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Does fertilization help or hinder? Nutrient inputs shape competition dynamics

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ABSTRACT

Invasive grasses such as Urochloa brizantha pose a major challenge to tropical forest restoration, often outcompeting native species and altering successional dynamics. Success in forest restoration often depends on initial cultivation practices and the competitive dynamics between native species and invasive grasses. This study evaluated the interaction between Senegalia polyphylla, a native tree species recommended for restoration, and Urochloa brizantha, an invasive grass, under different mineral and organic fertilization regimes. A greenhouse experiment was conducted using a completely randomized design with a factorial arrangement involving three cultivation types (monocultures of each species and interspecific competition), six fertilization treatments combining different proportions of mineral and organic fertilizers and a control without fertilization, and four replicates. Biomass production, nutrient content, and nutrient use efficiency were assessed.Our results indicate that, in the absence of fertilization, S. polyphylla facilitates the growth of U. brizantha, promoting a 96 % increase in grass biomass production. However, nutrient addition transforms facilitation into competition, particularly with organic fertilization. Although S. polyphylla showed near-optimal phosphorus uptake even without fertilization, competition with U. brizantha limited its efficient use of nutrients, particularly P and K. Moreover, the invasive grass demonstrated more efficient nitrogen use across all fertilization regimes, highlighting its competitive potential. S. polyphylla biomass was not significantly redistributed aboveground as a strategy to overcome light competition, suggesting that belowground competition was equally intense. We conclude that fertilization, while beneficial for initial revegetation, must be carefully planned in restoration projects, as it may favor invasive grasses and hinder native tree growth.

1. Introduction

Exotic grasses, particularly Urochloa species, dominate over 90 % of Brazilian pastures, occupying approximately 75 % (211 million hectares) of deforested land (Mello et al., 2020). Introduced for forage, ornamental purposes, or unintentionally via contaminated seeds, these African grasses threaten tropical ecosystems by reducing biodiversity, altering nutrient cycles, and impairing the establishment of native tree species (Duque et al., 2022; Damasceno and Fidelis, 2023; Rabelo et al., 2023). Their high growthand biomass further increase restoration costs and seedling mortality (Damasceno et al., 2018; Vieira et al., 2019; Souza et al., 2020).

To restore invaded landscapes, plant native species like *Senegalia polyphylla* (DC.) Britton & Rose (Fabaceae) has gained attention due to its capacity to enhance nutrient cycling, improve soil quality, and facilitate native plant recruitment (Souza et al., 2020; Barbosa et al., 2022). However, while S. polyphylla can improve soil fertility, this may also intensify competition with invasive grasses, potentially hindering its own establishment. Additionally, fertilization practices are often applied indiscriminately, following conventional methods used in

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commercial plantations without considering their effects on species interactions in restoration settings (Brancalion et al., 2019; Ornelas et al., 2022).

Effective management strategies, including fertilization, are crucial to overcoming these challenges and promoting native species establishment (Jaquetti and Gonçalves, 2021; Araújo et al., 2024). Mineral fertilizers, characterized by rapid nutrient availability, often favor fast-growing invasive grasses such as *Urochloa. brizantha* by providing an immediate resource advantage (Schott et al., 2016; Wang et al., 2019). In contrast, organic fertilizers release nutrients more gradually through microbial mineralization, potentially reducing competition and sustaining nutrient availability over extended periods (Arif et al., 2017; Otero et al., 2019). Identifying fertilization strategies that balance competition is critical to restoration success, particularly in areas invaded by *U. brizantha* (Walker et al., 2015; Zhao et al., 2020).

Nutrient availability influences how plants compete or coexist, and their ability to adjust nutrient uptake strategies may affect the outcome of competition. In ecosystems with low nutrient availability, the coexistence of exotic grasses and native leguminous trees involves complex interactions of competition and facilitation (Biro et al., 2024). Through biological nitrogen fixation, *S. polyphylla* can enhance soil nitrogen availability, potentially benefiting nearby plants, including invasive species (Meli et al., 2018; Meena et al., 2018). However, invasive grasses such as *U. brizantha* may exploit this additional nitrogen, increasing their competitive advantage (Dornbush et al., 2018). These dynamics raise concerns about whether legumes' facilitative role inadvertently strengthens invasive grasses' persistence, particularly in nutrient-poor soils.

Under high nutrient availability, the theory of asymmetric competition suggests that early resource acquisition provides a lasting competitive advantage to fast-growing species (Schwinning and Weiner, 1998). This dynamic is evident in *U. brizantha*, which exhibits superior nitrogen uptake capacity in nutrient-rich environments (Li et al., 2024a). Mineral fertilization may amplify this asymmetry by rapidly increasing nutrient availability, favoring *U. brizantha*. In contrast, the gradual nutrient release from organic fertilization could mitigate competitive imbalances and support native species (Sloan et al., 2016; Krapfl et al., 2016; Ornelas et al., 2022). Additionally, *S. polyphylla* has demonstrated an increased capacity to absorb organic nitrogen in competition with invasive grasses, highlighting the potential for optimizing fertilization strategies in restoration efforts (Bueno et al., 2019a, 2019b).

In response to nutrient availability, plants can adopt different strategies to mitigate competition, influencing their survival and growth under varying resource conditions. The coexistence of trees and grasses under nutrient competition can be explained by two main hypotheses (Biro et al., 2024). The first suggests resource specialization, where grasses like U. brizantha excel in nitrogen (N) acquisition (Valliere et al., 2022), while legumes such as S. polyphylla rely on higher phosphorus (P) availability for optimal growth (Yang et al., 2023). This specialization minimizes competition in nutrient-poor soils, with grasses showing higher foliar N content and trees higher P content. The second hypothesis highlights differences in resource allocation, with grasses investing in root biomass and trees prioritizing aboveground growth, especially in nutrient-rich environments (Bhandari et al., 2023).

This study investigates how different fertilization regimes—mineral, organic, and combined—affect the competitive dynamics between *S. polyphylla* and *U. brizantha*. Understanding these dynamics can guide fertilization strategies in forest restoration projects, especially given the lack of consensus in the literature regarding the effects of different fertilization types on competition outcomes. We hypothesize that (i) different fertilization regimes alter the coexistence dynamics between *S. polyphylla* and *U. brizantha* by shifting the balance between competition and facilitation, and *S. polyphylla* and *U. brizantha* adapt their competitive strategies to nutrient availability, (ii) with resource specialization dominating in nutrient-poor soils and (iii) shifts to aboveground and belowground competition in nutrient-rich environments. The findings aim to inform fertilization strategies that balance competition and enhance native species establishment in degraded tropical ecosystems.

2. Material and methods

2.1. Experimental design and plant cultivation

We conducted the experiments in a greenhouse in Diamantina, Minas Gerais, Brazil (18°12′S; 43°34′W, altitude 1370 m). As a substrate, we used a medium-textured dystrophic RED LATOSOL (Santos et al., 2018), collected from the surface layer (0–0.20 m), clod-free, air-dried, and sieved through a 5 mm mesh (Table S1). The soil was collected from a pasture area naturally colonized by U. brizantha and designated for future forest restoration interventions, located within the Fartura Private Natural Heritage Reserve (Reserva Particular do Patrimônio Natural – RPPN Fartura) in Aricanduva, Minas Gerais (15°30′S; 39°50′W), part of the Atlantic Forest biome. This setting ensured realistic conditions for evaluating interactions between native and invasive species in restoration contexts. A 15 cm^3 subsample was sieved through a 2 mm mesh and submitted to physical and chemical analyses following Teixeira et al. (2017).S. polyphylla seedlings were produced from seeds collected in the RPPN Fartura. Seeds were processed and sown in tubes containing 0.29 dm^3 of a 1:1:1 (v:v:v) sterilized mixture of local soil, carbonized rice husk, and sand. Seedlings with four pairs of leaves and approximately 0.08 m in height were selected, gently removed from the tubes, their roots washed in deionized water, and transplanted into 6 dm^3 polyethylene pots filled with the experimental soil. U. brizantha plants were established by direct sowing immediately after transplanting the tree seedlings. A density of three individuals per pot, equivalent to 60 plants m^2, was used to simulate typical infestation levels in degraded pasture areas (Vieira et al., 2019).

The experiment was set up in a completely randomized design, in a factorial arrangement, with three types of cultivation, six types of fertilization, and four replications. The three types of cultivation included *S. polyphylla* and *U. brizantha* grown alone (A) and in competition (C). The fertilizations consisted of six proportions of mineral fertilizer (MF) and organic fertilizer (OF) recommendations for *S. polyphylla*: %MF-OF: 100–0, 75–25, 50–50, 25–75, 0–100, and 0–0 % (Table S2).

Mineral fertilization (100–0 %) consisted of 50 mg of N (ammonium sulfate), 150 mg of P (single superphosphate), and 50 mg of K (potassium chloride) applied per dm^3 of soil (Gonçalves et al., 2008). Organic fertilization (0–100 %) included 5 g of cured cattle manure per dm^3 of soil (CFSEMG, 1999). Manure nutrient composition was determined by nitroperchloric digestion (Silva, 2009), with levels of 3.1 % N, 1.8 % P, 2.1 % K, 12.3 % Ca, 2.1 % Mg, and 26.1 % S. Intermediate treatments involved proportional mixes of mineral and organic fertilization. Fertilization occurred 15 days before transplanting *S. polyphylla* seedlings or sowing grass.

