode direcionar estudos futuros, que não devem se limitar a simplesmente avaliar a existência de quaisquer efeitos de alívio de estresse do Si, mas também compreender a variação que existe nesses mecanismos e que depende do tipo de estresse e dos fatores envolvidos na redução desses efeitos.

Palavras-chave: Mecanismos de alívio. Revisão sistemática. Efeito reduzido. Biomassa.

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*Author for correspondence
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[2]Department of Biology, Postgraduate programme in Ecology and Natural Resources, Federal University of Ceará (UFC), Fortaleza-CE, Brazil, samia.paiva@ifce.edu.br (ORCID ID 0000-0003-4736-3290), tchesca@ufc.br (ORCID ID 0000-0003-4661-6137)
[3]Biological Sciences Institute, Postgraduate programme in Ecology and Evolution, Federal University of Goiás (UFG), Goiânia-GO, Brazil fabriciorodrigues303@gmail.com (ORCID ID 0000-0002-1914-4093)
[4]Department of Soil Science, Postgraduate programme in Soil Science, Federal University of Ceará (UFC), Fortaleza-CE, Brazil, mariaeugenia@ufc.br (ORCID ID 0000-0001-7530-3338)
[5]Department of Soil Science, Postgraduate programme in Soils and Plant Nutrition, Federal University of Viçosa (UFV), Viçosa-MG, Brazil, teo@ufv.br (ORCID ID 0000-9904-6708)

INTRODUCTION

All plants grown in soil contain silicon (Si) in their tissue (COOKE; LEISHMAN, 2011; EPSTEIN, 1994). Si is the second most abundant element in the Earth's crust, accounts for approximately 32% of its weight (NEERU *et al*., 2019) and its ubiquity in the biosphere makes it difficult to prove its essentiality for plants. Unfortunately, the benefits of Si were mostly neglected until the early 20th century, in part due to the element's abundance in nature, but also due to the lack of visible symptoms of deficiency or toxicity (ZELLNER *et al*., 2021).

However, several dysfunctions in plant growth and development can be cause by Si deficiency (CHAKMA *et al*., 2021), which together with numerous evidences proving beneficial effects on plants, especially under abiotic stress conditions (ARAÚJO *et al*., 2022; DHIMAN *et al*., 2021), makes it "almost essential".

Most of these abiotic stresses are due to climate change and threaten agricultural productivity, with significant losses in crop yields, for example (KHAN *et al*., 2020, 2021; ZÖRB; GEILFUS; DIETZ, 2019). Plant exposure to multiple abiotic stresses results in changes in physiological responses ranging from seed germination to maturity and causing severe losses in growth and productivity (KHAN *et al*., 2021; MAHALINGAM, 2015). Numerous studies in the literature, recent or not, establish the ability of Si to neutralize the effects of various stresses such as water deficit (HABIBI, 2014; OTHMANI *et al*., 2020), salinity (ABDELAAL; MAZROU; HAFEZ, 2020; LIU *et al*., 2014) heat (KHAN *et al*., 2020), toxicity of heavy metals (DRESLER *et al*., 2015; JESUS; BATISTA; LOBATO, 2017), among others. Therefore, the element has been widely used over decades as an important ally of crops of agricultural interest, even though there is still a gap in understanding the action of Si in various metabolic processes of different plant species. Functions of Si associated with agricultural studies carried out in domestic plants are the most discussed (COOKE; LEISHMAN, 2016). In these cases, the main benefits from Si in terms of a reduction in the effects of biotic and abiotic stress in agricultural systems are well-documented under conditions of Si fertilisation; with most studies focusing mainly on surveying data from almost 30 years of the use of the element in agriculture (ADREES *et al*., 2015; COOKE; LEISHMAN, 2016; LIANG *et al*., 2007; SAVANT *et al*., 1999). Besides that, hundreds of studies have assessed the capacity of Si to alleviate abiotic stresses in single species by single-stress experiments (COOKE; LEISHMAN, 2016). Therefore, it is important to have access to a systematic review that objectively synthesises the effects of Si on different types of stress over time and confirms whether studies have been conducted to obtain advances in scientific knowledge about Si.

We assumed that 1) There is a difference in the effect of Si depending on the type of stress to which the plant is subjected, and 2) The effect of relief to abiotic stress is confirmed by the studies carried out with the element over time. For this, we search for publications in the literature about the influence of Si on plant response to the different types of abiotic stress: salinity, water, and heavy metal, thereby providing a meta-analysis evaluating silicon effects in plants under stress conditions, a relevant information to plant and soil scientists. Based on that, we aimed to perform a systematic quantitative review linking Si to the relief of abiotic stress in plants and contribute to the advancement of Si studies in the soil and serve as a basis for future research with the element.

