



Long-term crop diversity improves soil chemical attributes, nutrient cycling and soybean yield

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Abstract Cover crops have the potential to reduce agricultural inputs, but the long-term impacts of cover crops on soil chemical properties and nutrient cycling in tropical systems are not fully understood. This study evaluated the impact of different cover crop systems under long-term no-tillage on shoot dry mass (SDM) production, nutrient cycling, soil chemical properties, and soybean yield in succession in the

Cerrado region of Mato Grosso State, Brazil. The treatments consisted of different second crops after soybean cultivation: MC (soybean monocropped), fallow; CS1, *Crotalaria spectabilis*; CS2, *Pennisetum glaucum*; CS3, *Urochloa ruziziensis*; CS4, *Cajanus cajan*; and MIX, *C. spectabilis* + *P. glaucum* + *U. ruziziensis* + *C. cajan*. SDM was evaluated at 0, 90, 105, 120, 150, 180, and 210 days after chemical desiccation of the cover crop using herbicides in the crop years from 2014/15 to 2020/21. Soil chemical properties were evaluated after the 2019/20 soybean

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harvest. MIX increased SDM by approximately 22% compared with CS2 and CS3 and 60% compared with MC. In years 6 and 7, soybean yields were significantly higher in MIX, CS3, and CS4 than in MC, increasing by approximately 840 kg ha⁻¹. MIX resulted in the greatest long-term improvements in soil cation exchange capacity, pH, nutrient release and concentration, organic matter, and soybean yield. Even when grown individually, *U. ruziziensis*, *C. cajan*, and *C. spectabilis* also had positive effects on these parameters. Thus, crop successions with cover crops promote improvements in soil fertility and are a sustainable long-term strategy to enhance soybean productivity in the Brazilian Cerrado.

Keywords Long-term crop rotation · Nutrient use · Soil quality · *Urochloa ruziziensis* · *Cajanus cajan*

Abbreviations

N ₂	Atmospheric nitrogen
Ca	Calcium
C	Carbon
CEC	Cation exchange capacity
CM	Cover crop management
CS	Crop succession

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K ⁺	Exchangeable potassium
Ca ²⁺	Calcium
Mg ²⁺	Magnesium
UFLA	Federal University of Lavras
UFMT	Federal University of Mato Grosso
UFPR	Federal University of Paraná
UFR	Federal University of Rondonópolis
UFSC	Federal University of Santa Catarina
IC	Intercropped
Mg	Magnesium
MC	Monocropped
MIX	Four crops intercropped in the same plot
N	Nitrogen
NTS	No-tillage system
OAs	Organic acids
P	Phosphorus
K	Potassium
UNESP	São Paulo State University
SDM	Shoot dry mass
SOM	Soil Organic Matter
SO ₄ ²⁻	Sulfate
S	Sulfur
UNIMAR	University of Marília

Introduction

Production costs associated with agricultural inputs have increased considerably worldwide in the last two years (CONAB 2022). These increases are expected to continue in Brazil, emphasizing the need for changes in agricultural production management to target energy efficiency through nutrient cycling and reduced use of mineral fertilizers and natural resources (Obour et al. 2021). Sustainable production models such as no-tillage systems (NTSs) prioritize the synergy of crops in rotation or succession. Crop synergy is particularly relevant in the Brazilian Cerrado, where there are three cultivation periods: the first crop season (October–February), when water availability is favorable for the development of main crops such as soybean (*Glycine max* (L.) Merr.); the second crop season (February–June), when reduced water availability leads to periods of water stress and corn (*Zea mays* L.) or wheat (*Triticum aestivum* L.) are commonly cultivated; and the off-season (July–September), which is characterized by periods of drought and the cultivation of cover crops, sorghum (*Sorghum bicolor* (L.) Moench) and

other species. Diversifying the species planted in the second crop season, such as incorporating different legume and/or grass species or those with distinct phenological cycles, can improve nutrient use efficiency by increasing organic matter via carbon (C) sequestration (Crusciol et al. 2021a; Baptistella et al. 2020), strengthening the efficiency and resilience of the production system. In this context, the adoption of cover crops during the second growing season implies changes in the production system compared to the cultivation of commercial crops, resulting from gradual adaptation processes to technical, economic, and environmental conditions. These changes represent adjustments in agricultural management that must be analyzed in light of the specific context of each farm, including soil type, machinery availability, climate conditions, and other factors that characterize agricultural systems worldwide.