2.2. Interspecific competition intensity (RII)

The effect of competition between *S. polyphylla* and *U. brizantha* was assessed in each treatment using the Relative Interspecific Competition Index (RII) as described by Wang et al. (2020). This index quantifies the intensity and direction of interspecific interactions, with values ranging from −1 to 1. Positive values indicate facilitation, while negative values represent competition; the closer the value is to ±1, the stronger the facilitation or competition. The RII was calculated using the formula: $RII_{Fertilization} = (DMT_C - DMT_A)/ (DMT_C + DMT_A)$, where $RII_{Fertilization}$ where $RII_{Fertilization}$ represents the relative competition index for each fertilization treatment, DMT_C is the total dry mass of the species grown in competition, and DMT_A is the total dry mass of the species grown in monoculture.

The calculations followed two sequential steps. First, an RII value was calculated for *S. polyphylla* under each fertilization treatment by substituting the biomass of *S. polyphylla* into the formula. Second, the same calculation was performed for *U. brizantha* under each fertilization treatment. The DMT_A values were obtained as the average dry mass of four individuals grown in monoculture under the same fertilization treatment.

2.3. *Dry mass, N, P, and K content and accumulation*

The shoot and root systems of the plants were collected, washed in running water, and immersed in diluted detergent, distilled water, 0.1 mol L^{-1} HCl solution, and deionized water. The plant material (shoot and root) was placed in paper bags, dried in a forced-air oven at 65 °C until a constant weight was achieved, and weighed to determine the dry mass of leaves (DML), stem (DMSt), shoot (DMSh), roots (DMR), and total dry mass (DMT).

The collected shoot material was ground and subjected to sulfuric acid digestion for determining N content, and nitric-perchloric digestion for P and K in the leaves (Silva et al., 2009). N content was determined using the Kjadall method, P via UV–Vis spectrophotometer, and K via flame spectrophotometer. Total N accumulation in leaves was calculated as $CN = T_N \times DML$, where $CN = N$ accumulated in leaves (g), $T_N = N$ content in leaves (%), and $DML =$ dry mass of leaves (g). P accumulation in leaves was calculated as $CP = T_P \times DML$, and K accumulation as $CK = T_K \times DML$ (Figure S1).

Nutrient use efficiency in this context refers to the ability of native trees and invasive grasses to absorb and utilize available soil nutrients to promote growth. We calculated N (NUE), P (PUE), and K (KUE) use efficiency to assess if nutrients from fertilization were converted into new tissues by *S. polyphylla* and *U. brizantha*. Nutrient use efficiency (NUE, PUE, KUE) for the production of leaf dry mass (DML) was obtained by the ratio of DML^2 to the accumulation of N ($NUE = DML^2/CN$), P ($PUE = DML^2/CP$), and K ($KUE = DML^2/CK$) (Siddiqui, 1981; Ramos et al., 2020)).

2.4. *Dry mass production rate and leaf growth rate, height and diameter growth*

The relative growth rate is a critical metric for understanding how native trees compete with invasive grasses. We calculated production and growth rates to assess how plants allocate resources according to their competitive abilities. The production and growth rate were calculated for leaf dry mass (DML), stem dry mass (DMSt), shoot dry mass, root dry mass (DMR), height (H), diameter (D), and number of leaves (N. leaves). The formula used was: production or growth rate = ((final variable value – initial value)/experimental period), where the final and initial values correspond to the measurements at the end and start of the experiment, respectively, for the variables mentioned.

2.5. *Height, diameter, number of leaves and tillers*

The height of the plants (cm) from the base to the apical bud in *S. polyphylla* and from the base to the leaf tip in *U. brizantha* was measured 120 days after planting using a 1.0 mm precision ruler. The stem diameter of *S. polyphylla* was measured with a digital caliper with 0.01 mm precision. The number of leaves and tillers was manually counted.

2.6. *Expected values (EV) of leaf N, P, and K levels in competition*

The effect of interspecific competition on foliar N and P levels was determined by the difference between the observed values (OVs) and the expected values (EVs), as outlined by Wang et al. (2020). The OVs were obtained through direct measurement of leaf N, P, and K levels and calculated as the average for the two species in each competitive treatment.

The EVs were calculated for both species jointly for each treatment and nutrient as follows: $EVNutrient_C = (DMT_{C,i} \text{ x } TN_{A,i} + DMT_{C,j} \text{ x } TN_{A,j}) / (DMT_{C\ i+j})$, where $EVNutrient_C =$ expected value of the nutrient leaf level in competitive cultivation; $DMT_{C,i} =$ total dry mass of species i in competition; $TN_{A,i} =$ nutrient leaf level of species i in isolated cultivation; $DMT_{C,j} =$ total dry mass of species j in competition; $TN_{A,j} =$ nutrient leaf level of species j in isolated cultivation; and $DMT_{C\ i+j} =$ total dry mass of species i plus species j in competition. If the OVs are less than the EVs, the effect of competition is negative; if greater, it is positive. The values of DMSh or DMR for isolated cultivation were calculated using the average of the four plants for each treatment.

2.7. *Nutrient sufficiency ranges*

Foliar tissue analysis is a well-established tool for assessing whether fertilization levels are adequate to support plant growth (Owen, 2020). In this study, nutrient sufficiency ranges were used to evaluate whether fertilization effectively enhanced nutrient availability. The foliar concentrations of nitrogen (N), phosphorus (P), and potassium (K) were compared to established sufficiency thresholds (Berghetti et al., 2021). For S. polyphylla, sufficiency ranges reported in the literature are 2.00–3.00 % for N (Voigtlaender et al., 2019), 0.10–0.12 % for P (Manghabati et al., 2018), and 1.00–1.20 % for K (Lamontagne et al., 2019). For U. brizantha, sufficiency ranges are 1.13–1.50 % for N (Neves et al., 2019), 0.08–0.11 % for P (Lutosa Filho et al., 2020), and 1.43–1.84 % for K (Rodrigues et al., 2019). A literature review was conducted to identify studies focusing on the nutritional requirements of fast-growing trees and Urochloa grasses under conditions similar to those of this study (O'Brien et al., 2020).

2.8. *Nutritional status using vector analysis of monograms*

Nutritional status refers to the level and balance of nutrients present in a plant's tissues. We evaluated the nutritional status to determine how fertilizations maintained nutrient balance in the plant's tissues. Total dry mass (DMT) and the leaf nutritional status of *S. polyphylla* and *U. brizantha* were assessed using vector analysis to evaluate nutrient responses under different fertilization treatments. Responses were expressed relative to the control (0–0 %), normalized to 100 % for easier comparison among treatments, as recommended by Pokharel et al. (2017). The vector's direction relative to the control indicates nutrient concentration or dilution: upwards suggests nutrient concentration in leaves, downwards suggests dilution, and parallel indicates nutrient balance is maintained. The vector's size indicates the magnitude of the effect, either dilution or concentration, and the plant's relative growth.

2.9. *Statistical analysis*

Statistical analyses were performed using the "ExpDes.pt" package within the R environment (R Core Team, 2023). Prior to conducting ANOVA, the normality of residuals was assessed using the Shapiro-Wilk test, confirming that all data were normally distributed. A two-way ANOVA was conducted to evaluate the effects of the factors "Fertilization" (F) and "Type of Cultivation" (C), as well as their interaction ($F \times C$), on the response variables. Interactions were included to determine whether the effect of one factor depended on the levels of the other factor.

When main effects or interactions were found to be significant, the Scott-Knott test was employed as a post hoc procedure to compare treatment means. This test is effective in precisely distinguishing homogeneous groups without excessive splitting, providing clear statistical interpretations in experiments with multiple fertilization regimes (Scott & Knott, 1974). The test was applied to both the comparison of cultivation types (C) and the interaction between Fertilization and Type of Cultivation ($F \times C$).

To fulfill the objectives of this study with clarity and precision, we focused our discussion on the sources of variation related to "Types of Cultivation" and the interaction "Fertilization × Type of Coexistence" within the competitive cultivation system. The indices RII (Relative Interaction Index) and EVs-OVs (Expected Value of Species vs. Observed Value) were compared solely concerning the Fertilization factor (F), as these indices consider the difference between species grown individually and in competition.

3. Results

3.1. Relative interaction index (RII) of competition

The Relative Interaction Index (RII) for S. polyphylla was negative across all treatments, with the most substantial competitive effect observed under mineral fertilization (Fig. 1A). In contrast, U. brizantha exhibited the highest RII (0.94) without fertilization, indicating a highly beneficial facilitative interaction (Fig. 1B). Under fertilization, interaction patterns shifted, with competition prevailing under organic fertilization, while mineral fertilization still resulted in facilitation, albeit at a lower intensity than the unfertilized condition.

3.2. Dry mass production rate and morphology of S. polyphylla and U. brizantha

The dry mass production rate of leaves (DML), stem (DMSt), shoot (DMSh), and roots (DMR), as well as the growth rate in height (H) and diameter (⌀) of *S. polyphylla*, were significantly lower under competitive cultivation (Table 1). On the other hand, *U. brizantha* maintained its dry mass production rate and growth nearlyunchanged under both cultivation regimes. In our study, an average reduction of 50 % in biomass production of *S. polyphylla* was observed after 120 days of competition, while *U. brizantha* remained stable.