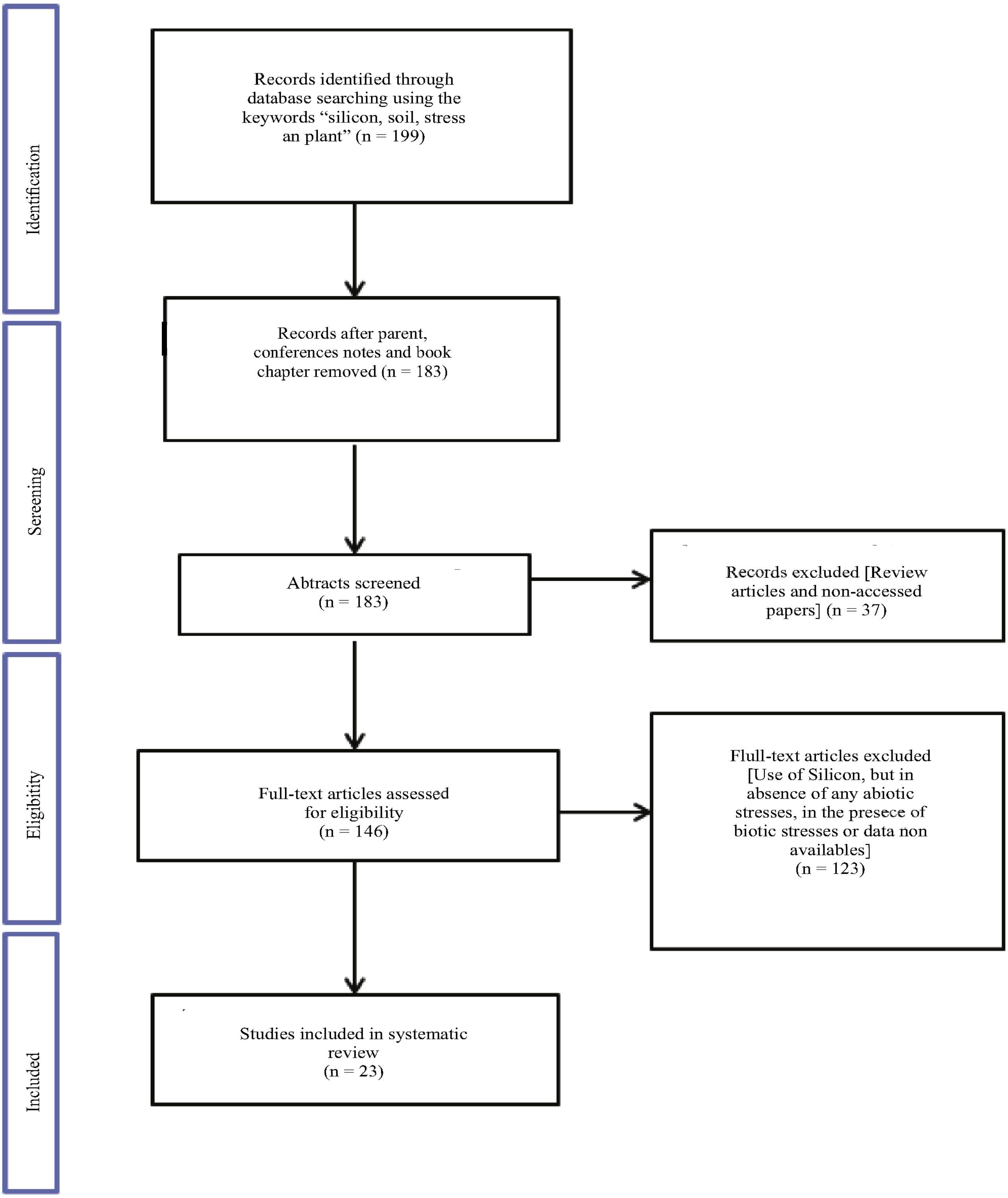
MATERIAL AND METHODS

The literature in the ISI Web of Science database was searched with reference to the influence of Si on the response of plants to stress ("silicon" and "soil" and "stress" and "plant"). See Figure 1 for a detailed explanation of the inclusion criteria used for selecting the papers and Supporting Information for the references of the studies included in the meta-analysis. Within the resulting data, the references of two consistence review articles (SACALA, 2009; ZHU; GONG, 2014) were also checked for further papers.

The same approach described in Figure 1 was followed to select studies from these reviews (See Fig. 2).