Increasing crop diversity in the Cerrado and elsewhere in Brazil is challenging due to the dominance of the soybean–corn model, which offers farmers high short-term profitability. Moreover, careful selection of the cover crops to be sown in the second crop season is required, as this period is best suited to drought-tolerant species with genetic potential for efficient nutrient cycling through high shoot dry matter (SDM) production, which is the dry organic matter formed from the aboveground parts of the plant (stems, leaves, and flowers) (Dalla Côt et al. 2021; Pacheco et al. 2018). Several studies have demonstrated that planting *Urochloa ruziziensis* (ruzigrass), *Pennisetum glaucum* (millet), *Cajanus cajan* (pigeon pea), or *Crotalaria spectabilis* (crotalaria) as a second crop is an efficient option that can improve soil biophysiochemical properties (Dalla Côt et al. 2021; Volf et al. 2021; Bossolani et al. 2020; Ferreira et al. 2020; Franzluebbers and Gastal 2019; São Miguel et al. 2018; Pacheco et al. 2017). Each of these cover crops has specific morphophysiological characteristics that impact the system. The expansive root systems of grasses promote soil exploration, nutrient uptake, and the accumulation of biomass covering the soil, while legumes perform biological nitrogen fixation. This functional diversity is reinforced by phenological diversity: annual species favor early nutrient release, whereas the sustained growth of perennial species enables nutrient cycling and soil cover over time (Baptistella et al. 2021; Almeida et al. 2020, 2018; Osterholz et al. 2018). All of these cover crops

translocate nutrients extracted from the soil to the photosynthetic apparatus to produce energy sources and C skeletons, which are subsequently transformed into SDM.

Planting these four cover crops simultaneously in an NTS (MIX) is an innovative consortium model that targets the extraction of nutrients located in deep layers of the soil, which are sometimes inaccessible to genetically improved crops such as soybean and corn. The variety of root systems in MIX allows the exploration of a greater volume of soil, the formation of biopores, and the release of a diversity of mucilages and exudates, creating a specific rhizosphere for each species (Baptistella et al. 2020; Bertollo et al. 2020). The latter high-quality plant materials favor the formation of a diverse edaphic fauna that can transform this labile material into stable soil organic matter (SOM) that is protected within soil aggregates and can serve as a nutrient reservoir for subsequent crops (Nair and Ngouajio 2012). In addition to enhancing nutrient cycling, crop diversification through MIX systems can improve soil resilience to climate change. This is primarily achieved through increased atmospheric C sequestration via incorporation into SOM, which promotes soil aggregation and serves as a C source to support microbial diversity and activity. These processes, combined with the soil cover provided by the NTS and root development of cover crops, improve water infiltration and retention for the succeeding crop. Collectively, these benefits help mitigate climate-related stresses and may contribute to higher grain yields (Obour et al. 2021; Franzluebbers and Gastal 2019; Pacheco et al. 2017).

These properties of MIX suggest that appropriate management of each cover crop and, especially, their mixture may increase soil nutrient availability and, in turn, the efficiency of mineral fertilizers and other inputs. However, the contribution of MIX as a second crop under NTS to nutrient cycling and possible changes in soil fertility and long-term soybean yield are unknown. Analyses of long-term effects are necessary to determine whether intercropping a mixture of cover crops in the same area provides superior results compared with cropping each species individually. Improvements may not be observed immediately because the system needs time to stabilize. This study evaluated the impact of single cover crops and MIX under long-term NTS on SDM production, nutrient cycling, soil chemical properties, and

soybean yield in succession. We hypothesized that higher cover crop diversity in the second crop season under NTS enhances long-term soil properties, including SOM, cation exchange capacity (CEC), pH and the concentrations of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and sulfur (S), thereby improving nutrient cycling and soybean yield.

Material and Methods

Experimental site

The experiment was conducted at the Experimental Station of the Federal University of Rondonópolis-MT (UFR) (16° 27' 41.75" S, 54° 34' 52.55" W, altitude of 292 m) (Supplemental Fig. S1) during the 2013/14 to 2020/21 seasons to evaluate the evolution of the systems over 7 years of implementation. The soil in the area is classified as a dystrophic Oxisol (Santos 2018) with flat relief. The local climate is tropical, with hot and humid conditions, and is characterized as Aw, tropical savanna, according to the Köppen classification (Souza et al. 2013). Supplemental Fig. S2 provides meteorological data since the implementation of the experiment.

Soil samples were collected in 2013 for chemical analysis (Table 1) to guide soil correction, neutralizing pH and eliminating toxic elements, such as aluminum, through liming and fertilization prior to experiment implementation. In all plots, soil amendments were applied only once, on October 8, 2013 following the recommendations of Souza and Lobato (2004). Liming for the implementation of the experiment was carried out in October 2013 with 1800 kg ha⁻¹ of filling limestone (90% effective equivalent of calcium carbonate, ECCE; equivalent

to Brazilian PRNT), which was incorporated into the soil by harrowing and disc plough leveling. For soil correction in September 2016, 2000 kg ha⁻¹ of filling limestone (90% ECCE) and 2,000 kg ha⁻¹ of agricultural gypsum were applied superficially. In total, these changes contributed approximately 1834 kg Ca ha⁻¹ during the experiment.