The DML production of *S. polyphylla* was higher in treatments with mineral fertilization (100–0 %, 75–25 %, 50–50 %, and 25–75 %), with biomass allocation to the roots being superior to that allocated to the aerial part (Fig. 2A and G). The DMSt and DMR values were relatively similar across treatments, while DMSh was higher in all fertilized treatments than the unfertilized control (0–0 %) (Fig. 2B,C and D). In contrast, the DMSh and DMR production rates of *U. brizantha* were higher in the higher proportions of mineral fertilizer (100–0 % and 75–25 %) (Fig. 2E and F). Although mineral fertilization benefits *S. polyphylla*, the significant increase in biomass of *U. brizantha*, which was up to 600 and 900 % higher compared to the treatment without fertilization (0–0 %). Notably, the DMSh/DMR ratio for U. brizantha remained consistent across treatments, indicating a proportional allocation of biomass above and below ground regardless of the fertilization regime (Figura 2H).

Table 1
Production rate (mg.day^{-1}) of dry leaf mass (DML), stem dry mass (DMSt), shoot dry mass (DMSh), root dry mass (DMR), DMSh/DMR ratio, height (H) (mm. day^{-1}), collar diameter (⌀) (mm.day^{-1}), number of leaves (Leaves.day^{-1}), and number of tillers (Tillers) of *Senegalia polyphylla* and *Urochloa brizantha* grown alone or in competition, 120 days after transplanting in substrate containing dystrophic Red Latosol. The symbol (±) indicates the standard deviation. Lowercase letters differ at 5 % by the F test.

Species	DM (g)	*p*-value	Type of cultivation	
			Alone	Competition
S. polyphylla	DML	<0001	32,61 ± 14,46^{a}	8,50 ± 3,96^{b}
	DMSt	<0001	36,71 ± 14,28^{a}	15,590 ± 8,56^{b}
	DMSh	<0001	97,69 ± 44,82^{a}	40,944 ± 24,56^{b}
	DMR	<0001	70,35 ± 27,96^{a}	27,16 ± 10,35^{b}
	DMSh/DMR	0,26	0,84 ± 0,33	0,72 ± 0,40
	H	<0001	0,83 ± 0,94^{a}	0,07 ± 0,10^{b}
	⌀	0006	0,02 ± 0,01^{a}	0,01 ± 0,01^{b}
	Leaves	<0001	0,41 ± 0,25^{a}	0,08 ± 0,08^{b}
U. brizantha	DMSh	0,7	81,32 ± 51,14	87,16 ± 54,62
	DMR	0,08	194,38 ± 120,50	276,32 ± 187,00
	DMSh/DMR	0,03	0,47 ± 0,25^{a}	0,35 ± 0,09^{b}
	H	0,31	2,93 ± 1,37	2,60 ± 0,75
	Tiller	<0001	0,07 ± 0,04^{a}	0,03 ± 0,01^{b}

The leaf production rate of *S. polyphylla* was highest under mineral fertilization (100–0 %) compared to other fertilization treatments (Fig. 3C). However, height and diameter growth rates did not differ significantly among fertilization types (Fig. 3A and B). In contrast, *U. brizantha* exhibited the highest height growth rate under fertilization treatments containing mineral nutrients, while tiller production remained similar across all fertilization treatments (Fig. 3D and E).

3.3. Observed values (OV) minus estimated values (EV) of leaf N, P, and K content

The difference between the observed values (OV) and estimated values (EV) of N and P content in the leaves of *S. polyphylla* + *U. brizantha* was positive in all treatments (Fig. 4A and B). The difference between OV and EV was more significant in mineral fertilization (100–0 %), demonstrating that fertilizers with rapid availability promote an increase in leaf N, P, and K contents. In the other fertilizations, the difference between OV and EV was higher than the treatment without fertilization (0–0 %) for N and similar for P. Conversely, the difference between OV and EV was negative for leaf K in the 50–50, 25–75, and 0–100 % fertilizations and in the treatment without fertilization (0–0 %), with competition reducing the contents (Fig. 4C).

The leaf N and K concentrations in S. polyphylla were highest under

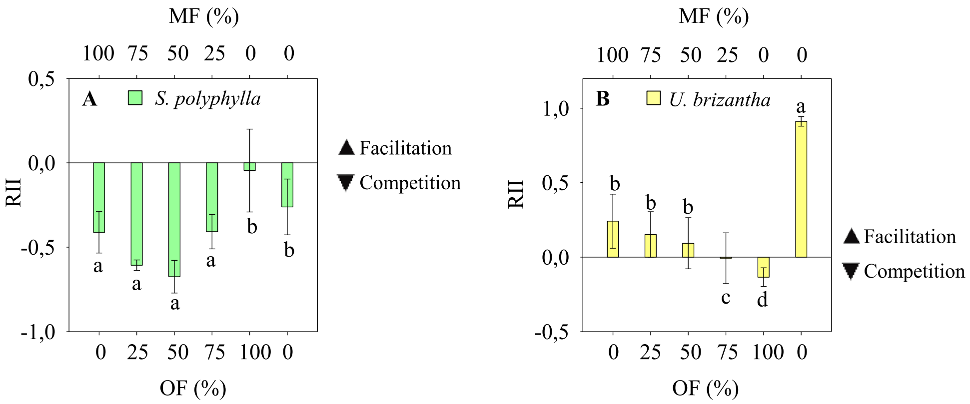

Fig. 1. Relative Inter-specific Competition Index (RII) of, *S. polyphylla* (Fig. 1A) and *U. brizantha* (Fig. 1B) in competition cultivation 120 days after transplanting in substrate containing dystrophic Red Latosol. The upper and lower axes of each graph show, respectively, the combination between MF and OF. Lowercase letters differ between fertilizations (F) at 5 % by the Scott-Knott test.

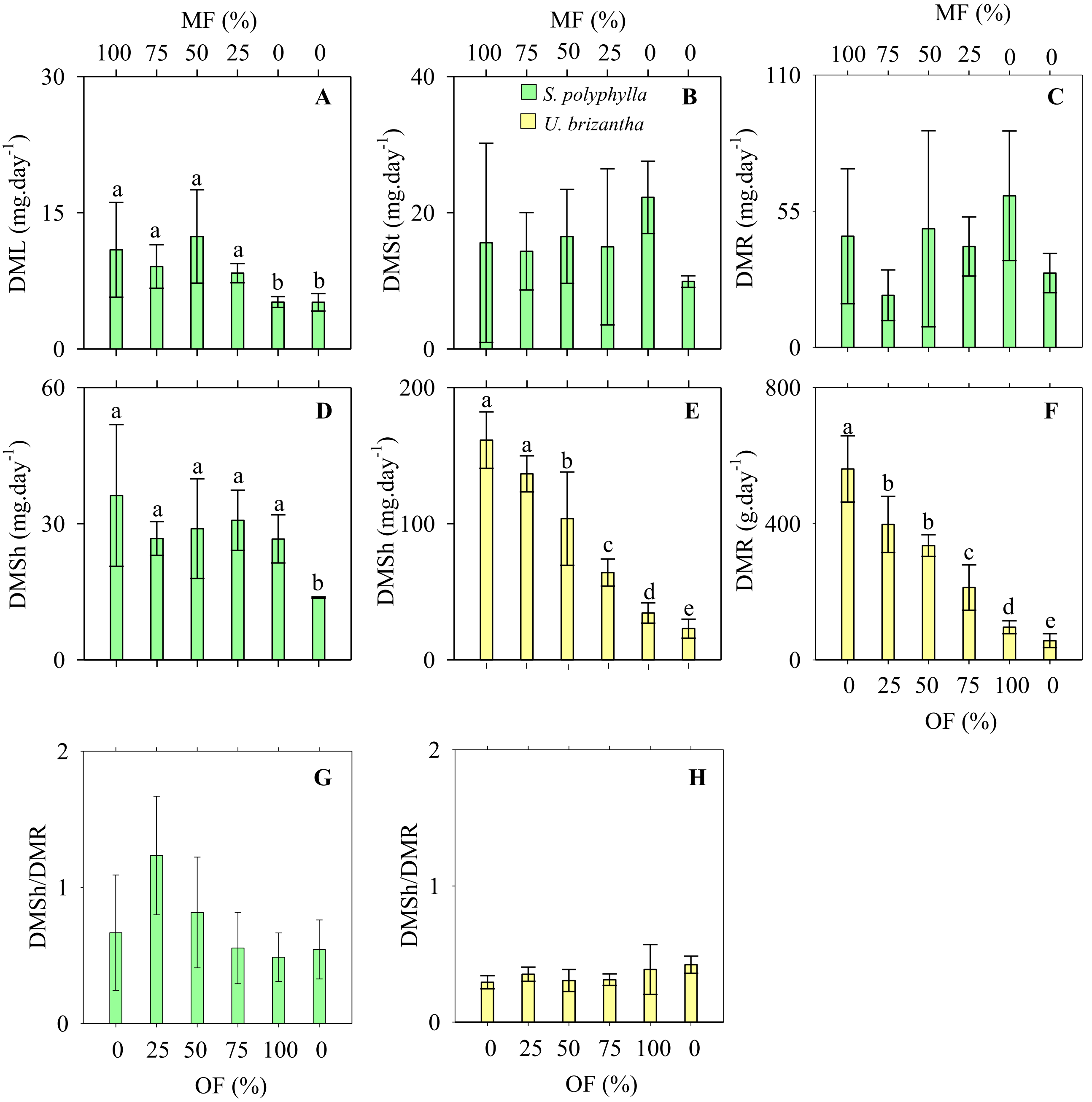

Fig. 2. Production rate (mg.day^{-1}) of dry mass of leaves (DML), stem (DMSt), shoot (DMSh), root (DMR), and DMSh/DMR ratio of *Senegalia polyphylla* (Figs. 2A, B, C, D and G) and *Urochloa brizantha* cv. Marandu (Figs. 2E, F and H) in competition cultivation, 120 days after transplanting in a substrate containing dystrophic Red Latosol. The upper and lower axes of each graph show, respectively, the combination of mineral (MF) and organic (OF) fertilization. Lowercase letters indicate significant differences at 5 % between fertilizations in the competitive cultivation (F vs C) by the Scott-Knott test.