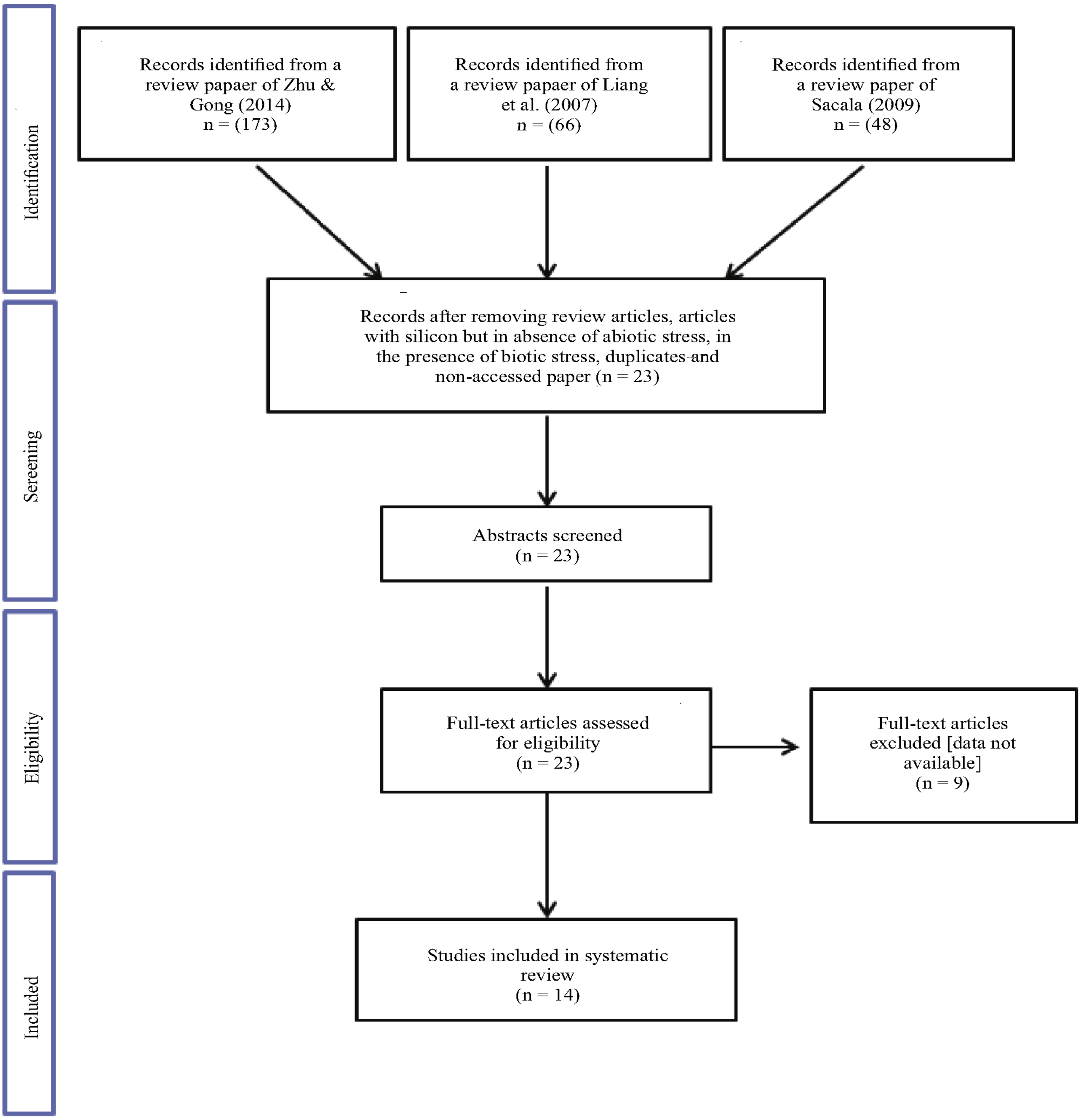
Hedges' g was used as a measure of effect size, with a correction factor that reduces problems related to low sample sizes (BORENSTEIN *et al*., 2009). To calculate this index for each study, one of the following approaches was employed depending whether the response variable of each study was mass or silicon concentration: 1) when the response variable of the study was any measure of plant weight, the experimental group under stress conditions with Si was compared with the group under stress conditions with no silicon (Mass of the Treatment$_{stress+Si}$–Mass of the Treatment$_{stress}$); 2) when the response variable of the study was Si concentration, the experimental group under stress conditions with Si was compared to the group under non-stress conditions with Si (Concentration of the Treatment$_{stress+Si}$–Concentration of the Treatment$_{Si}$). Positive values for Hedges' g represent the positive effects of Si in plants under stress conditions. For studies with multiple treatments, the mean and variance were determined for the effect group following Borenstein *et al.* (2009), by calculating a weighted mean for the mean values and the pooled variance respectively. When the studies had multiple outcomes, causing problems of lack of independence among the data, the formula proposed by Borenstein *et al.* (2009) was used, where the non-independent effect sizes from each outcome were combined in a single value for each study. However, using this approach demands to specify the correlation between the different related results of a study, information which is generally absent from the papers. This combination was carried out therefore, using three different correlation values (0.25, 0.5 and 0.75) in order to cover a range of possible relationships between the variables, as suggested by Borenstein *et al.* (2009).