Crop systems and experimental design

The experiment was carried out in a randomized block design with six production systems and four replications, resulting in 24 plots with dimensions of 7.40 m×9.50 m each. The first crop was soybean sown as a commercial crop, and cover crops were used as the second crop, desiccated in June, and the area was kept under mandatory sanitary fallow period before the next soybean crop. Figure 1 presents the treatments used since the implementation of the experiment in 2013 through the 2020/21 harvest. Some systems were modified after a few years due to species adaptation to Cerrado conditions, advances in cover crop research and to align more closely with cropping practices commonly used by Brazilian farmers. Figure 1 shows that four of the treatments remained unchanged over the years: MC, monocropped (fallow); CS1, *Crotalaria spectabilis*; CS2, *Pennisetum glaucum*; and CS3: *Urochloa ruziziensis*. Modifications occurred only in the second crop of CS4 (*Cajanus cajan*) and MIX (*C. spectabilis* + *P. glaucum* + *U. ruziziensis* + *C. cajan*). In CS4, *Stylosanthes* was sown in the 2013/14 and 2014/15 seasons, followed by *Vigna unguiculata* in 2015/16 and 2016/17 and *C. cajan* from 2017/18 to 2020/21. While the changes introduced different species over time, the cover crops used in CS4 were all legumes from the Fabaceae family. In MIX, the second crop consisted of *C. cajan* in 2013/14 and 2014/15,

Table 1 Chemical and textural properties of the dystrophic Oxisol at the experimental site in Rondonópolis-MT, 2013 (beginning of experiment)

Soil depth	pH	P	K	Ca	Mg	H + Al	CEC	BS	SOM	Sand	Silt	Clay
(m)	CaCl ₂	mg dm ⁻³		cmol _c dm ⁻³				%	g kg ⁻¹			
0.00–0.10	4.1	5.4	55	0.5	0.2	6.8	7.6	11	17.6	450	125	425
0.10–0.20	4.0	1.4	49	0.2	0.2	7.2	7.6	5.6	19.9	500	100	400
0.20–0.30	4.1	0.2	31	0.3	0.1	6.2	6.7	7.2	13.7	500	100	400

P: available phosphorus (Mehlich 1); exchangeable K⁺, Ca²⁺, and Mg²⁺; CEC: cation exchange capacity at pH 7.0; BS: base saturation; SOM: soil organic matter

