

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

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Abstract

In cultivated soils with pastures in different regions of the world, phosphorus (P) imbalances are recurrent. In addition to P deficiency, the occurrence of areas with excess P in the soil has increased, with damage to pasture production. This reality requires the search for thoughtful strategies such as the use of silicon (Si), which is an element known to attenuate stress in plants. However, the action of Si on morphogenetic and chemical characteristics of grasses forages cultivated in different soils is not known. Therefore, this study aimed to evaluate the effects of P deficiency and excess on morphogenetic and chemical parameters, and on the digestibility of Zuri guinea grass cultivated in Oxisol and Entisol, and to analyze whether fertirrigation with nanosilica can mitigate the damage caused by these nutritional stresses. P deficiency decreased tiller number and grass protein content, and increased lignin content, while P excess increased the percentage of dead material and lignin, and decreased the leaf:stem ratio of plants, and both stresses decreased dry matter (DM) production. Fertirrigation with Si promoted better tillering and protein in deficient plants. In the excess of P, Si reduced tiller mortality and the lignin content of the plants, increasing the leaf:stem ratio and DM production, also increasing the production of plants with P sufficiency, without affecting the digestibility of the grass. Thus, the perspective is that the use of Si can improve the growth and chemical characteristics of forage grasses under P stress, and optimize production in nourished adapted plants, confident for more sustainable pasture production.

1. BACKGROUND

Production in pastoral ecosystems worldwide is subject to phosphorus limitation, especially regarding deficiency in tropical regions ^[1]. In these places, the advanced degree of weathering and the high phosphate adsorption power of the soils decrease nutrient availability, mainly in clayey soils ^[2] requiring phosphate fertilization to sustainably increase forage production ^[3]. On the other hand, in intensive crops, using frequent high doses of phosphorus (P) fertilizers from conventional or organic sources can contribute to more P than what is exported from the areas ^[4], causing nutritional imbalance and excess P in plant tissues ^[5, 6]. The risk of excess P may be even greater in soils with a sandy texture (clay content < 15%), which have greater availability of phosphate because the adsorption of the element in the soil is relatively low ^[2].

In plants, the cellular balance of inorganic phosphate (Pi) is fundamental for converting nutrients, such as carbon (C) and nitrogen (N), into biomass since P has essential metabolic and structural functions in plants ^[5, 7]. Phosphorus imbalances compromise the physiological processes of the plant ^[8] and, consequently, the morphogenic processes determining forage growth. For example, this disturbance of P in the plant decreases the appearance and elongation of leaves and stems ^[9, 10] and plant tillering ^[11, 12, 13], which may reduce forage production and pasture perenniality.

The damage from P imbalances in the plant can go beyond the growth rate and biomass production and affect forage quality. Forage grasses comprise carbohydrates, proteins, lipids, fibers, lignin, minerals, and

vitamins. These nutritional components are decisive for the productivity of herds ^[14]. Nutritional imbalances modify these components and can also affect the nutritional value of the pasture ^[15, 16]. However, there must be more studies to better understand these losses.

The worldwide occurrence of P imbalances in plants ^[4, 1] implies the urgent need for strategies to mitigate these losses. Research has invested in more efficient ways to sustainably perform phosphate nutrition in forage plants ^[17]. An option for mitigating these imbalances has recently started with silicon (Si), with promising initial reports for mitigating nutritional deficiency ^[18]. However, these studies were carried out in soilless hydroponic cultivation ^[19, 20], and the role of Si in the morphogenetic responses of grasses under P deficiency cultivated in the soil is unknown. Furthermore, the effects of excess P on grasses are also unknown, in addition to its damage to morphogenic aspects of the plant, and further studies are necessary for its mitigation. It is possible that Si also contributes to alleviating excess P, given its benefits to this group of plants (Poaceae) subjected to other nutritional stresses ^[21, 22].

It is worth highlighting that the beneficial potential of Si use in stress mitigation depends on the high absorption of the element by the plant and, consequently, on the source used. Recently, with nanotechnology breakthroughs, the option of nanoparticulate silicon ^[23] that could potentiate the element's absorption has emerged ^[24, 25] due to the monomeric size of the SiO₂ particles with stability in solution. Therefore, there is an expectation that using this source of Si is promising for mitigating nutritional stress, which should be investigated.

In order to elucidate the damage caused by P imbalances in forage grasses and the benefits of Si in alleviating these stresses, it is important to answer the following questions: (i) does damage from P deficiency and excess affect morphogenesis and impair P production in *Megathyrsus maximus* cv. Zuri grass? (ii) does it influence chemical parameters and digestibility of plant biomass? (iii) is nanosilica fertilization efficient? In other words, does it enhance the absorption of Si by the plant, allowing the mitigation of the damage caused by the deficiency and excess of P in the growth due to improvements in the plant's morphogenesis and the quality of the forage cultivated in clayey and sandy soils?

If these hypotheses are confirmed, the reaction of this forage grass species regarding morphogenic processes when subjected to P deficiency or excess, and its reflexes in the forage quality, will be known for the first time. Furthermore, it will still be possible to indicate whether using nanoparticulate Si in forage cultivation is useful to mitigate problems of deficiency or excess of P in soils of different textures. Thus, it could strengthen this species' sustainable cultivation in many regions limited by P imbalances.

2. METHODS

2.1 Experimental design and cultivation environment

Two assays were developed with *Megathyrsus maximus* cv. Zuri cultivated in Oxisol (experiment 1) and Entisol (Quartzipsamment) (experiment 2) ^[26] under greenhouse conditions. They were conducted at São

Paulo State University, in Jaboticabal, Brazil, from October 2021 to April 2022. During this period, the plants were subjected to six defoliation intervals, representing six growth cycles. The cultivation took place under full light. Inside the greenhouse, the average maximum air temperature was $47 \pm 5^\circ\text{C}$, the average minimum was $22 \pm 5^\circ\text{C}$, and the average relative humidity was $50 \pm 10\%$.

In both experiments, a 3x2 factorial scheme was used with three phosphorus nutritional states: deficient (without P application), sufficient (200 mg dm^{-3} of P) [27], and excessive (600 mg dm^{-3} of P). These were combined with the absence of Si (no application) and the presence of Si (1.5 mM solution) [28], arranged in a completely randomized design with four replications. The experimental unit comprised a plastic pot with a volume of 7.2 L (height: 32 cm; bottom base 14 x 14 cm; and top 16 x 16 cm) filled with Oxisol or Entisol samples, with two plants per pot.

2.2 Characterization of soils and application of treatments

The soil samples used were obtained from native forest and submitted to chemical analysis according to [29], with the following results for Oxisol and Entisol, respectively: pH $\text{CaCl}_2 = 3.8$ and 4.3 ; organic matter (OM) = 34 and 9.0 mg dm^{-3} ; P in resin extractor = 12 and 2 mg dm^{-3} ; K = 1.4 and 3.0 ; Ca = 6 and 3.0 ; Mg = 2 and $1.0 \text{ mmolc dm}^{-3}$; H + Al = 85 and 16 ; and cation exchange capacity (CEC) = 94 and $20.3 \text{ mmolc dm}^{-3}$. The Si contents were determined [30] and showed the following results: 3.0 and 1.0 g dm^{-3} for Oxisol and Entisol, respectively. The granulometric analysis carried out according to [31] presented the following results for Oxisol and Entisol, respectively: 51 and 94% sand, 6 and 1% silt, and 43 and 5% clay.

The soils were limed using limestone (total neutralization power: 125% ; CaO: 58.5% ; MgO: 9%). Forty days after liming, P was incorporated into the soil at doses equal to 0 , 200 [27], and 600 mg dm^{-3} of P in the form of triple superphosphate, corresponding to treatments with deficiency, sufficiency, and excess of P, respectively. Furthermore, 225 , 50 , 5 , and 0.5 mg dm^{-3} of K, S, Zn, and B were also applied in both soils. Moreover, in Entisol, it was also necessary to apply 5 mg dm^{-3} of Fe using the sources potassium, calcium sulfate dihydrate, zinc sulfate heptahydrate, boric acid, and iron chelate (EDDHA), respectively. Nitrogen (300 mg dm^{-3}) was supplied in installments during each regrowth period in the form of urea and subsequent irrigation.