Figure 1 - PRISMA flow diagram detailing how the literature search was performed



Fonte: Adapted from Koricheva and Gurevitch (2014)

Figure 2 - PRISMA flow diagram detailing how the literature search was performed



Fonte: Adapted from Koricheva and Gurevitch (2014)

As there was no evidence suggesting that all the different studies should converge in a single effect size, a meta-analysis with random effects was performed. Furthermore, since the study units were species, a mixed-effect model was used to incorporate the relationship between the species in the analyses. The taxonomic distances between species were calculated following an approach proposed by Clarke and Warwick (1998), since there was no phylogeny available which covered all the studied species together with their varieties. These distances were used as a correlation matrix between species to correct the phylogenetic dependence among the variety of species after performing simple standardisation [(100 – distance) / 100), where 100 is the maximum distance provided by the formula of Clarke and Warwick], making the main diagonal equal to 1, following the correlation matrix commonly used in meta-analyses (NAKAGAWA; SANTOS, 2012).

The significance of the overall influence of Si in plants under stress conditions was evaluated by checking whether the 95% interval confidence (CI) for the overall effect size (a weighted mean of the effect sizes for each study) crossed zero. The Q statistic was employed, evaluated using a Chi-square distribution, to measure heterogeneity in models from the present work (BORENSTEIN *et al.*, 2009). In order to investigate the causes of variation in plant response to stress conditions, two moderators (or explanatory variables) were included in the meta-analysis: 1) the type of stress evaluated in the study (salt, hydric or heavy metal) and 2) the year the study was carried out. Since the mechanism of the effect of Si in plants under stress conditions changes according to the type of stress, it is expected that different stress situations should produce different effect sizes. In the current work, salt, hydric and heavy metal stress were used because they were the abiotic stress that most appeared in the literature. The year of publication was also included to account for temporal changes in effect size (KORICHEVA; GUREVITCH, 2014). The Akaike Information Criterion, corrected for small sample sizes (AICc), was used to select which model containing moderators best described the selected data. Differences in AICc greater than 2 were considered as evidence of difference between models. Since some studies included in our search evaluated different varieties of a plant and the present work considered each variety as an independent study, previous analyses were rerun using study reference (ID) as a random effect, to account for possible problems of non-independence existing in the studies carried out by the same research group (KORICHEVA; GUREVITCH, 2014).

Publication bias was verified using a funnel plot of effect sizes; this analysis was also carried out using the residuals of the meta-regressions. The residual approach appears to be better than using effect size, as there may be a large amount of heterogeneity with the latter, causing funnel plot asymmetry that is not due to publication bias (NAKAGAWA; SANTOS, 2012). In order to assess asymmetry in the funnel plot, an adaptation of Egger's regression test was used, which uses residuals instead of effect size and has been used in other studies (NAKAGAWA; SANTOS, 2012). The presence of publication bias in an analysis is supported when the intercept of the regression line is significantly different from zero (NAKAGAWA; SANTOS, 2012).

All analyses were performed with the R metafor package (VIECHTBAUER, 2010). Taxonomic distances were calculated in Vegan (OKSANEN *et al.*, 2013).

RESULTS AND DISCUSSION

After applying all the inclusion criteria, 37 studies were included in the meta-analysis which provided standardised mean differences and variances for 81 different varieties of plants. Sensitivity analysis, using three different correlation values (0.25, 0.50 and 0.75) gave very similar results; only the results of those analyses for a correlation value of 0.50 are presented here, this being an intermediate value among those used in the study (see Supporting Information for results using the remaining correlation values).

In general, the plants produced more biomass or accumulated more Si under stress conditions. The overall influence of Si in plants under stress conditions was not significant when study identification (ID) was not used as a random effect ($g = 1.36$, CI = - 0.45–3.17), but changed with the inclusion of this random effect ($g = 1.73$, CI = 0.31–3.17; see Supporting Information, Figures S1-S3 and Table S1). The result highlights the positive effect of Si in plants under stress conditions. Heterogeneity was both very high and significant in the two models ($Q = 491.55$, $P < 0.001$), reinforcing the importance of using moderators to understand the causes of variation between studies and between the varieties of plants.