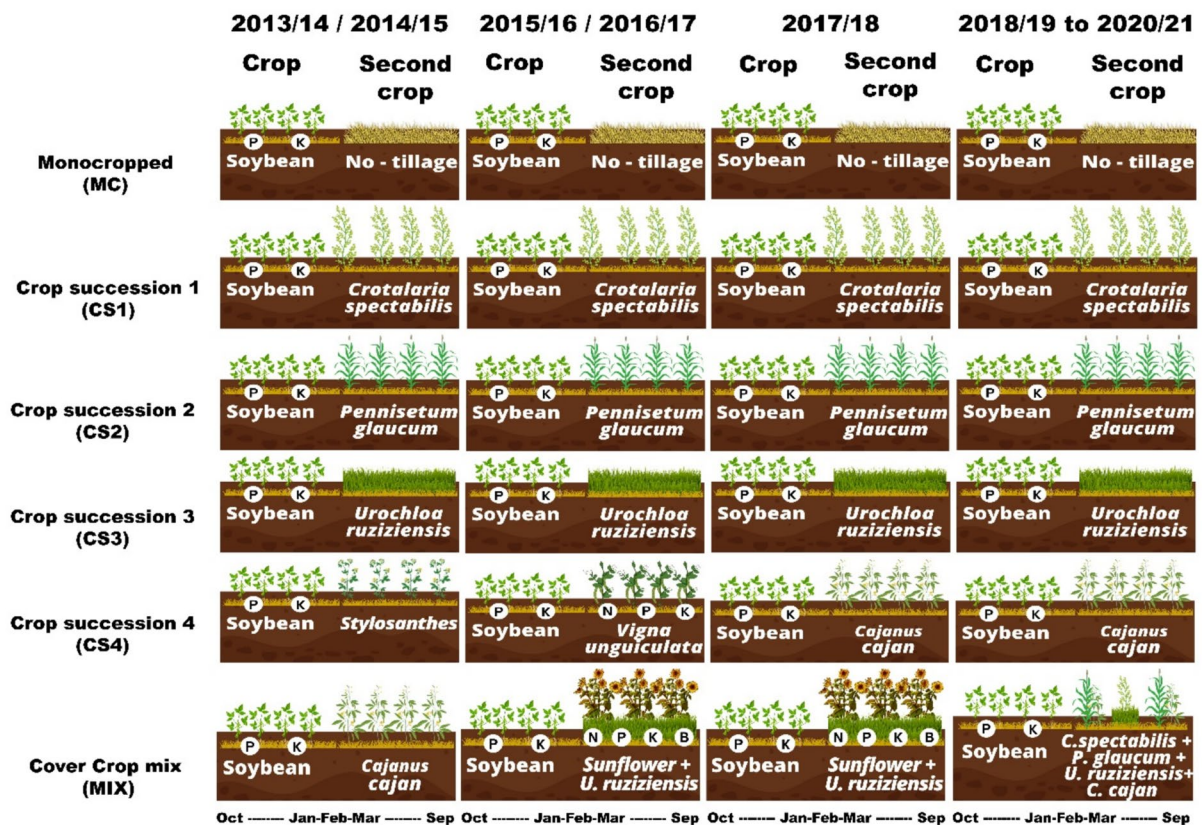


Fig. 1 Compositions of the crop systems implemented in the second crop in all crop years. Fertilizers applied to soybean and some cover crops are represented as N: nitrogen; P: phosphorus; K: potassium; and B: boron

followed by a combination of sunflower + *U. ruziziensis* from 2015/16 to 2017/18. From 2018/19 to 2020/21, a more diverse mixture of *C. spectabilis* + *P. glaucum* + *U. ruziziensis* + *C. cajan* was used. These changes were considered improvements to the trial's scope, as they promote the inclusion of a greater number of different cover crops, which may enhance nutrient cycling dynamics and further amplify effects on soil properties.

Soybean was sown between September and October under NTS, and the cultivars were selected according to technical recommendations for the region and market availability. Soybean was grown with a row spacing of 0.45 m and harvested in February of the following year. The second crops were sown manually each year between February and March with a spacing of 0.45 m between rows. The seeding rates were as follows: *C. spectabilis*, 30 kg ha⁻¹ (226 g per plot, approximately 30 seeds per meter); *P. glaucum*, 30 kg ha⁻¹ (225 g per plot,

approximately 20 seeds per meter); *U. ruziziensis*, 25 kg ha⁻¹ (187 g per plot, approximately 30 seeds per meter); and *C. cajan*, 60 kg ha⁻¹ (450 g per plot). The mixed treatment consisted of *C. spectabilis* (18 kg ha⁻¹; 113 g per plot), *P. glaucum* (18 kg ha⁻¹; 113 g per plot), *U. ruziziensis* (15 kg ha⁻¹; 94 g per plot), and *C. cajan* (36 kg ha⁻¹; 227 g per plot).

Sunflower is an important second-crop in the Brazilian Cerrado, whether grown alone or intercropped crop. Initially, it was sown so that production data could be calculated. However, the harvest of the second crop with the sunflower system was not performed in 2016/17 and 2017/18 due to operational constraints. In the MIX treatment, with sunflower and *U. ruziziensis* planted as the second crop in 2015/16 and 2016/17, the grass was sown between the sunflower rows. From 2018/19 to 2020/21, *P. glaucum* and *C. spectabilis* were sown in one row in MIX, while *U. ruziziensis* and *C. cajan* were sown in the adjacent row, resulting in an interspersed planting

pattern across the plots. In all production systems, cover crops were desiccated after second-crop harvest in June using the herbicides glyphosate (5 L ha^{-1}) and 2,4-D (1.5 L ha^{-1}).

Fertilization

In the first five years of the study, soybean was fertilized to correct soil chemical properties. Specifically, 60 kg ha^{-1} of P was applied in the sowing furrow, 20 kg ha^{-1} of K was spread pre-sowing, and an additional 20 kg ha^{-1} of K was applied when the soybean was at the V4 phenological stage. As the NTS stabilized, the amounts of K and P fertilizers were reduced by half to 30 kg ha^{-1} of P and 20 kg ha^{-1} of K as maintenance fertilization in the last two agricultural years (2019/20 and 2020/21), considering nutrient release from cover crop residue decomposition (Teixeira et al. 2012). In all growing seasons where sowing and/or topdressing fertilization was carried out, MAP (mono-ammonium phosphate, 11-52-00 [$\text{N-P}_2\text{O}_5\text{-K}_2\text{O}$]), KCl (potassium chloride, 60.5% K_2O) and urea (46-00-00 [$\text{N-P}_2\text{O}_5\text{-K}_2\text{O}$]) were used. The soybean seeds were inoculated at a dose of 150 mL of inoculant for every 50 kg of seeds with liquid inoculant (Nitragin Cell Tech® HC, Monsanto BioAg Office, Buenos Aires, Argentina) containing 3×10^9 colony-forming units of *Bradyrhizobium japonicum* per milliliter.