Sowing was direct in the soil, and each pot contained two plants. The plants were subjected to a standardization cut at 17 cm from the ground 30 days after sowing. From that point on, the data collection phase began. On the day of the standardization cut, there was a need to enable the minimum growth of the plants in the treatment deficient in Entisol (0 mg dm^{-3} of P). Thus, 4 mg dm^{-3} of P was applied in these plots. In turn, the Oxisol did not require it for minimal plant growth. For irrigation management, the water retention capacity of the soils was maintained at 70% , based on the daily weighing of the pots and the replacement of water losses due to evapotranspiration [32, 33].

Silicon application was carried out every day since sowing, with a solution of 1.5 mmol L^{-1} of Si [28], using colloidal nanosilica as a source (particles between 8.5 and 9.7 nm , specific surface of $300 \text{ m}^2 \text{ g}^{-1}$,

and pH of 10.5). The same volume of solution was applied in all treatments. This volume was defined daily by the treatment with the lowest water demand. On average, 102 and 69 mg dm⁻³ of Si were applied at each forage regrowth in Oxisol and Entisol, respectively. In the treatment without Si application, irrigation was performed with deionized water. The cuts were made whenever the plants under P sufficiency reached 70 cm in height, leaving a residual biomass of 30 cm in height [34].

2.3 Variables analyzed

Morphogenic and structural

Growth monitoring was carried out during six regrowths of the plants. In each regrowth, two tillers per pot were selected and identified with colored ribbons. They were evaluated every three days regarding ligule exposure, length of the stem, and length of leaf blades in expansion, expanded, or undergoing senescence. At the end of each growth cycle, the number of leaves per tiller, number of tillers per pot, number of live and dead leaves, and tiller diameter were measured using a digital caliper immediately before cutting the plants.

After data collection, the following variables were calculated according to [10]: leaf appearance rate (LA, leaf per tiller per day), leaf elongation rate (LE, mm per day), number of live leaves per tiller, stem elongation rate (SE, mm day⁻¹), and stem diameter (SD, mm). Tillering was also evaluated: the number of tillers per pot, tiller appearance rate (TA = number of new tillers per total tillers alive in the previous cycle)/days of regrowth, tiller mortality rate (TM = number of dead tillers per total tillers alive in the previous cycle)/number of regrowth days, and tiller survival rate (TS = 1-TM) [35, 36].

Production and morphological fractions: The average dry matter (DM) production was determined using six collections of biomass from the plant's grazing stratum [34]. In each collection, the morphological components of the leaf blade, stem, and dead material was separated from the biomass was carried out, measuring its fresh weight in grams. The material was packed in paper bags and taken to an oven with forced air circulation (65 ± 5 °C) until it reached constant mass. Thus, leaf blade, stem, and material DM were obtained. Finally, the percentage of each morphological component, the leaf blade:stem ratio, and the total DM production (g per pot) were calculated.

Chemical composition of forage: The material went through a Willey-type mill and was used to determine the percentages of neutral detergent fiber (NDF), acid detergent fiber (ADF), and lignin in the dry mass [37, 38], through which the hemicellulose (difference between NDF and ADF) and cellulose (difference between ADF and lignin) contents were calculated. The percentages of mineral matter (MM), non-fiber carbohydrates (NFCs), and crude protein (PB% = N content x 6.25, N being determined using a LECO Truspec CHNS analyzer) (AOAC, 2012) were also calculated, in addition to in vitro dry matter digestibility (IVDM) [39]. The following equation estimated total digestible nutrients: TDN (%) = Deg + (1.25*EE) – MM. Where Deg = degradability; 1.25 = correction factor; EE = ether extract; MM = mineral matter [40].

2.4 Statistical analyzes

The data were submitted to analyses of normality, homogeneity, and independence of the residues. Then, the analysis of variance was performed (F test with $p < 0.05$). When there was a difference between the means, they were compared through Tukey ($p < 0.05$) using the statistical software SPEED Stat version 2.8 [41].

3. RESULTS

3.1 Morphogenic and structural characteristics

There was a significant PxSi interaction ($p < 0.05$) for most results of the morphogenetic and structural variables studied (Figs. 1a-j), except for leaf elongation on Oxisol and stem diameter and leaf appearance rate on Entisol. In Oxisol, P deficiency regarding the adequate state increased the leaf appearance rate and the number of live leaves per tiller (Figs. 1a and 1e). It increased the elongation and diameter of the stem compared to plants under P sufficiency (Figs. 1g and 1i). Phosphorus deficiency also decreased the tiller mortality rate in Oxisol (Fig. 2c). In Entisol, P deficiency reduced the tiller appearance rate (Fig. 1b). Furthermore, it decreased the number of tillers per pot in the forage, both in Oxisol (55%) and Entisol (35%) (Figs. 2a-h).

Compared to P sufficiency, excess P increased the rate of leaf appearance and leaf elongation and decreased the number of live leaves per tiller in both soils (Figs. 1a-f). Stem elongation increased in plants under P excess in Oxisol. However, stem diameter decreased in both soils (Figs. 2g-j). Excess P also increased the tiller appearance rate in both soils, reflected in higher tiller numbers. However, it also increased the tiller mortality rate in Oxisol and Entisol (Figs. 2a-h).

There was PxSi interaction for the variables leaf appearance, number of leaves per tiller, and stem elongation in both soils and leaf elongation in Entisol and stem diameter in Oxisol (Figs. 1a-j). In P deficiency in Oxisol, the presence of Si compared to its absence decreased the number of live leaves per tiller (Fig. 1e). It increased the tiller appearance rate, which did not occur in Entisol (Figs. 2a, b). In Entisol, Si application to forage under P deficiency increased leaf appearance and elongation rates, decreased stem elongation, and increased stem diameter (Figs. 1b, d, h, j).

In plants with excess P applied in Oxisol, the presence of Si regarding the non-application of Si decreased the leaf appearance rate and stem elongation (Figs. 1a, g). Moreover, it increased the number of live leaves per tiller and the stem diameter (Figs. 1e, i). In excess P in Entisol, the plants that received Si showed a decrease in the rate of appearance and leaf elongation and in stem elongation (Figs. 1b, c, g) and an increase in the number of live leaves and stem diameter (Figs. 1f, i). In both soils, Si fertilization in plants under excess P resulted in a decrease in the tiller mortality rate and an increase in the number of tillers per pot with an increase in the tiller survival rate in Entisol (Figs. 2a-h). In the sufficiency of P in Oxisol, the presence of Si increased the number of live leaves per tiller (Figs. 1e) and the number of tillers per pot (Figs. 2g), while in Entisol the P sufficient plants showed a decrease in P elongation rates leaf and stem (Figs. 1d, g).

3.2 Morphological composition and dry matter production

There was a significant PxSi interaction ($p < 0.05$) for the morphological variables' percentage of the leaf blade and dead material in both soils and for stem percentage in Entisol, but not for dry matter production (Figs. 3a-j). When compared to P sufficiency, *M. maximus* plants grown in Oxisol under P deficiency had an increase in the green leaf blade (19%) and in the stem (100%) and a decrease in the leaf:stem ratio (49%) and in dead material (100%), with a 39% decrease in DM production (Figs. 3a, c, e, g, i). On Entisol, when compared to P-sufficient plants, P-deficient plants had an increase in leaf blade (9%), and a decrease in dead material, and DM production decreased by 20% (Figs. 3b, d, f, h, j). There was no effect of the presence of Si in the plants under P deficiency for the morphological variables and DM production in the studied soils.

Cultivation under excess P in the absence of Si regarding P sufficiency decreased green leaf blade (19 and 27%) and increased dead material (45 and 71%) in Oxisol and Entisol, respectively. It did not influence the stem fraction of the plants. However, it increased the leaf:stem ratio in both soils (Figs. 3a-h). Excess P decreased final DM production by 14% in Entisol, which did not occur in Oxisol (Figs. 4i, j).