mineral fertilization (100–0 %) (Fig. 5A and C). In contrast, leaf P concentrations were similar between the unfertilized and mineral fertilization treatments, which were higher than the other fertilization regimes (Fig. 5B). Regarding sufficiency ranges, N and K concentrations in S. polyphylla remained below the adequate threshold, while P concentrations fell within the sufficiency range. For U. brizantha, the highest N concentration was observed in the absence of fertilization, while the highest K concentration occurred under organic fertilization, and P concentrations remained similar across treatments (Fig. 5D, E, and F). Despite these variations, U. brizantha exhibited leaf N and K concentrations below the sufficiency range, while P levels were near the lower sufficiency limit. Leaf N and P concentrations in both species were similar whether plants were grown alone or in competition (Fig. 5G and I). In contrast, K concentrations were lower for both species under competitive conditions, suggesting stronger competition for potassium uptake (Figure H).

3.4. Monograms, accumulation, and efficient use of N, P, and K

The concentration of N and K in the leaves of S. polyphylla was highest under mineral fertilization (100–0 %), while P concentrations remained unchanged compared to the unfertilized treatment (0–0 %) (Fig. 6A, B, and C). In contrast, all other fertilization regimes resulted in a dilution effect for N, P, and K in S. polyphylla leaves. For U. brizantha, N dilution was observed across treatments, whereas P and K concentrations varied (Figure D, E, and F). Organic fertilization produced the

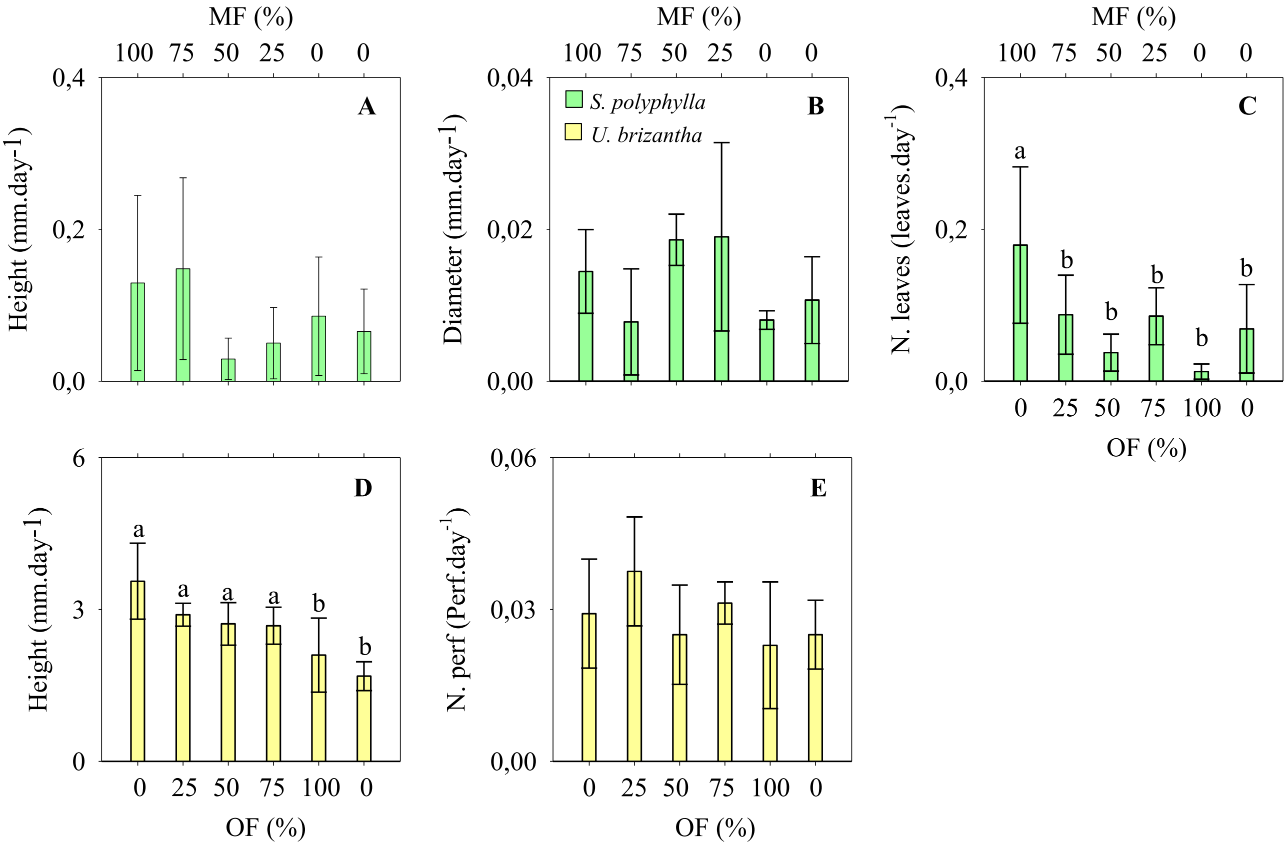

Fig. 3. Growth rate in height (mm.day^{-1}) and diameter (mm.day^{-1}), leaf production rate (Leaves.day^{-1}), and tiller production rate (Tillers.day^{-1}) of *Senegalia polyphylla* (Figs. 3A, B and C) and *Urochloa brizantha* cv. Marandu (Figs. 3D and E) in competition cultivation, 120 days after transplanting in a substrate containing dystrophic Red Latosol. The upper and lower axes of each graph show, respectively, the combination of mineral (MF) and organic (OF) fertilization. Lowercase letters indicate significant differences at 5 % between fertilizations in the competitive cultivation (F vs C) by the Scott-Knott test.

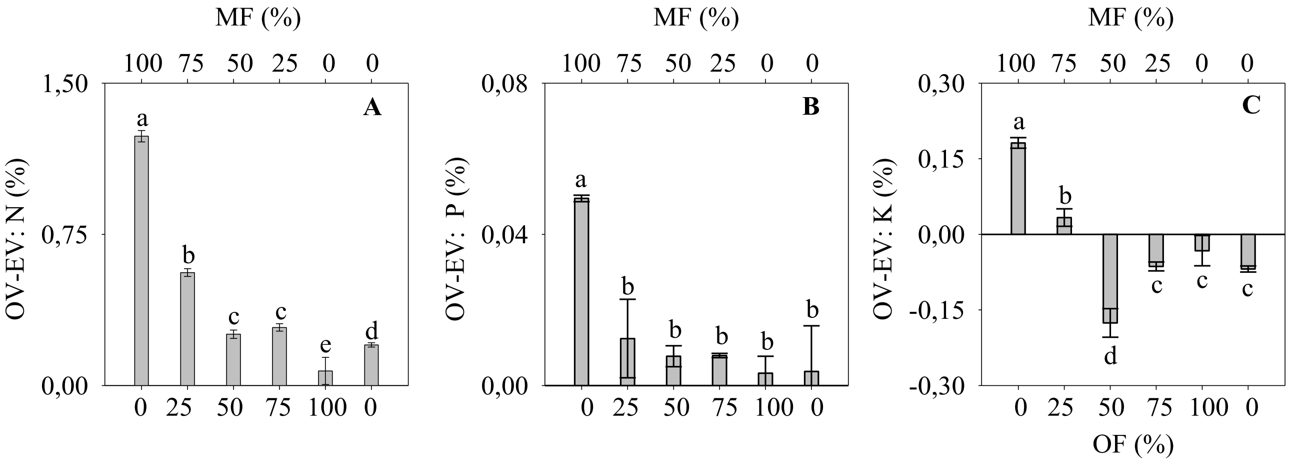

Fig. 4. Observed values (OV) (mean of both species) minus expected values (EV) of leaf N (Fig. 4A), P (Fig. 4B), and K (Fig. 4C) contents (%) of *S. polyphylla* + *U. brizantha* grown in competition cultivation. The upper and lower axes of each graph show, respectively, the combination of mineral (MF) and organic (OF) fertilization. Lowercase letters indicate significant differences at 5 % between fertilizations (F) by the Scott-Knott test.

highest P and K concentrations in U. brizantha leaves.

The efficient use of N, P, and K by S. polyphylla was lower under mineral fertilization (100–0 %), implying less utilization for new tissue formation (Fig. 7A, B, and C). In contrast, *U. brizantha* exhibited higher N use efficiency in fertilized treatments compared to the unfertilized control (0–0 %), while phosphorus and potassium use efficiency remained similar across treatments. (Fig. 7D, E and F).. However, for both S. polyphylla and U. brizantha, competition did not influence the of N and P efficient use. In contrast, both species exhibited higher K efficient use (Fig. 7G, H and I).

4. Discussion

The results demonstrate that fertilization strongly influences competitive interactions between S. polyphylla and U. brizantha, altering their growth, nutrient dynamics, and resource allocation.