No fertilizers were applied in the second crop season to the treatments with single cover crops (MC, CS1, CS2, CS3, and CS4) after 2017/18 season. In MIX, fertilization of sunflower as a second crop in consortium with *U. ruziziensis* was carried out following the recommendations of Souza and Lobato (2004). However, no fertilizers were used in the second crop season after the final MIX treatment implementation in the 2018/19 season.

Evaluations of SDM, nutrients, and soil properties

The SDM of the cover crops was evaluated at 0, 90, 105, 120, 150, 180, and 210 days after desiccation. Day 0 was defined as the maximum accumulation of SDM and nutrients at cover crop management (CM), which refers specifically to the cover crop termination process, particularly the timing and method of desiccation, stopping nutrient uptake and C assimilation. The dried plants remaining standing in the field, and SDM was collected at the second

harvest in all years. The second management desiccation (September/October) was carried out at 90 days after first desiccation (CM) (i.e., prior to soybean sowing) using the herbicide glyphosate (5 L ha^{-1}). SDM accumulation was evaluated according to the methodology described by Crusciol et al. (2005). In brief, the biomass of cover crops within an iron square measuring $50 \times 50 \text{ cm}$ was randomly collected at two sampling points per plot. The collected biomass was dried in an oven at 60°C until a constant mass was obtained, and the SDM was determined. To determine nutrient concentrations, the dried samples were ground in a Wiley mill and passed through a 2-mm mesh sieve before determining the concentrations of nutrients from a subsample following the methodologies proposed by Malavolta et al. (1997). Nitrogen (N) was extracted by sulfuric acid digestion and determined by the semimicro-Kjeldahl method. Phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and sulfur (S) were determined by nitric-perchloric acid digestion. P was determined by molecular absorption spectrometry, K by emission flame photometry, Ca and Mg by atomic absorption spectrophotometry, and S by barium sulfate turbidimetry.

To describe the decomposition of SDM and nutrient release from the cover crops after desiccation, the data collected at 0, 90, 105, 120, 150, 180, and 210 days after CM were fit to the exponentially decreasing mathematical model (Eq. 1) described by Wieder and Lang (1982):

$$PL = Po \times e^{-kt} \quad (1)$$

where PL is the amount of SDM and nutrients at time t in days (kg ha^{-1}), Po is the fraction of SDM and nutrients potentially released (kg ha^{-1}), and k is the constant for SDM and nutrient release (g g^{-1}).

The value of k was used to calculate the half-life ($T_{1/2}$) of the SDM and remaining nutrients, i.e., the time required for half of the SDM to decompose and half of the nutrients to be released, using the formula $T_{1/2} = 0.693/k$, as proposed by Paul and Clark (1989).

Soybean grain yield was evaluated by sampling the crops in 2-m lengths of two rows and expressed in kg ha^{-1} , corrected for 13% moisture. For soybean yield and all shoot variables, historical series were constructed using the averages of SDM and nutrient accumulation and release from the 2014/15 to

2020/21 seasons to allow comparisons between crop systems under NTS over time.

For the analysis of chemical properties, soil sampling was carried out after harvesting the 2019/20 soybean crop by collecting four subsamples from the central area of each plot (5 m × 5 m). Samples were collected with a probe-type tract at depths of 0.00–0.05, 0.05–0.10, 0.10–0.20, and 0.20–0.30 m. The soil was packed in plastic bags and taken to a greenhouse, where the bags were opened to obtain air-dried fine earth. After drying, the samples were sieved (2-mm mesh) and ground in a ball mill for analyses of SOM, CEC, pH, and soil concentrations of P, K, Ca, Mg, and S according to the methodology proposed by Raij et al. (2001). SOM ($\text{cmol}_c \text{ dm}^{-3}$) was determined following the Walkley–Black method (Walkley and Black 1934). CEC ($\text{cmol}_c \text{ dm}^{-3}$) was calculated as the sum of exchangeable cations (Ca^{2+} , Mg^{2+} , and K^+) extracted with cation exchange resin and determined by atomic absorption spectrophotometry in $\text{cmol}_c \text{ dm}^{-3}$ and acid cations (H^+ and Al^{3+} , from potential acidity). Potential acidity ($\text{H} + \text{Al}$) was quantified using Shoemaker–McLean–Pratt (SMP) solution. pH was measured with a glass electrode after shaking 1 part soil in 25 parts 0.01 M CaCl_2 solution (v/v), followed by resting. Resin-extractable P (mg dm^{-3}) was determined using an anion exchange resin and quantified by spectrophotometry. S was extracted with 0.01 M $\text{Ca}(\text{H}_2\text{PO}_4)_2$ solution at a 1:2.5 (v/v) soil:solution ratio, and SO_4^{2-} (mg dm^{-3}) was determined by barium sulfate turbidimetry. Finally, the sum of exchangeable bases was calculated as the sum of Ca^{2+} , Mg^{2+} , and K^+ , and base saturation (BS), expressed as a percentage, was calculated as the ratio of exchangeable bases to CEC.