The plants of *M. maximus* under P excess that received SiO₂ nanoparticulate had an increase in the leaf blade (29 and 26%) and in the leaf:stem ratio, and a decrease in the dead material (84 and 67%), in Oxisol and Entisol, respectively (Figs. 3a-f). Furthermore, in plants with P sufficiency in the presence of Si compared to plants that did not receive Si, there was an increase in the leaf blade (16 and 7%) and the leaf:stem ratio and a decrease in dead material (88 and 55%) in Oxisol and Entisol, respectively. Fertilization with Si increased forage total DM production at P excess (9 and 18%) and P sufficiency (8 and 5%) in Oxisol and Entisol, respectively (Figs. 3i, j).

3.3 Chemical composition of forage

The results for variables related to chemical composition, fiber, and DM digestibility had a significant PxSi interaction ($p < 0.05$) only for the percentage of lignin and mineral matter in both soils and for non-fiber carbohydrates in Oxisol (Figs. 4a-h and Figs. 5a-h). Under P deficiency in Oxisol regarding adequate P status, *M. maximus* plants had an increase in the percentage of lignin, a decrease in non-fiber carbohydrates, and an increase in the mineral matter without affecting the CP content or the DM digestibility (Fig. 4 and Figs. 5a, c, e, g). In Entisol, the deficiency did not influence the fiber composition or the percentage of non-fiber carbohydrates. However, it decreased the CP content by 5.1%, decreasing the mineral matter (Fig. 4 and Figs. 5b, d, f, h).

Under P excess compared to Oxisol sufficiency, the plants showed a decrease in non-fiber carbohydrates and increased CP (15.4%) and mineral matter (Fig. 4g and Figs. 5a, c). Meanwhile, under Entisol, excess P caused a decrease in hemicellulose (28.5%) and mineral matter and an increase in lignin (1.1%), CP (28.6%), and DM digestibility (Figs. 4b, f; Figs. 5b, d, h).

In the presence of Si, plants deficient in P regarding nutrient sufficiency increased CP (4.9 and 9.4% in Oxisol and Entisol, respectively) and mineral matter (Figs. 5a-d) without affecting fiber composition and digestibility. In excess P in plants grown in Oxisol, Si fertilization increased non-fiber carbohydrates and mineral matter. Meanwhile, in Entisol, there was a decrease in lignin (1.3%) and increased CP (12.4%) and mineral matter. The presence of Si in P sufficiency compared to its absence decreased the percentage of lignin in both soils (1.0%). Moreover, it increased the CP content in Oxisol (4.1%) and Entisol (9.7%) and increased the mineral matter of plants in Oxisol. Fertilization with Si did not influence TDN percentage or digestibility, regardless of the P nutritional status.

4. DISCUSSION

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

The effects of P deficiency on grasses have been documented ^[1, 3, 42]. However, studies focusing on the morphogenic processes of grasses used in pastures under P deficiency are less abundant ^[43, 44]. It is a concern because the damage caused by nutritional disorders of the nutrient in the plant and its responses to this stress are not known in depth, which are unveiled with morphogenesis studies.

Overall, we discovered in this species of grass some plant strategies related to morphogenetic responses to minimize P deficiency, which occurred in plants cultivated in the two soils studied. The plant deficient in P compared to that under P sufficiency develops the strategy of increasing the number of live leaves per tiller without decreasing the elongation rate of the leaves. However, at the same time, there is a significant decrease in the appearance rate and the number of tillers and, consequently, damage to the plant's biomass production.

The growth and tillering dynamics of forage grasses involve morphogenic processes that guarantee forage production and pasture perenniality ^[11]. Our study allowed us to discover in *M. maximus* the strategies of the plant related to morphogenesis to alleviate the effects of P deficiency in clayey (Oxisol) and sandy (Entisol) soils. In Entisol, the morphophysiological changes in *M. maximus* under P deficiency were reflected in a lower tiller appearance rate due to the decrease in cell division and expansion. A similar effect was observed in perennial *Lolium* ^[45].

Low tillering under macronutrient deficiency occurred in both soils. However, Oxisol plants responded with increased appearance rates and leaf elongation. There was possibly a greater severity of P deficiency in the plants on Oxisol, which may have triggered the more efficient use of the nutrient by the plant. It is known that under P deficiency, the plant can allocate more P in metabolic processes ^[46, 47]. Furthermore, although each tiller has a genetically defined number of leaves ^[48], leaf elongation is a trait responsive to the genotype:environment relationship ^[49] in forage grasses, which this study observed regarding P.

The reduction in tillering caused a severe loss in forage production. These effects are commonly observed in grasses under P deficiency [50, 12, 47]. The lower production of plants with nutritional deficiency was expected, as they were grown in weathered soils with low available P content (12 and 2 mg dm⁻³ in Oxisol and Entisol, respectively). This limitation compromises cell division and slows the net photosynthesis rate [7, 42].

The loss in DM production under P deficiency was 18% higher in Oxisol than Entisol, as plants cultivated in Entisol possibly used the small amount of P added (4 mg dm⁻³) after the standardization cut with high efficiency to enable minimal plant growth. This amount corresponds to 2% of the recommended dose [27]. However, it was enough for the deficiency of this nutrient to be more moderate in Entisol. It occurs because this soil has a lower phosphate adsorption capacity [2, 42, 44].

Plants grown with excess P were impaired, possibly due to loss of cellular Pi homeostasis. This imbalance impairs the essential functions of P in plants, with a consequent depression in photosynthesis and biomass production [5, 8]. It was observed for the first time in our first study that the excess of P in the soil reduced the homeostasis between C, N and P in grasses, which impairs the efficiency of use of these nutrients [51]. However, there are still few studies describing the effects of excess P on grass, even in nutrient solution [52], so our study may be the first to identify the morphogenic responses of forage grass to P excess in different soils.

Our study allowed a better understanding of the morphogenic mechanisms of *M. maximus* and to know the reaction strategies of the plant when subjected to excess P compared to plants with adequate P in both soils. In an unprecedented way, we report that the forage studied under toxic P levels has an increase in the leaf appearance rate and elongation. However, it maintains a reduced number of live leaves on the tiller. Then, there is an increase in the appearance and number of tillers in the plant but with a smaller diameter and high tiller mortality rate, followed by a low percentage of live leaf blades and a high amount of dead material in the plant and, consequently, low dry matter production.

Our study shows that contrary to deficiency, excess P accelerates the dynamics of growth variables of *M. maximus*. However, the higher tiller mortality of plants grown in both soils under P excess may have resulted not only from the high stimulus to cell division processes by P excess but also from the synergy between P and N. Under P excess, N can be absorbed in greater quantities for plants, contributing to high tissue renewal [53, 54]. [47] also observed that the process of tissue renewal in Massai grass (*M. maximus* x *M. infestum*) is accelerated with increasing doses of phosphorus, even without a toxic dose of P.

Losses due to early leaf senescence occurred in plants in both soils. However, total DM production was impaired by excess P only in Entisol, which corroborates the greater availability of phosphate applied in sandy soils [2]. Moreover, in soils rich in oxidic clays, such as Oxisol, there is a decrease in P availability the longer the phosphate exposure time to the adsorption sites [55]. Thus, the excess of P in pastures is even more worrying when it comes to sandy soils, which allows us to partially accept the first hypothesis.

Although both P imbalances altered the growth and tillering of plants in both soils, the excess of P decreased DM production of Zuri grass only when cultivated in sandy soil.

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

We observed that P imbalances also caused changes in the morphogenetic and structural characteristics, chemical composition, and nutritional value of *M. maximus* grass. However, although P deficiency increased hemicellulose and decreased protein in plants grown in one soil (Entisol), increased lignin and mineral material, and decreased non-fibrous carbohydrates in another soil (Oxisol), these changes were not sufficient to alter the total digestible nutrients and DM digestibility of grasses cultivated in both soils. The increase in lignin content in P-deficient plants grown in Oxisol is an effect reported in plants under abiotic and biotic stress as a natural defense mechanism ^[56]. However, it is a route with a high energy cost for the plant ^[57].

The lack of effect of P deficiency on digestibility can be explained by the fact that these plants kept a greater number of young leaves. It occurred because there were plants with a low number of tillers in this condition, which induced an increase in leaf blade and stem production in response to stress. Furthermore, plants under P deficiency did not produce dead material due to slow leaf senescence, which contributes positively to forage digestibility.