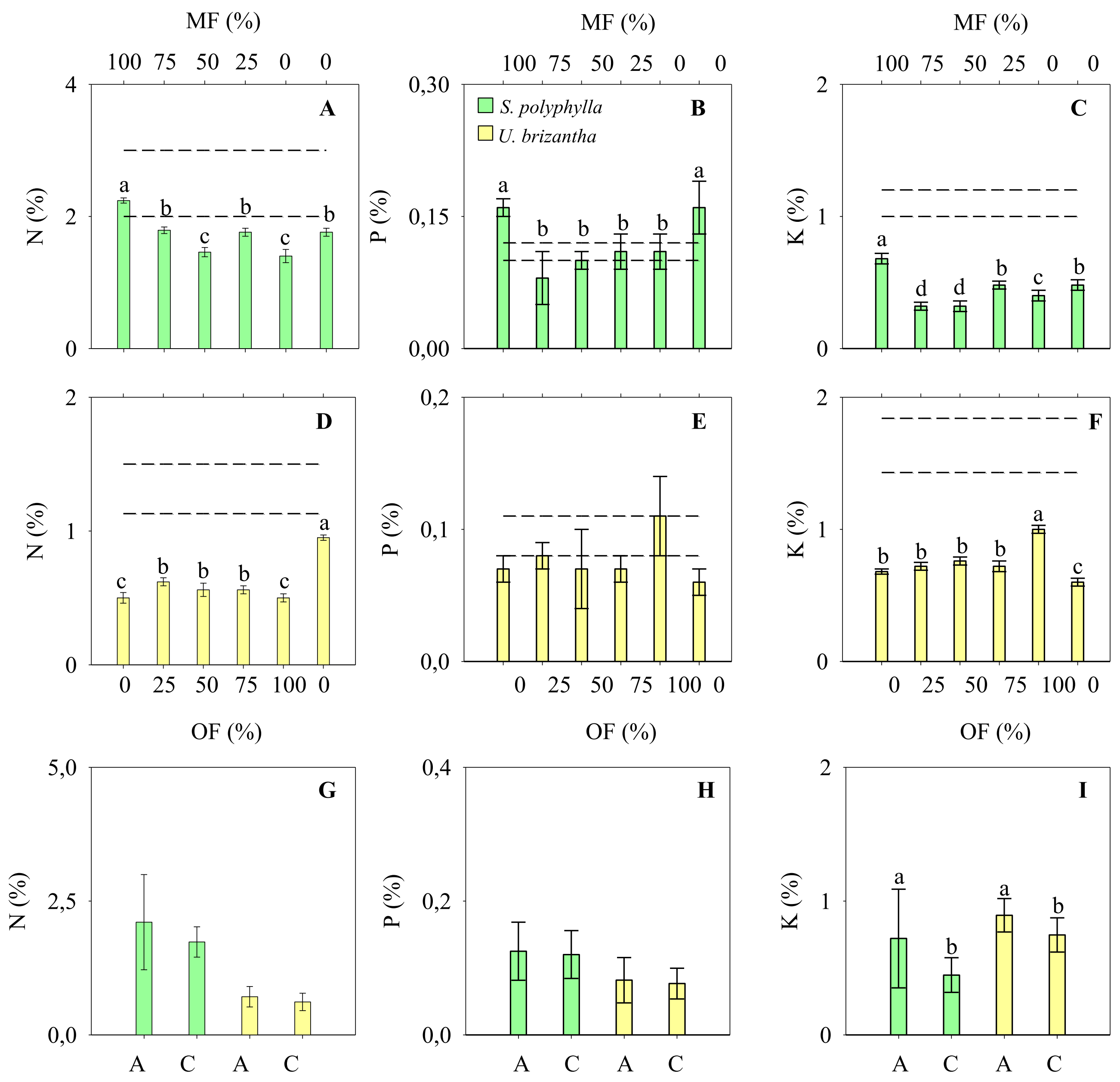

Fig. 5. Nitrogen (N), phosphorus (P), and potassium (K) contents (%) in the leaves of *Senegalia polyphylla* (Figs. 5A, B and C) and *Urochloa brizantha* cv. Marandu (Figs. 5D, E and F) in competition cultivation, 120 days after transplanting in a substrate containing dystrophic Red Latosol. The dashed line (–) represents the upper and lower limits of the sufficiency ranges. The upper and lower axes of each graph show, respectively, the combination of mineral (MF) and organic (OF) fertilization. Lowercase letters indicate significant differences at 5 % between fertilizations in the competitive cultivation (F vs C) by the Scott-Knott test. Leaf N, P, and K contents (%) of *S. polyphylla* and *U. brizantha* grown alone (A) or in competition (C) (Figs. 5G, H, and I) 120 days after transplanting in a substrate containing dystrophic Red Latosol. Lowercase letters indicate significant differences between cultivation types (C) at 5 % by the F test.

Mineral fertilization intensified competition, favoring U. brizantha, which exhibited a 600 % increase in shoot biomass and a 900 % increase in root biomass, severely restricting S. polyphylla growth. In contrast, organic fertilization mitigated this imbalance by suppressing U. brizantha while supporting nutrient uptake by S. polyphylla. Despite allocating more nutrients to leaves, S. polyphylla did not overcome competition under high nutrient availability. Meanwhile, U. brizantha exhibited superior nutrient use efficiency, particularly for K, and benefited from facilitation in unfertilized conditions.

4.1. Different fertilization regimes alter the coexistence dynamics between S. polyphylla and U. brizantha

Our results support the idea that U. brizantha benefits more in the presence of S. polyphylla in the treatment without fertilization (0–0 %). In summary, when there is no fertilization, S. polyphylla facilitates the growth of U. brizantha. However, with the addition of fertilizers, this effect shifts from competition under organic fertilization to facilitation as the proportion of mineral fertilizer increases. For S. polyphylla, coexistence with U. brizantha reduces its growth in all scenarios, with the most severe adverse effects occurring under mineral fertilization.

The absence of a transition from facilitation to competition under mineral fertilization for *U. brizantha* may be explained by its reduced dependence on nitrogen derived from *S. polyphylla*. Studies indicate that mineral fertilization increases soil nitrogen availability, allowing grass species to rely less on nitrogen from legume-associated biological fixation (Bicharanloo et al., 2024). This effect likely results from a shift in microbial community composition, as higher nitrogen availability can

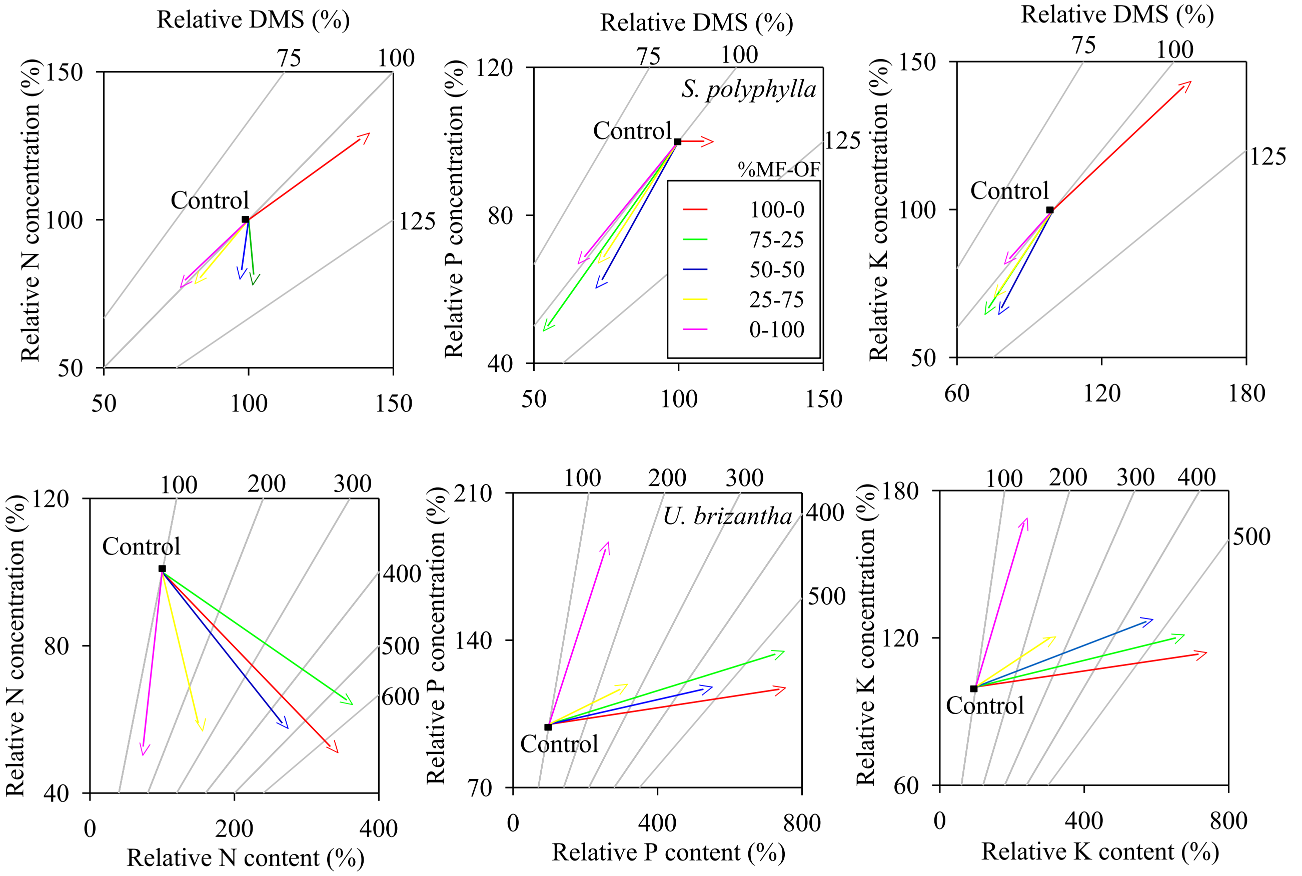

Fig. 6. Vector monograms of changes in shoot dry mass (DMS), nitrogen (N), phosphorus (P), and potassium (K) content and accumulation relative to the unfertilized treatment (0–0 %) of *Senegalia polyphylla* (Fig. 6A, B, and C) and *Urochloa brizantha* cv. Marandu (Fig. 6D, E and F) in competition cultivation, 120 days after transplanting in a substrate containing dystrophic Red Latosol. Control treatment values were normalized to 100 %.