Statistical analysis

The data were checked for normality and homoscedasticity, analyzed with analysis of variance (F test), and when significant, submitted to the Fisher least significant difference (LSD) test at $p \leq 0.10$, using SISVAR 5.6 software (Ferreira 2008), to identify biologically or agronomically relevant patterns in a long-term experimental setting with different cover crops. The data for SDM and nutrient concentrations in cover crops were fitted to decreasing exponential

equations using the software SigmaPlot 10.0 (Systat Software Inc., San Jose, CA, USA). Multivariate analysis of shoot data as a function of soil depth was performed by principal component analysis (PCA) and Pearson's correlation using R software (Lenth 2019; Oksanen et al. 2019; R Core Team 2020).

Results

Dry matter production and nutrient cycling differed significantly between the cover crop systems (Fig. 2). MIX enhanced SDM accumulation compared to the other treatments, with increases of approximately 22% compared with CS2 and CS3 and 60% compared with MC. All differences were statistically significant, as indicated by the distinct letters in Fig. 2A. The differences in N, K, P, S, Ca and Mg accumulation at desiccation between treatments followed the same pattern, with MIX, CS4 and CS3 showing higher nutrient accumulation in SDM than MC, CS1 and CS2. However, exceptions were observed, such as the higher Ca accumulation in CS1 compared to the other treatments and lower K, P, and Mg accumulation in CS4 compared to CS3 and MIX (Fig. 2B–D). Among CS1, CS2, CS3, and CS4, N accumulation was highest in CS4 (*Stylosanthes*, *V. unguiculata*, and *C. cajan*), P accumulation was highest in CS3 (*U. ruziziensis*), and Ca accumulation was highest in CS1 (*C. spectabilis*). Compared with MC, MIX increased P accumulation by 22%, K accumulation by 38%, and N accumulation by 43%, equivalent to 24.9 kg ha^{-1} of P, 185.9 kg ha^{-1} of K, and 49.3 kg ha^{-1} of N.

The temporal analysis revealed that nutrient release significantly declined most rapidly in the early days after desiccation (Fig. 3). All regression models used to characterize nutrient release dynamics showed strong goodness of fit, supporting the reliability of the half-life estimates presented. The decomposition rate of SDM was highest in CS4, with a $T_{1/2}$ of 71 days, followed by MIX and CS1, with an average $T_{1/2}$ of 93 days. The decomposition rate was slowest in MC. The differences in $T_{1/2}$ indicated that nutrient cycling was faster in CS4, CS1, and MIX than in MC. The rate of N release into the soil was highest in CS4 and MIX (Fig. 3B). P release was greater in MIX, CS3, and CS4 than in CS2 and MC (Fig. 3C). MIX also exhibited greater K release compared to the other treatments (Fig. 3D). Regarding Ca, CS1 and