In P-deficient plants cultivated in Entisol, attention was drawn to the decrease in the plant's CP content. This fraction comprises protein nitrogen (true protein) and non-protein nitrogen, such as amino acids and amines, which are essential for animal nutrition ^[58]. This decrease in protein in plants was because P comprises ribonucleic acid (RNA), which is required for the translation process ^[7] in protein synthesis. In addition, in P-deficient plants, there is a decrease in N absorption, which is vital for protein formation ^[59, 60].

Another effect of P deficiency in the plant cultivated in Oxisol was the increase in mineral matter. Possibly, this increase occurred due to an effect of the element's concentration in the dry matter since these plants had less growth and biomass production than those adequately nourished (Figs. 6a, b). Another possibility for increasing mineral matter is the absorption of residual Si from the soil, as plants under stress can release exudates into the rhizosphere, favoring the dissolution of phytoliths in the organic matter ^[61] and releasing the Si in these materials.

It can be inferred that pastures of *M. maximus* under P deficiency produce a lower amount of dry matter when compared to a pasture with an adequate supply of P and even with a lower protein content, but without damage to digestibility.

Another important nutritional problem would be the excess of P in the grass, but its effects on the nutritional value of the plant remained unknown until then. We observed that excess P initially decreased the leaf:stem ratio due to the lower percentage of live leaf blades, as described by ^[10]. Even this was

visually evidenced, being the first report of P toxicity symptoms for this species, which start with chlorosis and necrotic spots on the leaves (Figs. 6c, d) evolving to complete leaf necrosis. These symptoms result from biochemical disturbances caused in tissues by excess P, such as inhibition of photosynthesis and increased lipid peroxidation ^[8], added to accelerated senescence and decreased photosynthetically active area. In practice, this results in less accumulation of dry matter ^[9, 62] and biomass loss, as grazing animals select green leaf blades with greater nutritional value ^[63, 64].

We verified that the excess of P, and the deficiency, resulted in higher lignin content in *M. maximus* as a strategy to mitigate nutritional stress, similar to that described by ^[65]. Thus, it confirms that the lignin content of the fiber may vary with the input of nutrients ^[14]. However, even with the highest lignin content, we visually observed that the plants under P stress, mainly those under P excess, did not reach a phenotype similar to that of the plant adequately nourished with P, which would be the well-developed leaf blade with a green color, characteristic of most forage grasses (Figs. 6a-d).

Increased lignin content may compromise fiber digestibility by ruminants ^[54, 66]. However, in this study, the excess of P did not impair dry matter digestibility. It can be explained by the fact that the lignin studied here consists mainly of non-core lignin. In other words, it comprises phenolic compounds of low molecular weight, released from the cell wall by hydrolysis. These are represented by ester-linked p-hydroxycinnamic acids, unlike the core lignin, which features cell wall phenylpropanoid polymers, highly condensed and resistant to rumen microbial degradation ^[67, 68].

The increase in CP in plants under excess of P in Entisol goes back to the essentiality of P in protein synthesis. However, it is worth emphasizing that it may also be related to the fact that P stimulates N absorption ^[53]. Nevertheless, this higher protein content in the plant under P excess results in lost nutrients. In other words, nutrients cannot be redistributed in the plant and reused in its metabolism or used by animals in grazing, which usually do not consume the dead leaves.

In light of the results discussed, part of the second hypothesis was confirmed, as P imbalances altered the chemical composition of the plant. However, it did not affect forage digestibility. Nevertheless, the severe reduction in biomass production caused by excess P and early leaf senescence compromises the supply of quality pasture ^[63].

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

In this study, the damage of deficiency and excess of P in the studied forage that harms extensive areas of cultivation of these species in the world was clear and well-detailed from the morphogenesis studies. Thus, there is an urgent need for strategies to mitigate this damage without risking the environment. A potential strategy to mitigate the effects of P imbalances in *M. maximus* would be using silicon, especially with innovative sources of the element, such as nanosilica. In this scenario, it would be

opportune to deepen research on the effects of this element on forage morphogenesis, given the lack of research on this topic, which motivated this study.

We showed that the benefits of Si in the morphogenesis of P-deficient forage were very limited in plants grown in Oxisol, as it only increased the tiller appearance rate, and in plants grown in Entisol. There was an increase in the appearance rate, leaf elongation, and stem diameter. However, these improvements in the morphogenesis of the Si-induced P-deficient forage were not sufficient to increase plant dry mass production in the two soils studied. It possibly did not occur because there was no significant increase in the number of tillers, which is the basic unit of grass production ^[10].

In hydroponic studies, alleviation of Si-mediated P deficiency in wheat and rice is indicated ^[69, 70]. However, in these studies, there is greater control of P in the culture medium (nutritive solution), generating a more severe deficiency in the plant compared to cultivation in soil. There are indications that the beneficial effect of Si is more pronounced when stress is more severe ^[71]. Advances in forage regrowth cycles could further aggravate the P deficiency in the soil with nutrient export in the biomass, and Si could increase its benefits in the plant. Nevertheless, future research must prove it ^[51].

Regarding the role of Si in plants with excess P, it is something unprecedented in this species since this nutritional disorder has occurred in more restricted areas compared to the P deficiency problem. However, it is important to start research on this topic. We emphasize that Si induces some morphogenic processes in the plant to mitigate the damage caused by excess P in *M. maximus*, which occurred in plants cultivated in both soils. Nevertheless, there was a decrease in the appearance rate of new leaves due to controlling the flow of tissues in the plant, which increased the number of live leaves per tiller and decreased the stem's elongation rate. In turn, it favored an increase in the number of tillers and tiller diameter. These benefits in plant growth and structure led to an increase in plant dry mass production in Entisol.

However, in plants grown in Oxisol with the P dose used, it was not possible to reach P toxicity given the high capacity of this soil in adsorbing the nutrient in the soil. Thus, since there is no P toxicity in plants grown in this soil, it was not possible to study the effect of Si in mitigating this stress. Either way, the risk of P toxicity in Oxisol is relatively low. It requires future studies using higher doses of the element ($> 600 \text{ mg dm}^{-3}$ of P equivalent to 1200 kg ha^{-1} of P) because, according to ^[2], Oxisol's maximum P adsorption capacity is close to 575 mg dm^{-3} and may vary according to other soil properties, such as organic matter content.

Given these results obtained in plants cultivated in Entisol, mitigating damage caused by excess P in *M. maximus* may be among the many benefits of Si in other species ^[72, 73]. In a study on rice plants cultivated in a nutrient solution with an excess of P, Si negatively regulated the gene expression of Pi transporters, decreasing their absorption by the plant ^[74]. This aspect may be one of the Si mechanisms to mitigate P excess in grasses and should be the subject of future research.

Studies involving Si most often address stress, as it is believed that Si only benefits crops under stress, with no effect on plants without stress^[71]. However, this study evaluated the effects of Si on the morphogenesis of plants under P sufficiency, i.e., plants with no stress. We evidenced an increase in the number of live leaves per tiller and the number of tillers in plants grown in Oxisol, in addition to the decrease in stem elongation in plants grown in Entisol. These Si effects reflected in an increase in DM production in *M. maximus* in both soils, possibly due to different Si mechanisms reported in grasses, such as the promotion of adequate nutritional homeostasis to provide an increase in the efficiency of N and P use^[20, 75–77], even in plants without stress^[78].

Therefore, our results corroborate the fact that Si can influence the morphology of plants^[23], mainly in Si-accumulating species^[79]. It contributes to optimizing the productive potential of plants without stress and mitigating nutritional stress, as observed here.

Overall, this study showed that using Si to benefit *M. maximus* depends on the presence or absence of stress, the type of stress, and the cultivated soil class. Therefore, this study proved that Si is useful to *M. maximus* cultivated in different regions of the world since it can cover cultivation areas without nutritional stress in sandy or clayey soils. Furthermore, it can cover areas with excess P, especially in sandy soils, enabling its use in agriculture. This finding confirms the important role of Si as a tool for more sustainable agricultural production^[80].