The increase in biomass production with the addition of Si, confirmed in this study covering many species of plants of different taxonomic groups, is well-documented in studies focusing only in one species, whether with experiments are conducted in soil or under nutrient solution (KHAN *et al.*, 2017; MUSHTAQ *et al.*, 2020; OTHMANI *et al.*, 2020). According to a study conducted by Chen *et al.* (2019), Si increased the biomass of rice plants by approximately 50%. The reason for such beneficial effects of Si in increasing plant biomass, in addition to other gains, is still not well understood, but some research has pointed out that Si absorbed by the plant would deposit in the epidermis, forming a double-layer "cuticle structure -silicon". This could greatly increase the cell wall resistance, making the plant more erect and straight, with elongated leaves (FAROUK *et al*., 2020). In addition, Si can increase the chlorophyll content and optimize the light condition, reducing the angle between the stem and the leaf, which is beneficial for photosynthesis (FAN *et al*., 2016; HUSSAIN *et al*., 2019). It is important to highlight that Si considerably improves photosynthesis and ion homeostasis, as well as the activation of the antioxidant capacity, regulation of genes needed in several physiological processes and in the production of secondary metabolites (FAROUK *et al*., 2020). Furthermore, Si can promote the absorption of nutrients such as N, P and K, improving the oxidation efficiency and root absorption rate (KELLER *et al*., 2015; MA *et al*., 2021). More recently, Mir *et al*. (2022) extensively discussed the intervention of Si in triggering the synthesis of phytohormones, regulating gene expression in alleviating abiotic stress conditions, in addition to reinforcing the element's role in increasing plant growth and metabolism.

The meta-regression, whether including the study ID or not as a random effect, provided similar general results, although the models with ID had a lower AICc (Table 1 and Table S2).

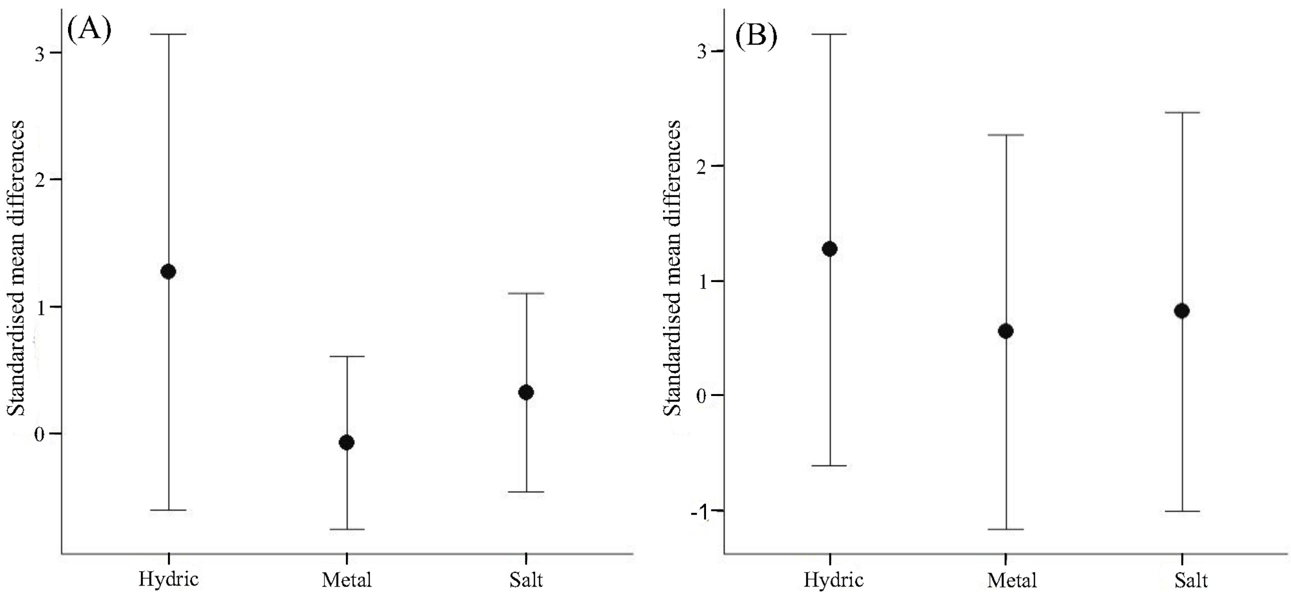
The best model was that using the year of publication as a moderator and including study ID as a random effect. The type of stress did not influence the effect of Si in plants under stress conditions (Figure 3 and Figure S4), but the year of publication had a negative effect (when using ID as a random effect: b (angular coefficient) = - 0.11, P = 0.02; when not using ID: b = - 0.10, P < 0.001; Figure 4).