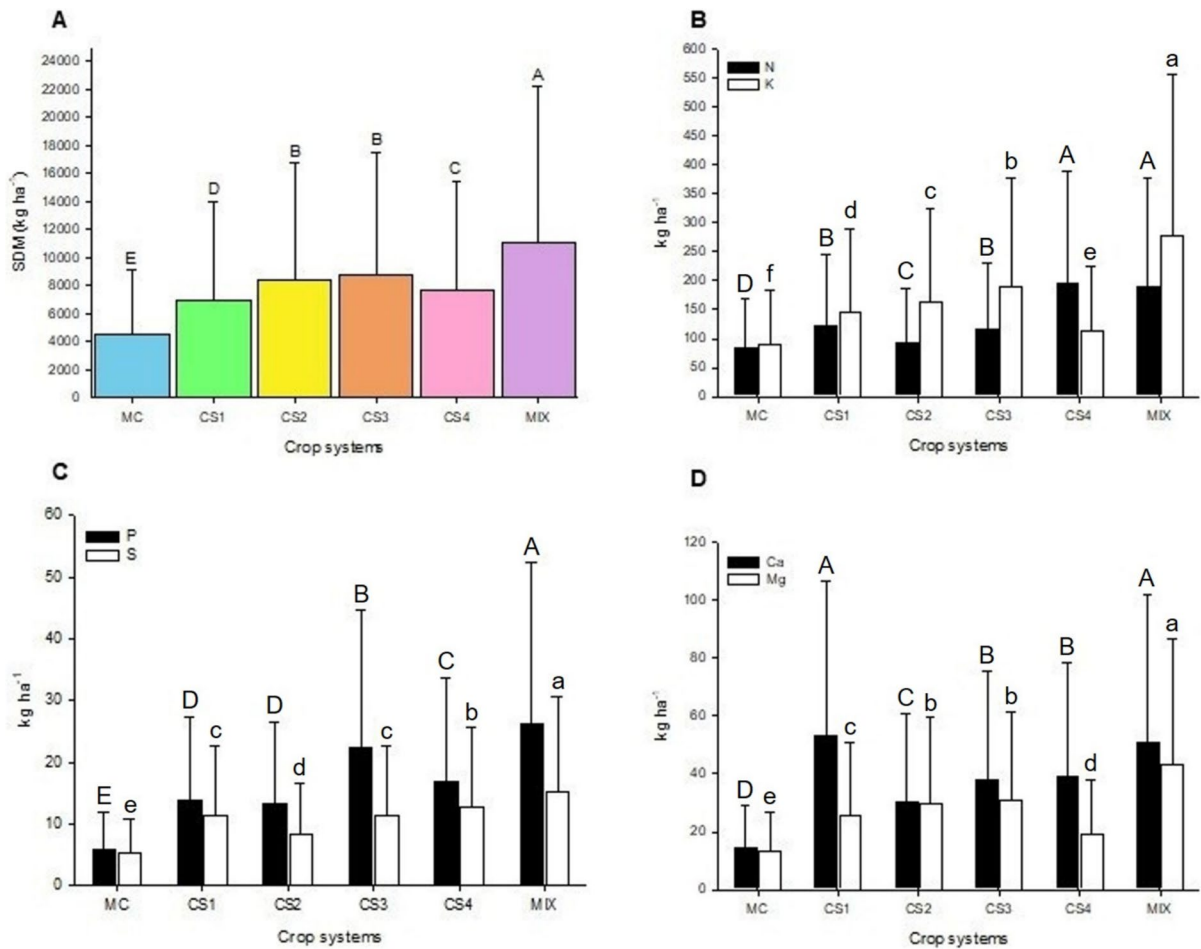


Fig. 2 Seven-year average (2014 to 2020) of **A** shoot dry mass (SDM) production and **(B–D)** accumulated amounts of **B** N and K, **C** P and S, and **D** Ca and Mg at desiccation of the second crop. Treatments in the 2018/19 to 2020/21 crop seasons: MC, monocropped (fallow); CS1, crop succession 1 (*Crotalaria spectabilis*); CS2, crop succession 2 (*Pennisetum glaucum*); CS3, crop succession 3 (*Urochloa ruziziensis*);

CS4, crop succession 4 (*Cajanus cajan*); MIX (*C. spectabilis* + *P. glaucum* + *U. ruziziensis* + *C. cajan*). In **(A)**, different uppercase letters indicate significant differences by Fisher's protected LSD test at $p \leq 0.10$. In **(B–D)**, black columns with different uppercase letters and white columns with different lowercase letters are significantly different by Fisher's protected LSD test at $p \leq 0.10$

MIX showed clear superiority over CS3, CS2 and MC (Fig. 4A). Mg release rates (Fig. 4B) were significantly higher in MIX and CS3 than in the other treatments. Finally, S release was higher in MIX and CS4 than in CS3, CS2, and MC (Fig. 4C). Consistent with their positive effects on nutrient release, soybean yield was highest in MIX, CS3, and CS4, with increases of 20% compared to MC, equivalent to an additional yield of approximately 840 kg ha⁻¹ (Fig. 4D).

The MIX system improved CEC in the 0.00 to 0.05 m layer (Fig. 5A), increased P and K concentrations in all soil layers (Figs. 5D and 6A), improved Ca

and Mg in the 0.00–0.05 m layer (Figs. 6B and C), increased S mainly between 0.05 and 0.30 m (Fig. 6D), increased SOM from 0.00 to 0.10 m (Fig. 5C), and increased soil pH in the 0.00–0.20 m layer (Fig. 5B). Compared to MC, the CS1, CS2, CS3, and CS4 systems improved CEC and SOM (Figs. 5A–C), reduced soil acidity (Fig. 5B), increased S availability at depth (Fig. 6D) and P, K, Ca, and Mg availability throughout the profile, especially in the first 0.00 to 0.20 m (Figs. 5D, 6A, B, C). This highlights the intermediate, yet significant, benefits provided by cover crops, even when used as a single second crop.