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

One of the concerns of the scientific community regarding Si in forage is that it can be an anti-nutritional element in the feed^[81]. Furthermore, it is not known whether the effect of Si in the forage is beneficial or not in the quality of the plant in different cultivation conditions, such as in areas without nutritional stress, to wit, areas with excellent soil fertility or with P-deficient or P-excess soils. It is a worrying fact because, as previously seen, there is no point in Si having an important benefit in morphogenesis and plant growth if there is a significant loss in forage quality, which would negatively affect the performance of the animal consuming this forage.

In order to answer this question, we showed that using nanosilica in P-deficient plants did not alter the morphological composition or fiber composition of *M. maximus* and even increased the CP and mineral matter contents. This increase in protein is likely because Si increased the absorption of P^[70] and N^[82] involved in protein synthesis in the plant. This finding is relevant given the importance of protein for the activity of the ruminal microbiota^[14]. The increase in the mineral matter in the presence of Si indicates the absorption of the beneficial element by stressed plants^[69, 19]. Using Si in these plants did not impair forage digestibility, possibly because Si did not increase lignification. However, in P-deficient wheat, Si favored lignin synthesis^[83], confirming that there are differences between species regarding lignification^[56], as each species may have a strategy to mitigate stress, using Si in the cell wall and/or activating enzymes involved in lignin synthesis.

This study clearly indicates that the supply of Si in *M. maximus*, even in the condition of P deficiency, does not risk jeopardizing the forage's nutritional value. This information is of great practical importance because most pastures cultivated in tropical regions have soils with P deficiency^[1] and could benefit from sustainably using this element.

For areas with excess P, using Si also allowed achieving promising results in *M. maximus*, with a better morphological composition of the plant cultivated in both soils, as it decreased dead material and increased the leaf blade fraction. Furthermore, it is worth noting the decrease in the tiller mortality rate, which^[11] is essential for the persistence of a pasture. It is important to highlight that similar to what was observed in studies with excess P in other cultures^[84, 85], the supply of Si in *M. maximus* under excess P caused a decrease in the lignin content in the fiber and an increase in the CP and mineral matter content, especially in plants grown in Entisol.

Some benefits of lignin for stressed plants have already been reported, such as improvement in leaf architecture^[86] and the antioxidant action of phenolic precursors in fighting reactive oxygen species^[87]. However, it is not an interesting strategy for forage plants since lignin is an anti-nutritional constituent for ruminants^[68]. This study verified that, in *M. maximus*, Si does not stimulate lignin synthesis, even in plants with excess P. It occurs because the plant may be using Si at a low energy cost to compose constituents of the cell wall, fulfilling the support function of plant tissue in place of lignin. Thus, its synthesis is decreased by the plant^[88].

These results show that fertilization with nanosilica contributed to a better morphological and chemical composition in grasses even under excess P. Thus, the third hypothesis was partially confirmed since fertilization with nanosilica alleviated the stress caused by excess P without compromising the forage quality. It was also clear that fertilization with SiO₂ nanoparticles in plants with P sufficiency allowed a decrease in lignin content, which may contribute to greater fiber digestibility^[56] and joins other promising results of Si in grasses without nutritional stress^[89]. In addition, we showed that using Si in plants with optimal P nutrition increased the protein content, which also occurred in Zuri (*M. maximus*) and Ipyporã (*Urochloa ruziziensis* x *U. brizantha*) grasses fertilized with silicates^[28].

However, plants absorb Si in greater amounts when subjected to stress^[89]. Thus, the decrease in forage lignin content under P sufficiency must have been triggered by a slight increase in Si content. In rice plants and sorghum without stress, a negative relationship between Si accumulation and lignin synthesis was verified^[84, 85] and observed in the sufficiency of P in this study. Further studies on the relationship between Si fertilization and lignin biosynthesis in grasses are required, including in properly nourished plants, as the results seem to depend on the crop and growing conditions.

Overall, these results support Si fertilization in forage grasses under P stress or adequately nourished to optimize the integrated soil:forage:animal system, resulting in the better formation of pastures, which, according to^[14], is the most economical food source for animal production.

5. CONCLUSIONS AND PERSPECTIVES

In general, we portray for the first time the origin of the losses in the growth of *M. maximus* cv. Zuri under P deficiency and excess P grown in two tropical soils. Moreover, we describe the morphogenic and structural strategies of the plant to mitigate these stresses, even though there is no loss in forage quality.

Furthermore, we found that fertilization with SiO₂ nanoparticles promotes a greater balance in the growth and senescence processes of the plant, alleviating the loss in biomass production, especially in plants cultivated under excess P in sandy soil. In addition, it increases production in P sufficiency in soils of different textures without impairing digestibility.

New studies should investigate Si-specific mechanisms with metabolomic approaches in mitigating P excess damage in grasses and optimizing production in non-stressed plants, especially its relationship with lower plant senescence, which was a vehement effect of Si observed here. The mitigation of P deficiency in forage grasses mediated by Si should be the subject of future research, given the potential observed here to improve the deficient plant's growth and protein content.

Abbreviations

ADF: acid detergent fiber

C: carbon

CP: crude protein

DM: dry matter

LA: Leaf appearance rate

LE: leaf elongation rate

MM: mineral matter

NDF: neutral detergent fiber

N: nitrogen

NFCs: non-fiber carbohydrates

P: phosphorus

SE: stem elongation rate

SD: stem diameter

Si: silicon

TA: tiller appearance rate

TDN: total digestible nutrients

TM: tiller mortality rate

TS: tiller survival rate

Declarations

AVAILABILITY OF DATA AND MATERIALS

The datasets generated and/or analyzed in this study are available from the corresponding author upon reasonable request.

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AUTHOR CONTRIBUTIONS

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

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RESEARCH INVOLVING PLANTS

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

ETHICS DECLARATIONS

Ethics approval and consent to participate: Not applicable.

Consent for publication: Not applicable.

COMPETING INTERESTS

The authors declare no competing interests.