Most data used in this analysis comes from studies that provided raw data relating the role of Si under isolated and controlled stress conditions. However, it is known that plants grown in field are constantly subjected to a number of different types of combined stresses. Despite the existence of an overall positive effect of Si under stress conditions, the heterogeneity observed in our general model suggests that the plant response to stress in the presence of Si can be explained by specific factors. It is necessary to better understand the function of Si in a larger number of species with more complex environmental interactions. Field studies would be needed to understand the functions of Si under multiple types of stress, as they would allow comparisons between Si-supplied plants and other stress coping mechanisms, such as wax accumulation in leaves, succulence, or other adaptations under stressful conditions, for example (COOKE; LEISHMAN, 2011).

Table 1 - Model selection based on the Akaike Information Criterion corrected for small differences in sample size (AICc). Moderator effect = amount of heterogeneity in effect size explained by the moderator (Q statistic); P = p-value evaluation of the moderator. The models presented in the table were obtained using effect sizes estimated for a correlation value of 0.50. (See supplementary material for results for other correlation values)

Model	Moderator effect	P	AICc	ΔAICc
Year + ID	Q = 5.55	0.02	338.02	0.00
Year	Q = 22.86	< 0.001	397.64	59.62
Stress + ID	Q = 0.71	0.70	340.11	2.09
Stress	Q = 1.37	0.50	418.26	80.24

Figure 3 - Standardised mean differences (Hedges' g) for the three groups: hydric, heavy metal and salt, a: without study identification (ID) as random variable, b: with study ID as random variable. The results are from data for a correlation value of 0.50



The effect of Si associated with plants under adverse stresses, expressed in terms of increases in element concentrations in plant tissues, was also confirmed in our analysis. The discussion about the wide variation in Si concentrations in plant tissue may be related to differences in the absorption and transport characteristics of the element within groups of plants before exposure to stress (EPSTEIN, 1994; LIANG *et al*., 2007). For example, grasses absorb much more Si than other species, while most dicots absorb it passively and others, such as legumes, exclude the element from absorption (LIANG *et al*., 2007). Such phylogenetic influences were considered in the present study with the inclusion of the variance-covariance distance matrix between the studied species, avoiding possible bias in the results due to the use of different proportions of monocotyledons and dicotyledons (indeed it was found that the AIC values for those models incorporating the distances between species were far lower than for models that did not incorporate this relationship – data not shown, reinforcing the phylogenetic effect on plant response). Several authors associate the different action mechanisms of Si with the type of stress the plants are subjected to. In general, under conditions of water or salt stress, the effects of Si for both conditions are associated with regulating the rates of transpiration (ZHU; GONG, 2014), and for salt stress, inhibiting the transport of Na and Cl to the leaves, and/or their accumulation in the roots (TUNA *et al*., 2008; ZHU; GONG, 2014). For stress caused by heavy metals, the most common mechanisms are a reduction in the absorption of these elements by the plant, and an improvement in gas exchange and photosynthetic pigments (ADREES *et al*., 2015). However, even with specific mechanisms for each type of stress, in the present study the Si displays a similar relieving effect regardless of the type of abiotic stress being tested. The data used in our meta-analysis and much of the Si research are from studies conducted in one or at most two types of stress at a time. It is understood that plants under natural conditions in field can be affected by more than one stress-producing factor, such as salt and water stress, for example, which has a strong association of occurrence, reinforcing the need for future case studies that cover different combinations of stress conditions.

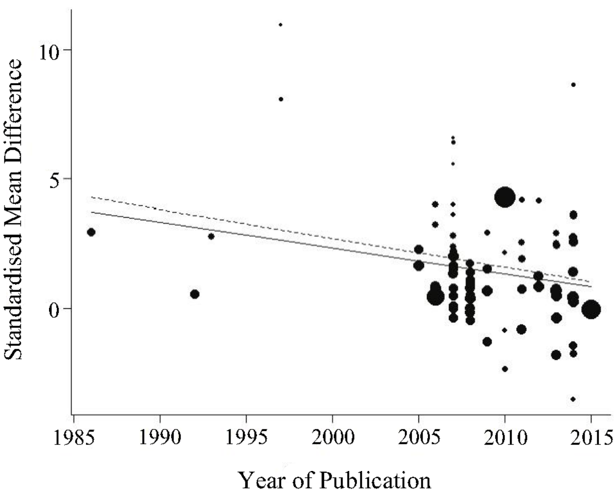
It is necessary to highlight that there is still a great variability in the benefits of adding Si when the environmental levels of the element are low (THORNE *et al*., 2022), in which some plants are even negatively impacted by Si, others do not respond, and others show positive results. The data suggest that the effectiveness of Si is greater in varieties that are more tolerant to one or more types of stress. Thus, it is important that cultivar-specific data be collected in broader studies, with the aim of evaluating the benefits of Si supplementation. In terms of practical applications and future studies, it would be very useful for such studies to include assessments of the economic viability of Si supplementation, especially with reference to different cultivation and production systems.