suppress the activity of nitrogen-fixing microorganisms associated with leguminous species (Tao et al., 2024). Consequently, *S. polyphylla* may experience greater competition for nitrogen as its reliance on biological fixation becomes less advantageous under elevated soil nitrogen levels (Ghafoor et al., 2024). Additionally, mineral fertilization can alter soil carbon-nitrogen dynamics, potentially reducing the rhizodeposition of *U. brizantha*, a key process for maintaining soil organic matter balance (Bicharanloo et al., 2024). These findings suggest mineral fertilization does not completely shift *U. brizantha* from facilitation to competition. However, it modifies competitive intensity by altering nitrogen acquisition strategies and below-ground interactions between the species.

The shift from facilitation to competition under organic fertilization may be associated not only with the gradual release of nutrients but also with soil-mediated interactions that influence the competitive dynamics between S. polyphylla and U. brizantha. Organic fertilizers stimulate microbial activity, which can initially intensify competition for nutrients between microorganisms and plants, temporarily reducing nutrient availability for both species (Álvarez-Carrillo et al., 2023). Additionally, while organic amendments contribute to long-term soil structure improvements, increased decomposition rates can alter the immediate availability of nutrients, making them less accessible in the short term (Abrol et al., 2024; Wang et al., 2024a). This effect may have disadvantaged U. brizantha, which relies on high nitrogen availability to sustain its rapid growth, whereas S. polyphylla, as a leguminous species, may have maintained nitrogen acquisition through biological fixation. Consequently, belowground competition may have intensified, diminishing the benefits that U. brizantha typically gains from S. polyphylla in nutrient-poor soils. These processes may explain the transition from facilitation to competition under organic fertilization, highlighting the necessity of considering not only nutrient sources but also their indirect effects on soil microbial dynamics when designing fertilization strategies for ecological restoration.

The exceptionally high conversion of N into biomass by *U. brizantha* under mineral fertilization—up to 600 % and 900 % increases in shoot and root biomass, respectively—highlights its superior nutrient exploitation capacity in nutrient-rich environments. In soils with low nitrogen availability, invasive grasses commonly invest in specialized mechanisms for nitrogen acquisition, including extensive root systems, root exudation, stimulation of rhizospheric microbial activity, and enhanced associations with decomposers or arbuscular mycorrhizal fungi (Morris et al., 2016; Craig et al., 2019; Duan and Kent, 2024). However, these investment costs are reduced when nitrogen is readily available through mineral fertilization (Feng et al., 2023). The grass no longer needs to allocate as many resources to nutrient-foraging mechanisms and can direct photosynthates more efficiently toward growth and reproduction (Li et al., 2024b). This ecological release results in accelerated biomass accumulation and reinforces the competitive dominance of *U. brizantha* over slower-growing native species. In this sense, mineral fertilization facilitates invasive performance, enhancing growth by simplifying nutrient acquisition and promoting physiological efficiency. These findings underscore the need for cautious fertilization management in restoration programs, as elevated nutrient availability may inadvertently favor aggressive invaders at the expense of native biodiversity.

In contrast to the invasive grass, *S. polyphylla* exhibited reduced nitrogen use efficiency under increased nitrogen availability, indicating a limited capacity to translate excess nitrogen into additional biomass. Notably, even in mineral fertilization treatments where the need for biological nitrogen fixation is likely diminished, the species did not exhibit gains in efficiency or biomass comparable to *U. brizantha*. This apparent inefficiency may be attributed to its evolutionary adaptation to

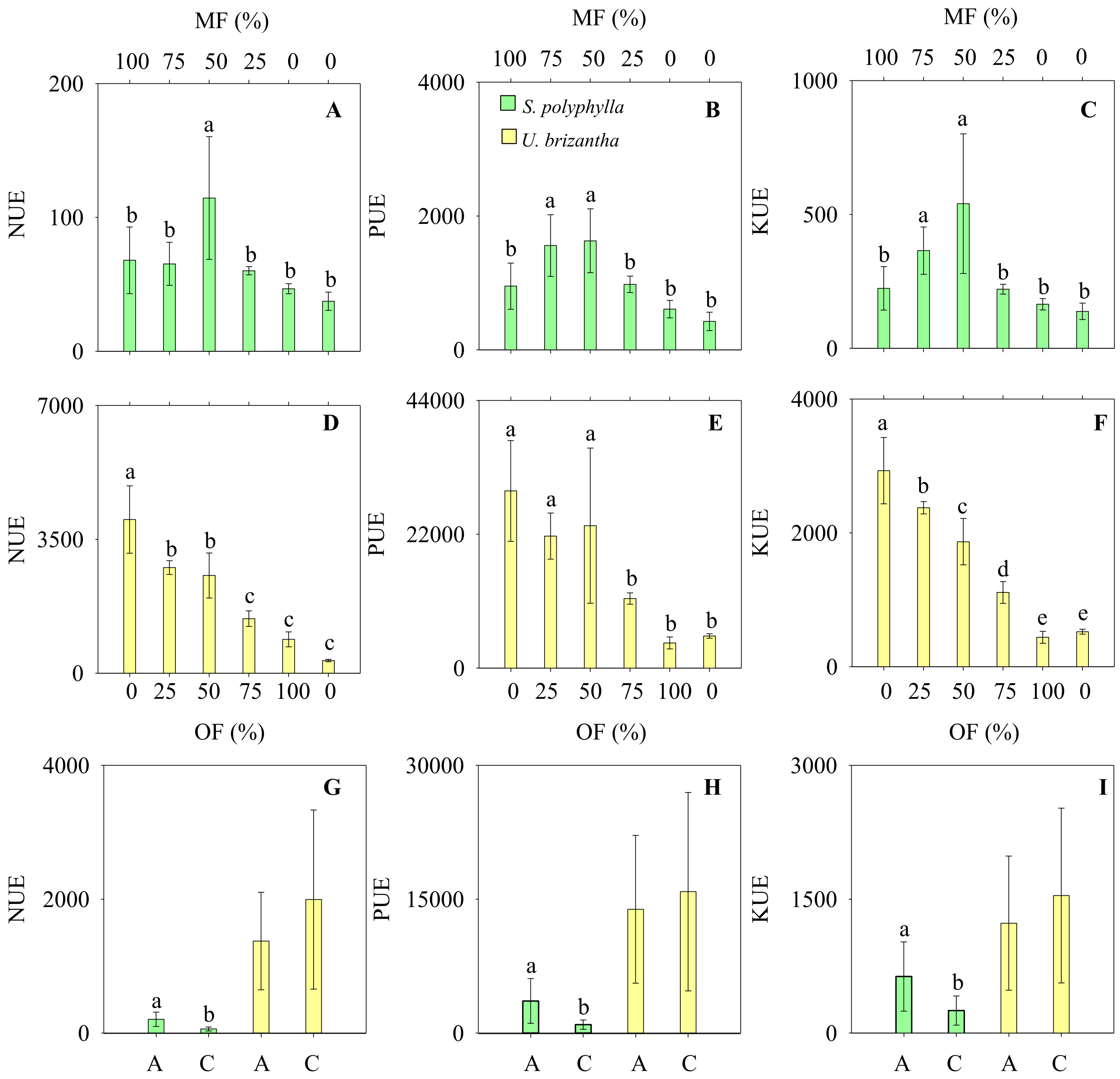

Fig. 7. Nitrogen (N) (NUE), phosphorus (P) (PUE), and potassium (K) (KUE) use efficiency (UE) in the leaves of *Senegalia polyphylla* (Figs. 7A, B, C) and *Urochloa brizantha* cv. Marandu (Figs. 7D, E, F) in competitive cultivation, 120 days after transplanting in a substrate containing dystrophic Red Latosol. The upper and lower axes of each chart show, respectively, the combination of mineral (MF) and organic (OF) fertilization. Lowercase letters differ between fertilizations in the competitive cultivation (F vs C) at 5 % by the Scott-Knott test. N (NUE), P (PUE), and K (KUE) use efficiency (UE) in the leaves of *S. polyphylla* and *U. brizantha* grown alone (A) or in competition (C) (Figs. 7G, H, and I), 120 days after transplanting in a substrate containing dystrophic Red Latosol. Lowercase letters differ between cultivation types (C) at 5 % by the F test.

low-nutrient environments, where conservative resource-use strategies prevail (Knauf et al., 2021). Native species such as *S. polyphylla* tend to maintain lower metabolic rates and slower growth, making them less responsive to high nutrient availability than invasive species (Li et al., 2024a). As a result, these trees may prioritize nutrient storage in leaves or structural investment over immediate growth responses (Sharma et al., 2024). Such conservatism, while advantageous in nutrient-poor systems, can limit competitiveness in fertilized conditions, especially when facing fast-growing, nutrient-responsive invaders (Knauf et al., 2021). This disparity emphasizes the importance of aligning fertilization strategies with the functional traits and ecological adaptations of native species in restoration efforts.