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Figures

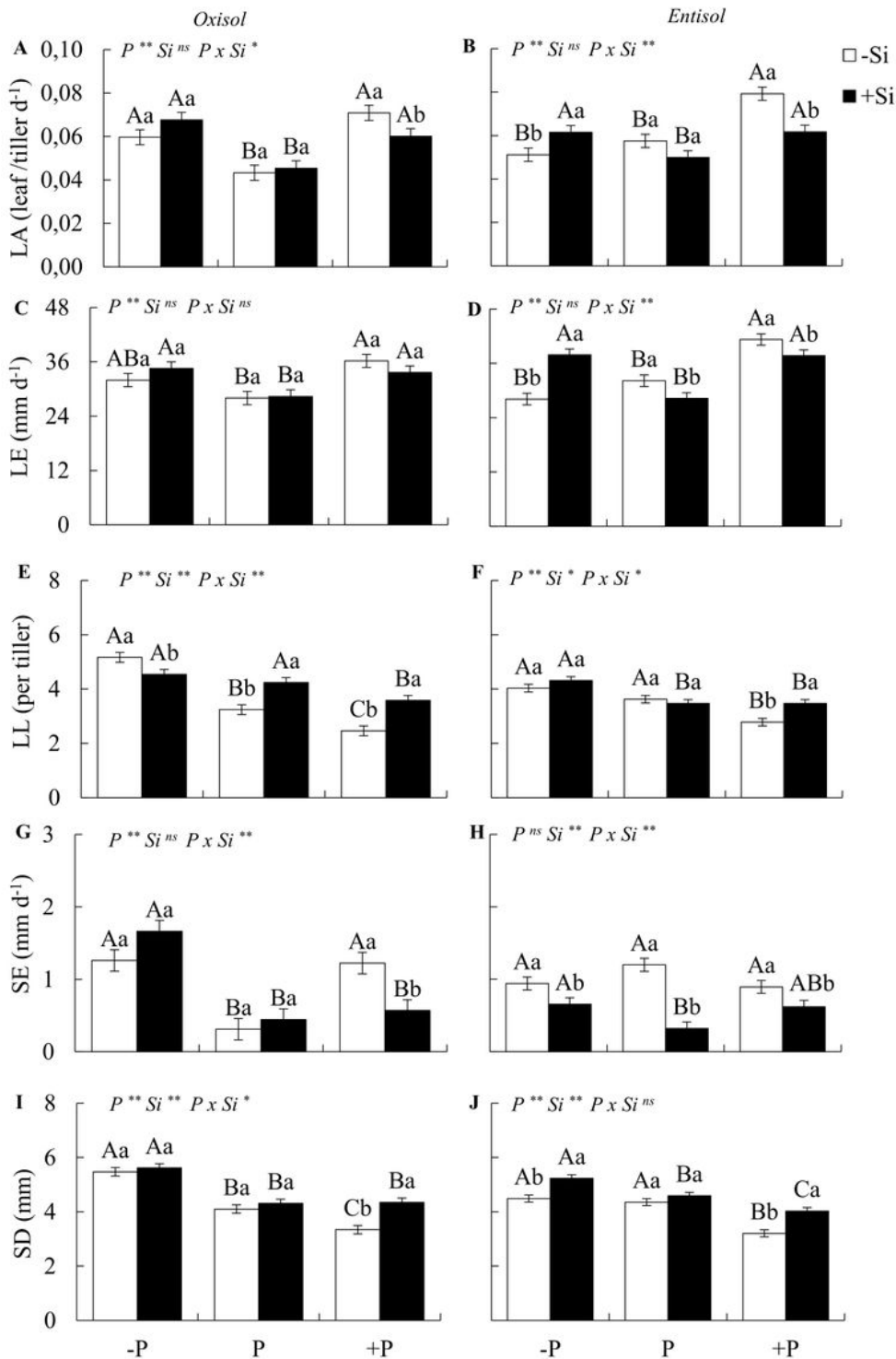


Figure 1

Leaf appearance rate (LA), leaf elongation rate (LE), number of live leaves per tiller (LL), stem elongation rate (SE), and stem diameter (SD) of Zuri guinea grass under phosphorus levels of deficiency (-P), sufficiency (P), and excess (+P) in Oxisol (A, C, E, G, and I) and Entisol (B, D, F, H, and J) in the absence (-Si) and presence of silicon (+Si, 1.5 mmol L⁻¹). *Ns*, *, ** refer to the F test as not significant and significant

at 5 and 1%, respectively. Nutritional states are compared in uppercase letters, and the effect of Si in lowercase letters (Tukey test, $p<0.05$). Bars correspond to the standard error of the mean.

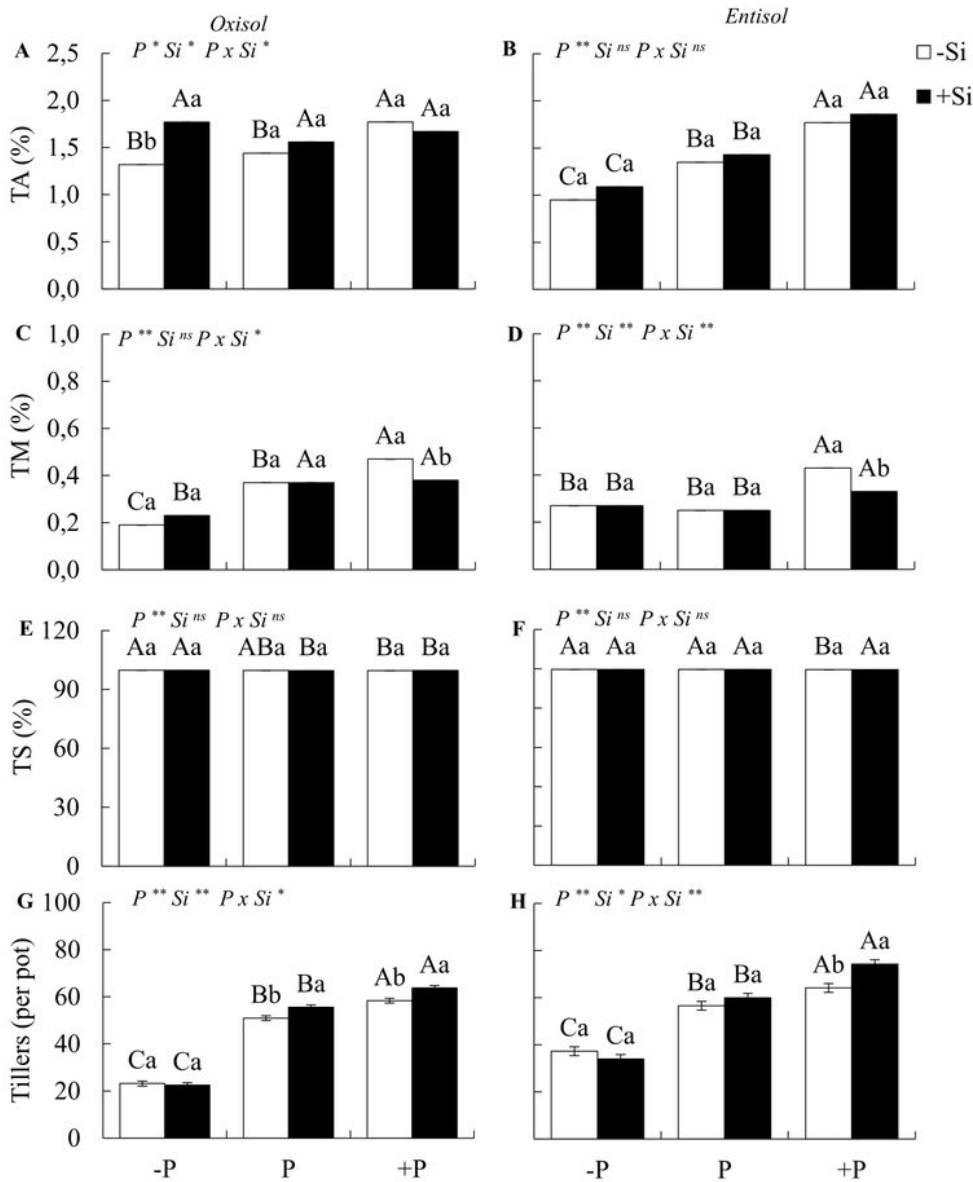


Figure 2

Tiller appearance rate (TA), tiller mortality rate (TM), tiller survival rate (TS), and number of tillers per pot of Zuri guinea grass under phosphorus levels of deficiency (-P), sufficiency (P), and excess (+P) in Oxisol

(A, C, E, and G) and Entisol (B, D, F, and H) in the absence (-Si) and presence of silicon (+Si, 1.5 mmol L⁻¹). Ns, *, ** refer to the F test as not significant and significant at 5 and 1%, respectively. Nutritional states are compared in uppercase letters, and the effect of Si in lowercase letters (Tukey test, p<0.05). Bars correspond to the standard error of the mean.