The occurrence of a defense mechanism stimulated by Si, common to the different types of stress used in these studies, would explain the absence of any difference found in this meta-analysis.

Si seems to act in general mechanisms common to most plant species, such as those that lead to the expression of stress-related genes. Increases in biomass and productivity, in addition to Si concentration, were common variables in the selected publications for this meta-analysis, for a wide variety of plant species. In some cases, these effects were associated with amorphous silica deposition while in others, a consequence of monosilicic acid bioactivity. Recently, Hall *et al*. (2019) reported that Si improves several defense responses through signal transduction, especially the regulatory pathway of jasmonic acid (JA). The application of Si can also increase the tolerance to abiotic stresses by modifying the homeostasis of phytohormones and regulating endogenous hormone levels (KHAN *et al*., 2021; MORADTALAB *et al*., 2018).

In the most recent studies used in our analysis, the beneficial functions of Si are associated with an increase in enzymatic and non-enzymatic antioxidants, demonstrated for adverse stress conditions. This is increasingly reported in the literature, such as in the studies by Rahman *et al*. (2017) and Liu *et al*. (2019). It is possible, then, that a common action of Si under these conditions explains this more general action of the element, regardless of the type of stress the plants are subjected to or the studied species.

Figure 4 - Scatterplot of the meta-regression, representing the influence of year of publication on the standardised mean difference (Hedges' g). Full line: model without study identification (ID) as a random effect; dashed line: model with study ID as random effect. Dot size is proportional to the weights (inverse of the square root of the variance) for each study



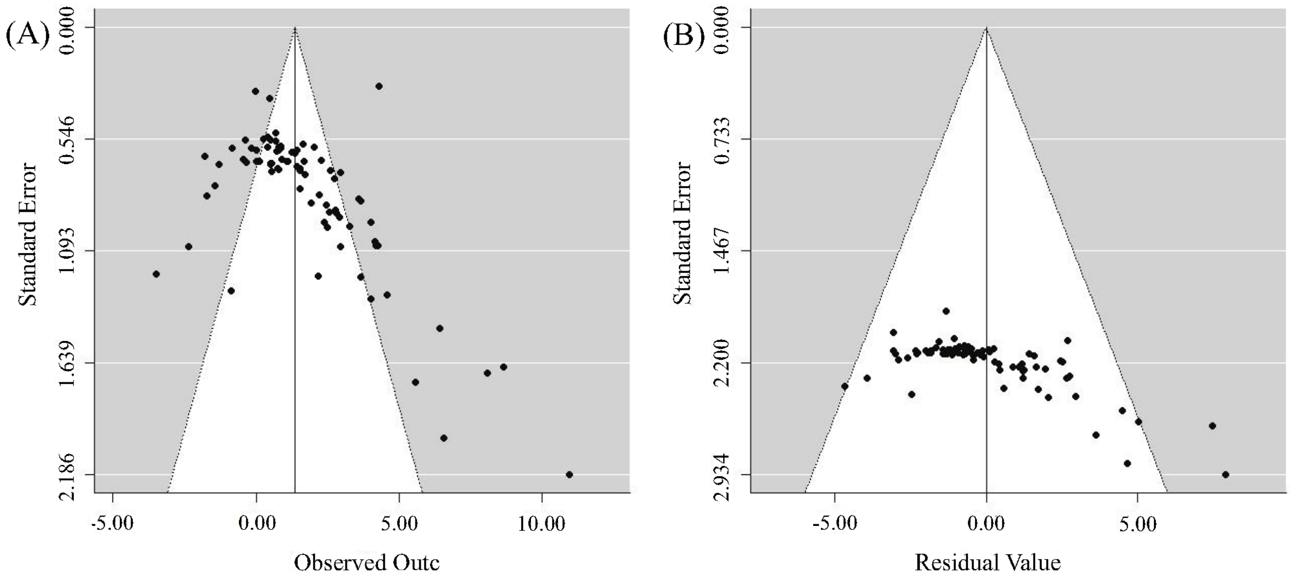
Funnel plots for the best model showed a low signal for publication bias, as most of the effect sizes and residuals are almost equally distributed around zero (Figure 5; see Figure S5 for graphs of publication bias in the dataset for correlation values of 0.25 and 0.75). Egger's regression test, using the residuals of the regression, suggests a low signal for publication bias (intercept = 1.55, t = 1.99, P = 0.05; see also Appendix S1).