4.2. S. polyphylla and U. brizantha adapt their competitive strategies to nutrient availability with resource specialization dominating in nutrient-poor soils

The competition between native trees and grasses for phosphorus (P) and potassium (K) reveals distinct strategies employed by these plant groups (Biro et al., 2024). Native trees exhibit specialized mechanisms for nutrient acquisition, notably P, which is crucial in nutrient-poor soils and higher P availability (Yang et al., 2023). Although phosphorus acquisition is often emphasized in native tree strategies, their deeper root systems may also confer a competitive advantage in potassium uptake by accessing nutrient pools beyond the reach of shallow-rooted grass (Bouillet et al., 2023).

Our findings align with previous studies regarding phosphorus (P) acquisition strategies in native leguminous trees, as S. polyphylla exhibited foliar P concentrations in the unfertilized treatment comparable to those under mineral fertilization, with both values exceeding the sufficiency threshold. This indicates an intrinsically efficient P acquisition mechanism, independent of external inputs. Such efficiency may be attributed to root-based adaptations, including the exudation of carboxylates and phosphatases, which enhance the mobilization of mineral-bound P (Shen et al., 2024). Nevertheless, when nutrient availability increased through fertilization, a dilution effect in foliar P concentrations was observed across all treatments except mineral fertilization. This phenomenon, defined as decreased nutrient concentration despite increased biomass, is commonly linked to nutrient remobilization from leaves to stems and roots as absorption reaches its maximum physiological (Manghabati et al., 2018; Berghetti et al., 2021).

Interestingly, despite no increase in root biomass, S. polyphylla showed higher phosphorus use efficiency for leaf biomass production under the 75–25 % and 50–50 % fertilization regimes. These results suggest that S. polyphylla retains its conservative P-acquisition strategy even under elevated nutrient availability. However, it responds to moderate fertilization by allocating absorbed P more effectively to leaf biomass production than unfertilized conditions. In contrast, N and K dynamics followed a similar pattern. However, foliar concentrations under no fertilization were lower than in mineral fertilization, reinforcing that S. polyphylla is particularly efficient in acquiring P.By contrast, under mineral fertilization (100–0 %), a concentration effect was observed for N, P, and K in S. polyphylla leaves. Such nutrient accumulation is ecologically relevant, as it enables plants to store excess nutrients when availability is high and remobilize them later during periods of scarcity or stress (Zhao et al., 2019). However, this capacity for accumulation appears decoupled from immediate biomass production. Despite elevated foliar nutrient concentrations, S. polyphylla did not exhibit corresponding leaf or total biomass increases under mineral fertilization. This finding is reinforced by the reduced nutrient use efficiency (NUE, PUE, and KUE) observed in the 100–0 % treatment compared to the 50–50 % treatment, indicating that the tree did not effectively convert the abundant nutrients into structural tissue. Such patterns are consistent with a conservative ecological strategy, in which S. polyphylla favors nutrient storage over rapid allocation to growth, especially for P and K.

This strategy may offer long-term resilience in nutrient-poor ecosystems by buffering against episodic nutrient deficits (Wang et al., 2024b). However, this conservative nutrient-use behavior becomes a disadvantage in nutrient-rich environments, particularly those invaded by highly responsive species such as U. brizantha. The inability to promptly translate nutrient abundance into competitive growth compromises S. polyphylla's performance, thereby facilitating the dominance of invasive species with more exploitative resource-use strategies (Fan et al., 2025). Thus, while S. polyphylla demonstrates the remarkable capacity for nutrient acquisition and internal regulation, its limited growth response under mineral fertilization highlights a critical ecological constraint in restoration scenarios where competition with invasive grasses is intense and nutrient availability is artificially elevated.

Unlike N and P, the K content in the leaves of *S. polyphylla* was influenced by competition with *U. brizantha*, and in both species, there was a reduction in content. Invasive grasses can release allelochemicals that inhibit the growth of native species, further limiting their K absorption (Morrison et al., 2023) and their access to nutrients (Zhang et al., 2024a). As a result, the expected value minus the observed K content in competition was positive only in fertilizations with a predominance of mineral fertilizer, indicating K absorption above expected. However, even in these fertilizations, the levels were below the sufficiency range but did not impact the concentration or dilution effect, similar to other nutrients. The accumulation and efficient use of K followed the same trend as other nutrients, indicating that even with adequate availability, *S. polyphylla* only concentrates the nutrients and does not form new tissues.

In contrast, Urochloa brizantha adopts an exploitative strategy, rapidly acquiring and efficiently allocating nutrients to structural biomass. Its superior N and K use efficiencies and consistent nutrient-use patterns across treatments reflect high physiological plasticity, enabling this invasive grass to promptly convert nutrient availability into increased shoot and root growth (Morrison et al., 2023). This strategy is particularly evident under mineral fertilization—in the nutrient recommendation level for S. polyphylla—where increased N and K availability was closely associated with enhanced biomass production, especially in leaves and roots. In these conditions, U. brizantha exhibited its highest nutrient use efficiency and maximized growth, underscoring its capacity to capitalize on resource pulses with minimal delay. Moreover, the observed reductions in foliar nutrient concentrations under competitive settings, particularly for K, suggest strong belowground interference mechanisms, potentially driven by allelopathic interactions or intense competition for nutrient-rich microsites.

This mechanistic divergence—between the conservative nutrient storage strategy of S. polyphylla and the aggressive resource exploitation of U. brizantha—helps explain the consistent competitive advantage of the grass in nutrient-enriched environments, especially under mineral fertilization regimes. Such findings emphasize the importance of aligning fertilization strategies with the functional traits of native species to avoid inadvertently favoring invasive competitors.

4.3. S. polyphylla and U. brizantha adapt their competitive strategies to nutrient availability with shifts to aboveground and belowground competition in nutrient-rich environments

The dry mass production of U. brizantha was significantly higher both above and below ground, indicating intense competition with S. polyphylla. This indicates that *U. brizantha* competed strongly, imposing an average reduction of 60 % in the dry mass of shoots (DMSh) and roots (DMR) of *S. polyphylla*. Under this solid competitive effect, the DMSh/DMR ratio was similar for *S. polyphylla* grown alone or in competition. Therefore, a similar pattern of dry mass allocation was observed above and below ground. Despite this, in our study, *S. polyphylla* seemed to timidly show a response in terms of above-ground dry mass allocation in fertilizations. This occurred due to the higher rate of leaf dry mass production (DML) in mineral fertilization and shoot dry mass (DMSh) in fertilizations. One hypothesis is that the higher growth rate in the height of *U. brizantha* may have helped to overshadow the leaves of *S. polyphylla* and reduced its capture of above-ground resources (Damasceno et al., 2018; Tang et al., 2022). The height of invasive grasses can hinder native trees from accessing resources, mainly through competition for light and changes in soil properties (Williams and Brewer, 2024).

Another possible explanation is that S. polyphylla invests in root development even in fertilized conditions, prioritizing below-ground competition (Biro et al., 2024). Some native trees maintain a conservative growth strategy, favoring root expansion to secure long-term nutrient acquisition rather than rapidly increasing shoot biomass (Li et al., 2017). This may help explain why, despite fertilization, S. polyphylla did not exhibit a pronounced above-ground growth response. Meanwhile, U. brizantha showed a significant increase in both shoot and root biomass, reinforcing its aggressive resource-acquisition strategy. Additionally, the investment in root biomass may enhance the symbiotic association with arbuscular mycorrhizal fungi (AMF), which are known to improve phosphorus uptake efficiency in nutrient-poor soils (Shen et al., 2023; Yao et al., 2024). This could be particularly beneficial in organic fertilization treatments, where nutrient release occurs gradually and is highly influenced by microbial activity.

On the other hand, The DMSh/DMR ratio of U. brizantha decreased under competition with S. polyphylla, indicating greater resource allocation below ground and a substantial increase in biomass production.

Compared to unfertilized conditions, mineral fertilization (100–0 %) led to a 600 % and 900 % rise in DMSh and DMR, respectively, while organic fertilization (0–100 %) resulted in 50 % and 70 % increases. This rapid shoot expansion under mineral fertilization likely enhanced light capture and photosynthetic rates (Xiang et al., 2024). At the same time, the substantial root biomass increase reflects an aggressive strategy to secure below-ground resources in response to competition (Liu et al., 2024). U. brizantha exhibits high plasticity in root architecture, adjusting allocation patterns to optimize nutrient and water uptake (Amrani, 2023; Fuji et al., 2024). Additionally, its root investment may accelerate organic matter turnover and microbial activity, altering soil dynamics (Wiesenbauer et al., 2024). These traits reinforce its competitive dominance, particularly in nutrient-rich environments, challenging native tree establishment in restoration settings.

4.4. Mineral fertilizers should be avoided in areas invaded by Urochloa brizantha

It is important to recognize that fertilization practices under greenhouse conditions differ in several respects from those used in field-based restoration. In this section, we focus on the similarities between the two approaches, while the differences and their implications are addressed in detail in Section 4.6.