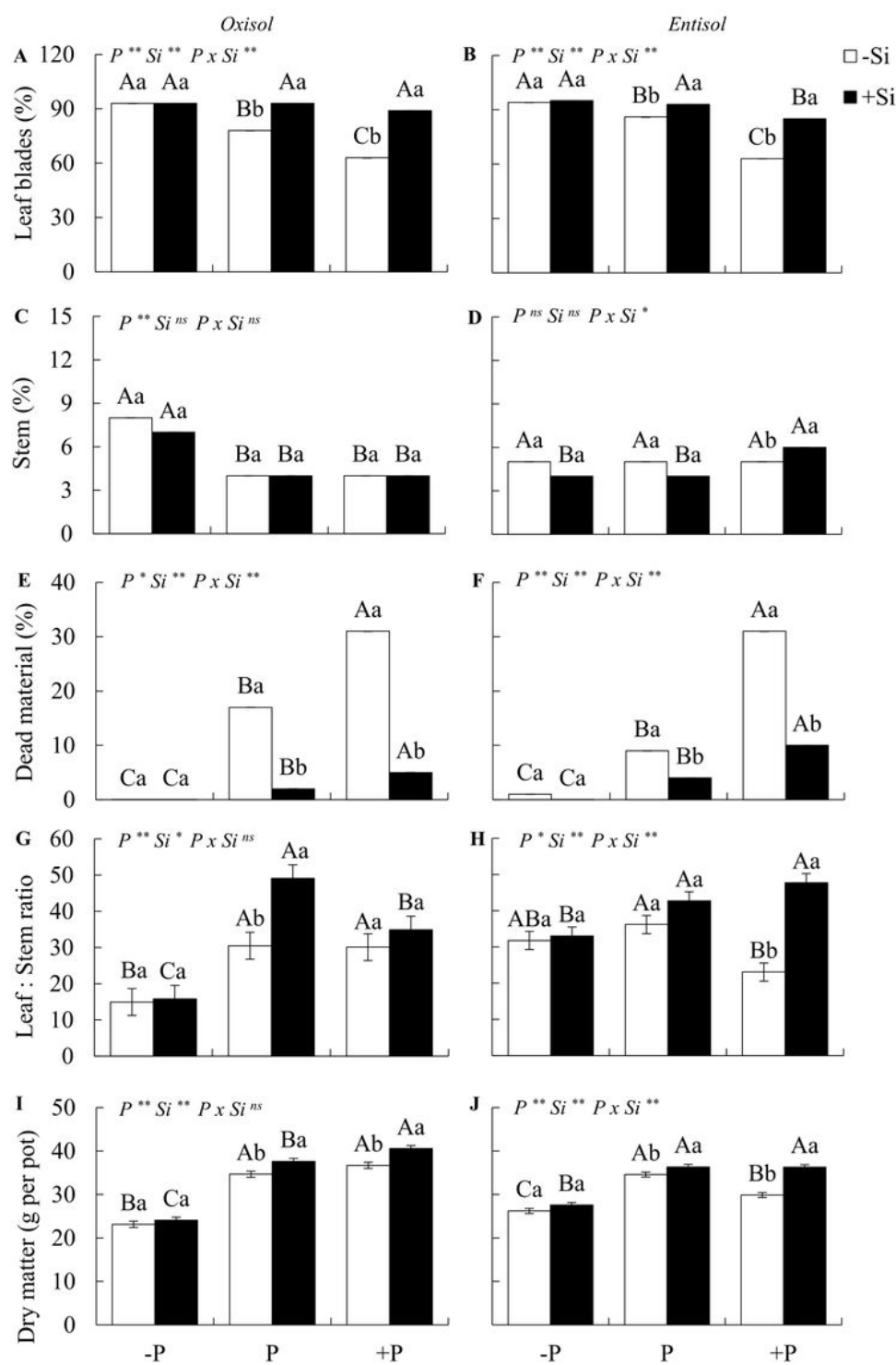


Figure 3

Percentage of leaf blade, stem, dead material, leaf:stem ratio, and dry matter production of Zuri guinea grass under phosphorus levels of deficiency (-P), sufficiency (P), and excess (+P) in Oxisol (A, C, E, G, and I) and Entisol (B, D, F, H, and J) in the absence (-Si) and presence of silicon (+Si, 1.5 mmol L⁻¹). Ns, *, ** refer to the F test as not significant and significant at 5 and 1%, respectively. Nutritional states are compared in uppercase letters, and the effect of Si in lowercase letters (Tukey test, p < 0.05). Bars correspond to the standard error of the mean.

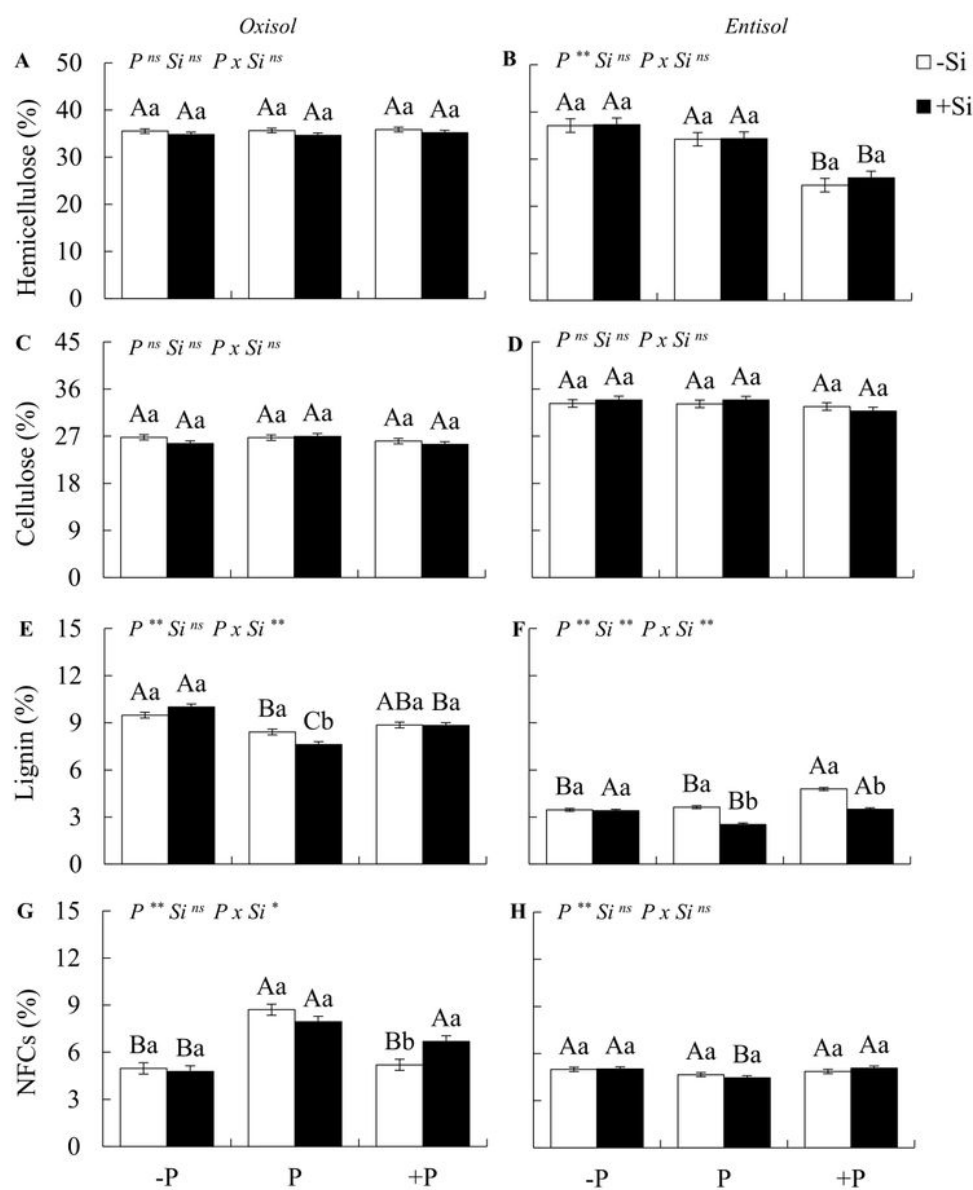


Figure 4

Percentage of hemicellulose, cellulose, lignin, and non-fiber carbohydrates (NFCs) in the dry matter of Zuri guinea grass cultivated by six regrowth cycles under phosphorus levels of deficiency (-P), sufficiency (P), and excess (+P) in Oxisol (A, C, E, and G) and Entisol (B, D, F, and H) in the absence (-Si) and presence of silicon (+Si, 1.5 mmol L⁻¹). Ns, *, ** refer to the F test as not significant and significant at 5 and 1%, respectively. Nutritional states are compared in uppercase letters, and the effect of Si in lowercase letters (Tukey test, $p < 0.05$). Bars correspond to the standard error of the mean.