The result that most caught attention in our research is that the effect of Si in conditions of abiotic stress has become less evident over time. There are many aspects that can be considered for this statement. One could be the lack of a universally applied method for the determination of Si available to plants in the soil, or even in plants.

According to Zellner *et al.* (2021), there is a lack of agreement on Si test procedures in soil and plant. The two main components of soil Si testing are the extraction procedure and the method of its quantification in the soil extracts. According to the authors, the establishment of different procedures for extracting Si from soil began in the 1960s. Since then, several procedures have been established, and almost all of them had several modifications made mainly to reduce the extraction time requirement (TUBAÑA; HECKMAN, 2015). The amount of Si extracted from the soil differs depending on the extraction procedure used (PAYE *et al*., 2018). In addition, the method by which the concentration of Si in soil extracts is quantified, also affects the soil Si test values, and current standard procedures for digestion of plant tissues can interfere with the determination of the contents, as they affect the solubility of the element. If we consider the number of crops cultivated, the soil classes in the landscapes and the amount of research that is multiplying rapidly, it is worrying that, after more than five decades, there is no agreement on the use of procedures, a database with critical Si levels and soil test interpretations for economically important crops that could more accurately guide the use of the element in agriculture.

In the studies used as database for this work, the use of different methods to determine Si concentrations in leaves was observed, using different extractors such as H_2SO_4 + HF (LIU *et al*., 2014), $CaCl_2$ (PULZ *et al*., 2008), NaOH + H_2O_2 (BALAKHNINA *et al*., 2012), as well as the use of modern equipments, such as inductively coupled plasma atomic emission spectroscopy (ICP-AES) (HABIBI, 2014) and electron microscopy transmission (SIDDIQUI *et al*., 2014). According to our analysis, current studies on the action of Si in plants under stress conditions do not confirm the results obtained in previous studies. These conditions may have been identified because of technological advances in the field of soil and plant research, thanks to the use of more modern equipment that ensure greater accuracy in data collection and, especially, less possibility of contamination (VERCHOT *et al*., 2007). Furthermore, it is important to consider that the most recent studies used in this review include the use of genetically modified species or species resistant to abiotic stress,

Figure 5 - Funnel plots of effect size (a) and residuals of the meta-regression (b)



such as the studies by Ahmed, Hassen and Khurshid (2011), Liu *et al*. (2014) and Habibi (2014). Although there has been a gradual increase in the production of major crops since the 1960s due to the development of agronomic practices such as the use of genetically modified plants, susceptibility to climate change has increased, resulting in the loss of harvests (MICKELBART; HASEGAWA; BAILEY-SERRES, 2015). As a result, the adoption of resistant plants has guaranteed global food security, allowing plants to successfully occupy differing environments under limiting conditions. In this scenario, the reliever function of Si will possibly be eliminated or become "unnecessary". Gene transcription analysis has shown that the addition of silicic acid has no impact on gene expression for Si absorption in the absence of stress (FAUTEUX *et al*., 2006), so any advantages provided by the Si may not be evident unless the plants are forced to (CHERIF *et al*., 1994; COOKE; LEISHMAN, 2011). If genetically modified plants are already seen as being resistant to stress, absorption of the element by the plants would be reduced.

CONCLUSIONS

1. No differences for Si responses in relation to the types of stress selected for this study were found, confirming a more general effect of the element. The identification of a common and general effect of a greater number of stresses, or under conditions where the species are subjected to more than one stress simultaneously, may direct further studies with the element and help to clarify the mechanisms of stress relief;

2. The main finding refers to the reduction in the effect of Si as a stress reliever over time; this should be better investigated aiming to identify any possible interference from advances in science and technology in studies that address resistance to various stresses. Future studies therefore should not be restricted to simply evaluating the existence of positive effects, but also to understanding the variations between them and whether they depend on the type of stress, and the factors involved in the reduction of these effects over time;

3. Considering the ability of Si to create a tolerance in plants to abiotic stress, future research should include aspects of plant adaptation to climate change and/or strategies for environmental remediation, making the element relevant to current research. In this way, plant scientists from other areas than agronomy could be involved, bringing new insights and ideas that would contribute to advances in the area.

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