In our greenhouse experiment, all mineral, organic, or combined fertilizers were thoroughly mixed into the soil volume within each pot, ensuring uniform nutrient distribution. In contrast, field fertilization typically involves planting seedlings in pits or furrows, with phosphate fertilizers placed at the bottom and nitrogen–potassium fertilizers applied in small lateral pits located a short distance from the seedlings (Matallana et al., 2022; Mauki and Kilonzo, 2022). Despite these operational differences, both approaches share a critical feature: the localization of nutrients near the planted seedlings. This spatial proximity is essential for nutrient uptake during early establishment and simultaneously creates nutrient-rich microsites that can intensify competition from aggressive invasive species (Wei et al., 2024). In this context, the experimental setup effectively reproduces key aspects of the nutrient dynamics observed in field conditions, supporting the applicability of our findings to restoration scenarios affected by U. brizantha.

The frequency and logistics of fertilization further complicate restoration interventions. In field settings, particularly in large-scale projects, fertilization is typically a one-time event performed at planting, as recurrent applications are logistically challenging and cost-prohibitive (Castro et al., 2021; Domevscik et al., 2023). This mirrors our experimental design, which also applied fertilizers only once. However, in field conditions, this single fertilization event can result in high nutrient availability for a period that favors the growth of *U. brizantha*. Maintaining low-competition zones through manual or mechanical weeding (i.e., using a crowning technique) can reduce grass interference (Pereira et al., 2025). However, this strategy becomes economically unfeasible at high planting densities (e.g., 2000–4000 seedlings per hectare) (Meli et al., 2018). The high labor demand and low operational efficiency limit the practicality of such interventions, especially in large-scale restoration (Castro et al., 2021). Even when using the fertilization treatment in which the native tree exhibited the highest nutrient use efficiency, reducing mineral fertilizer input by 50 %. *U. brizantha* increased its leaf biomass by over 350 % and root biomass by 500 %. This outcome underscores that minimizing or entirely avoiding using mineral fertilizers remains the most ecologically and economically sound strategy in restoration scenarios involving invasive grasses.

Alternative strategies must be explored to mitigate competition without relying on mineral fertilizers. One promising approach is using nutrient-enriched nursery seedlings, preconditioned to store nutrients in their tissues at non-toxic levels (Schott et al., 2016). These nutrient-loaded seedlings could rely on internal reserves to support early growth in nutrient-poor soils, reducing the need for external fertilization and minimizing the stimulation of invasive grasses (Doyle et al., 2021; Luo et al., 2024). Research is needed to assess the ability of such seedlings to remobilize stored nutrients for rapid leaf or root development, potentially enhancing competitiveness against invasive species. In parallel, studies should investigate whether these practices affect biological nitrogen fixation and its indirect facilitative effects on invasive grasses. Ultimately, field trials will be essential to validate these strategies under real-world environmental heterogeneity, including variable soil properties, rainfall patterns, and the dynamics of *U. brizantha* seed banks. Such trials will ensure that fertilization recommendations are practical and context-sensitive, improving the replicability and scalability of restoration efforts.

4.5. Organic fertilization can be a key tool in invasive grass management

In contrast to mineral fertilization, organic fertilization resulted in a competitive interaction between *S. polyphylla* and *U. brizantha*, where both species experienced reduced biomass production. Nevertheless, even under this regime, U. brizantha accumulated 40 % more shoot and 80 % more root mass relative to the unfertilized treatment. Localized organic fertilization is not recommended, as it primarily increases soil fertility, indirectly benefiting the invasive grass. However, organic fertilization has excellent potential for invasive grass control when applied to the entire restoration area (Choi et al., 2018; Cole and Zahawi, 2021). The most effective strategy would be to use organic matter as a surface mulch, covering the soil and potentially delaying *U. brizantha* regrowth (Lorenzo and Morais, 2024).

Future studies should focus on using green manure as a large-scale organic fertilization strategy (Pagoto et al., 2022). Green manure application is cost-effective, poses no risk of introducing invasive seeds, and may contribute to soil cover and nutrient cycling (Plaza et al., 2018). Research should prioritize identifying green manure species that produce high biomass yields to suppress *U. brizantha* effectively (César et al., 2013). Additionally, studies should evaluate whether nitrogen fixed by green manure species becomes available to native trees before invasive grasses recolonize the area. Another promising approach could be combining green manure application with pre-emergent herbicides to control the *U. brizantha* seed bank. However, it is essential to consider the potential toxicity of these herbicides to native species. Some Atlantic Forest species are known to tolerate the pre-emergent herbicide trifluralin (Santos et al., 2019), suggesting this could be a viable option for integrated management strategies.

4.6. From controlled conditions to complex landscapes: study limitations and directions for future research

Although this study offers meaningful contributions to understanding plant competition and fertilization in restoration ecology, important limitations must be acknowledged. Conducted under greenhouse conditions, the experiment ensured optimal water, light, and temperature for both species—conditions rarely sustained in the field. Such environmental stability likely enhanced biomass accumulation and may have intensified competitive interactions, particularly benefiting *U. brizantha*. In natural settings, variations in rainfall, temperature, radiation, and soil heterogeneity could dampen or shift these dynamics. Thus, validating our findings under field conditions is critical to assess the robustness of the observed effects and to fine-tune fertilization strategies for degraded tropical ecosystems. Field trials incorporating spatial and temporal variability would provide valuable insights into how competition and facilitation unfold under realistic restoration scenarios.

Another key limitation is the temporal scale. The study focused on early growth stages, which are vital for establishment but may not capture long-term competition dynamics. As roots expand and canopies develop, species interactions often shift in direction and intensity. Long-term experiments are necessary to determine whether the early competitive dominance of U. brizantha persists and how fertilization regimes influence succession and canopy closure over time. Such studies would directly inform species selection and adaptive management in restoration programs.

The study also employed a binary fertilization approach, comparing only mineral and organic sources. However, nutrient formulations vary widely in composition, solubility, and microbial effects. Future research should test different organic amendments (e.g., green manures, composts, biochar) and mineral combinations tailored to native species' needs, while minimizing grass proliferation. Understanding how different fertilization blends influence nutrient cycling and root-microbe interactions will improve ecological precision in restoration interventions.

Finally, the species pool in our experiment was limited to one native tree and one invasive grass. While this simplification allowed for mechanistic clarity, it does not reflect the multispecies complexity of real restoration sites. Interactions among multiple native trees, shrubs, and invasive species may buffer or amplify competition effects. Experimental designs that incorporate functional diversity will better capture the ecological processes relevant to species coexistence, competition, and facilitation. Such studies will also help define ideal species assemblages for restoration in invaded landscapes, contributing to more resilient ecosystem recovery.

5. Conclusion

Fertilization is pivotal in ecological restoration, influencing competitive interactions between native and invasive species. Our study demonstrates that different fertilization strategies distinctly shape the competitive balance between *S. polyphylla* and *U. brizantha*. Mineral fertilization significantly intensified competition in favor of *U. brizantha*, leading to an extraordinary increase of 600 % in aboveground biomass and 900 % in root biomass, which strongly suppressed the establishment of *S. polyphylla*. In contrast, organic fertilization mitigated these effects, promoting a more balanced competition dynamic.

These findings directly impact restoration practices in tropical ecosystems invaded by aggressive grasses. Readily available mineral fertilizers should be strictly avoided in areas with *U. brizantha* dominance unless combined with targeted herbicide application. Even in such cases, fertilization must be precisely calibrated to meet the initial demands of native trees while minimizing the resurgence of *U. brizantha*. When applied as a localized amendment, organic fertilization still conferred a competitive advantage to *U. brizantha*; however, when used as a surface cover across the restoration area, it holds tremendous potential for both nutrient enrichment and physical suppression of invasive grasses. Future studies should explore green manure as an organic fertilization alternative, evaluating its potential to enhance soil fertility while inhibiting *U. brizantha* through ground cover and competition for nitrogen.

Moreover, our results emphasize the importance of species selection in restoration programs. Nitrogen-fixing species, while often beneficial for ecosystem recovery, may unintentionally facilitate *U. brizanthaa* expansion in the early stages of restoration. Thus, a more strategic approach is required, prioritizing shade-tolerant species that modify environmental conditions without increasing soil nitrogen availability. The Anderson Cluster Method emerges as a promising alternative, allowing the controlled introduction of nitrogen-fixing trees within mixed-species groups that maximize shading and reduce *U. brizantha* growth. Further research should investigate the optimal species composition and spatial arrangement to balance soil improvement with invasive grass control.

By integrating targeted fertilization strategies with carefully selected native species, it is possible to enhance the success of restoration efforts in degraded ecosystems invaded by *U. brizantha*. Our findings highlight the need for an adaptive management approach, combining soil fertility management, species selection, and invasive species control to promote long-term forest recovery. Future research should further refine these strategies, focusing on long-term ecosystem dynamics, interactions among *Multiple species*, and the scalability of these approaches in large-scale restoration projects.

CRediT authorship contribution statement

Fillipe Vieira de Araújo: Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Wander Gladson Amaral:** Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Formal analysis, Conceptualization. **Naiane Maria Corrêa dos Santos:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Investigation. **Enilson de Barros Silva:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Conceptualization. **Evander Alves Ferreira:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Israel Marinho Pereira:** Writing – review & editing, Writing – original draft, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **José Barbosa dos Santos:** Writing – review & editing, Writing – original draft, Resources, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.tfp.2025.100887.

Data availability

Data will be made available on request.

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