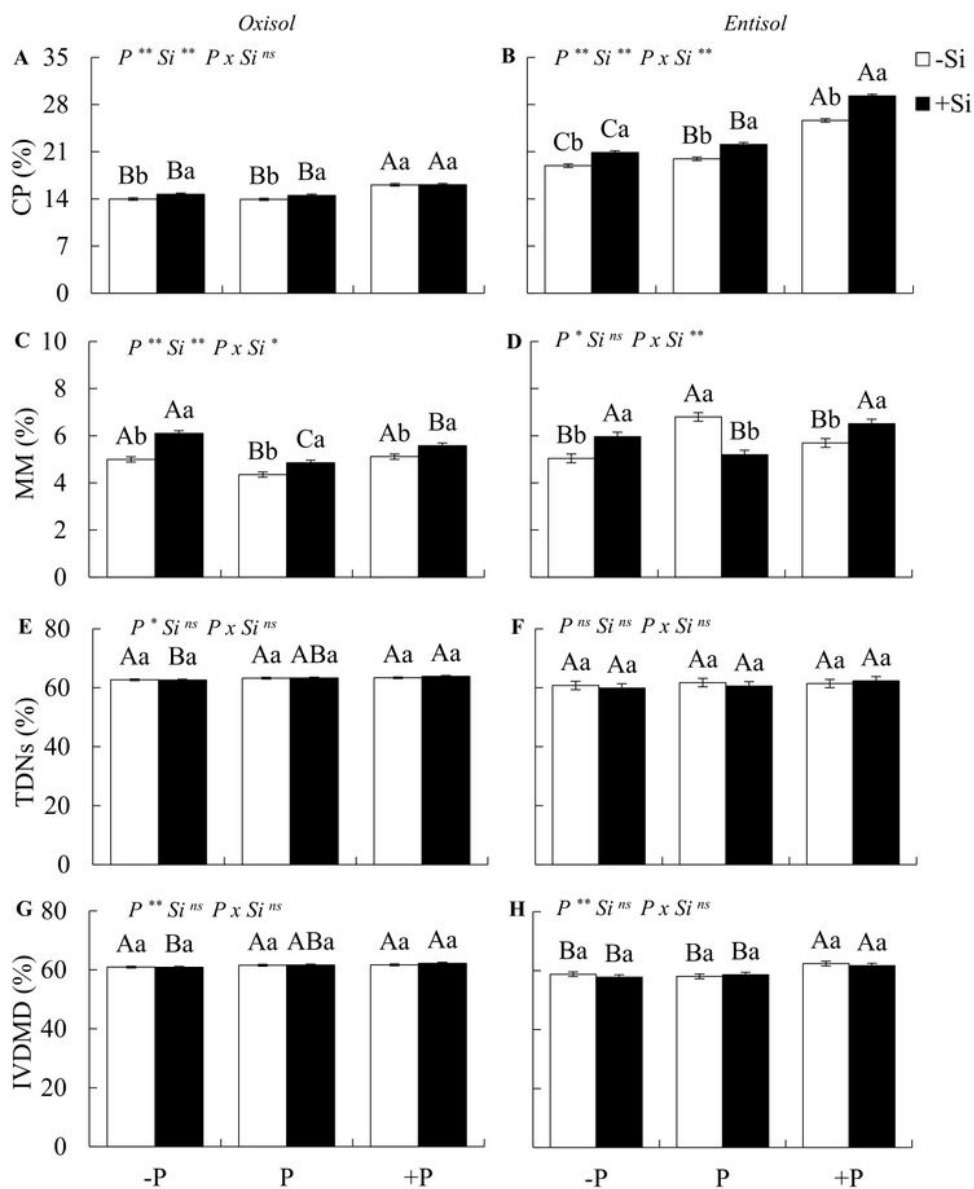


Figure 5

Percentage of crude protein (CP), mineral matter (MM), total digestible nutrients (TDNs), and in vitro dry matter digestibility (IVDMD) of Zuri guinea grass, cultivated by six regrowth cycles under phosphorus levels of deficiency (-P), sufficiency (P), and excess (+P) in *Oxisol* (A, C, E, and G) and *Entisol* (B, D, F, and H) in the absence (-Si) and presence of silicon (+Si, 1.5 mmol L⁻¹). ns, *, ** refer to the F test as not significant and significant at 5 and 1%, respectively. Nutritional states are compared in uppercase letters,

and the effect of Si in lowercase letters (Tukey test, $p < 0.05$). Bars correspond to the standard error of the mean.

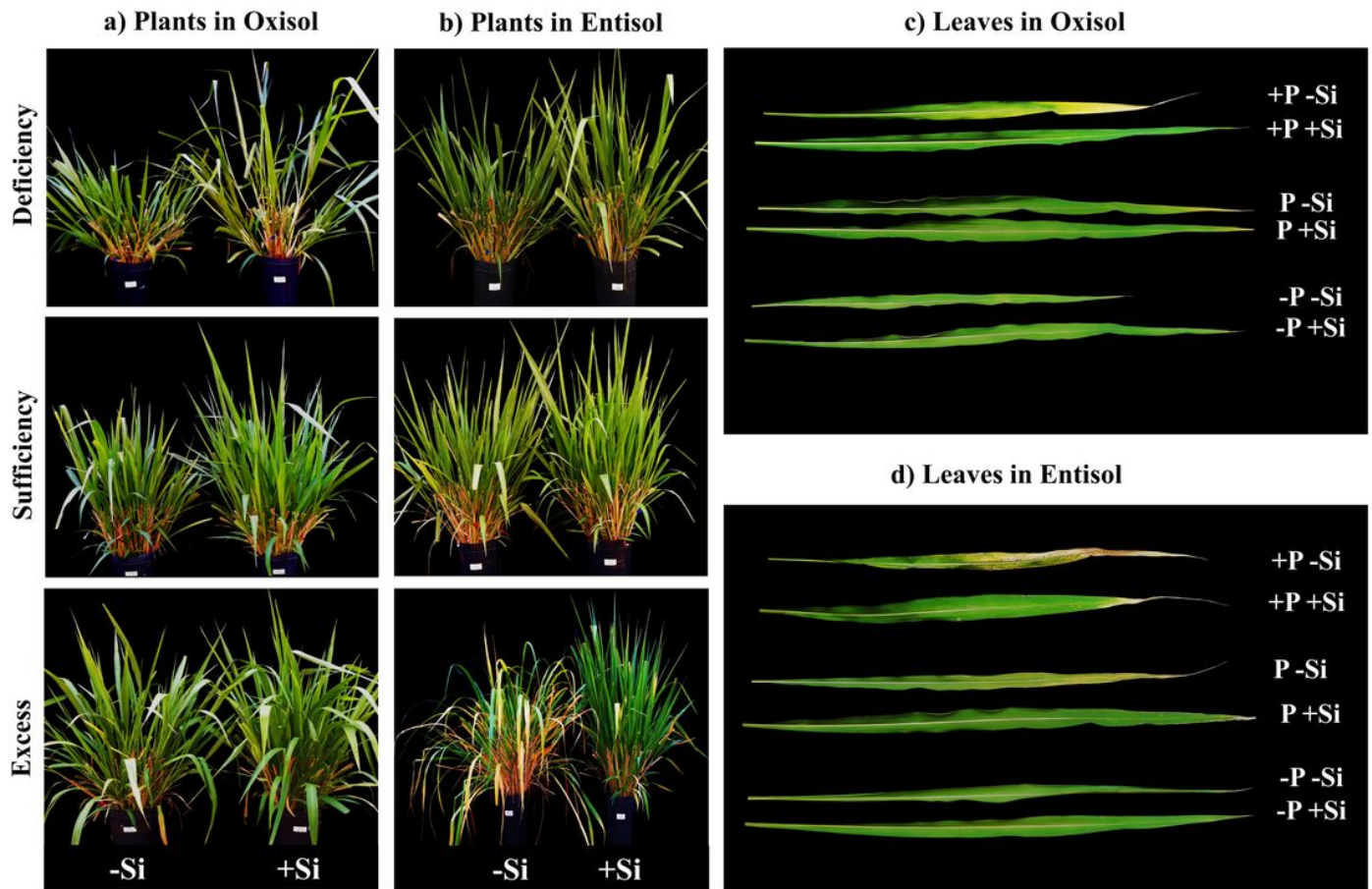


Figure 6

Plant phenotype and visual aspects of the leaf blades of *M. maximus* cv. Zuri grown under phosphorus deficiency, sufficiency, and toxicity, combined with the absence (-Si) or presence (+Si) of Si nanoparticles (1.5 mmol L⁻¹) in Oxisol (a) and Entisol (b) at the end of the fifth regrowth cycle.

Supplementary Files

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