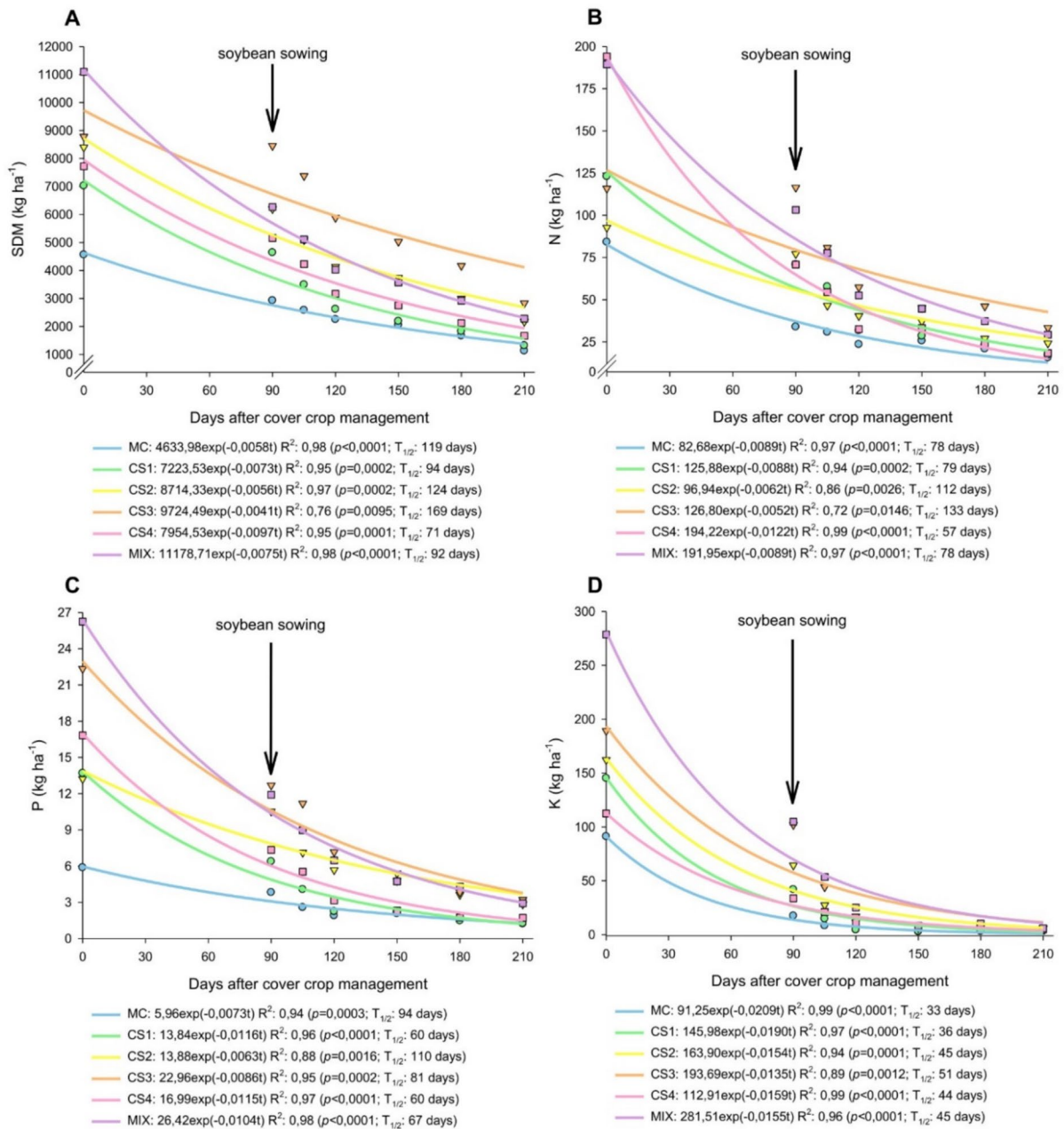


Fig. 3 Seven-year average (2014/15 to 2020/21) of **A** shoot dry mass (SDM) decomposition and **B** N, **C** P, and **D** K release after cover crop management (desiccation). MC: monocropped (fallow under no-tillage); CS1: crop succession 1 (*Crotalaria*

spectabilis); CS2: crop succession 2 (*Pennisetum glaucum*); CS3: crop succession 3 (*Urochloa ruziziensis*); CS4: crop succession 4 (*Cajanus cajan*); MIX (*C. spectabilis* + *P. glaucum* + *U. ruziziensis* + *C. cajan*). $T_{1/2}$: half-life

PCA confirmed the strong association between diversified cropping systems and soil properties. PC1 explained 48%–69% of the variation in soil fertility as a function of shoot variables, while PC2 explained

12%–27% (Fig. 7). These analyses revealed correlations of MIX and CS3 with soybean yield, SDM nutrient content, and soil fertility variables at the four evaluated depths, mainly in the later years of the experiment. In

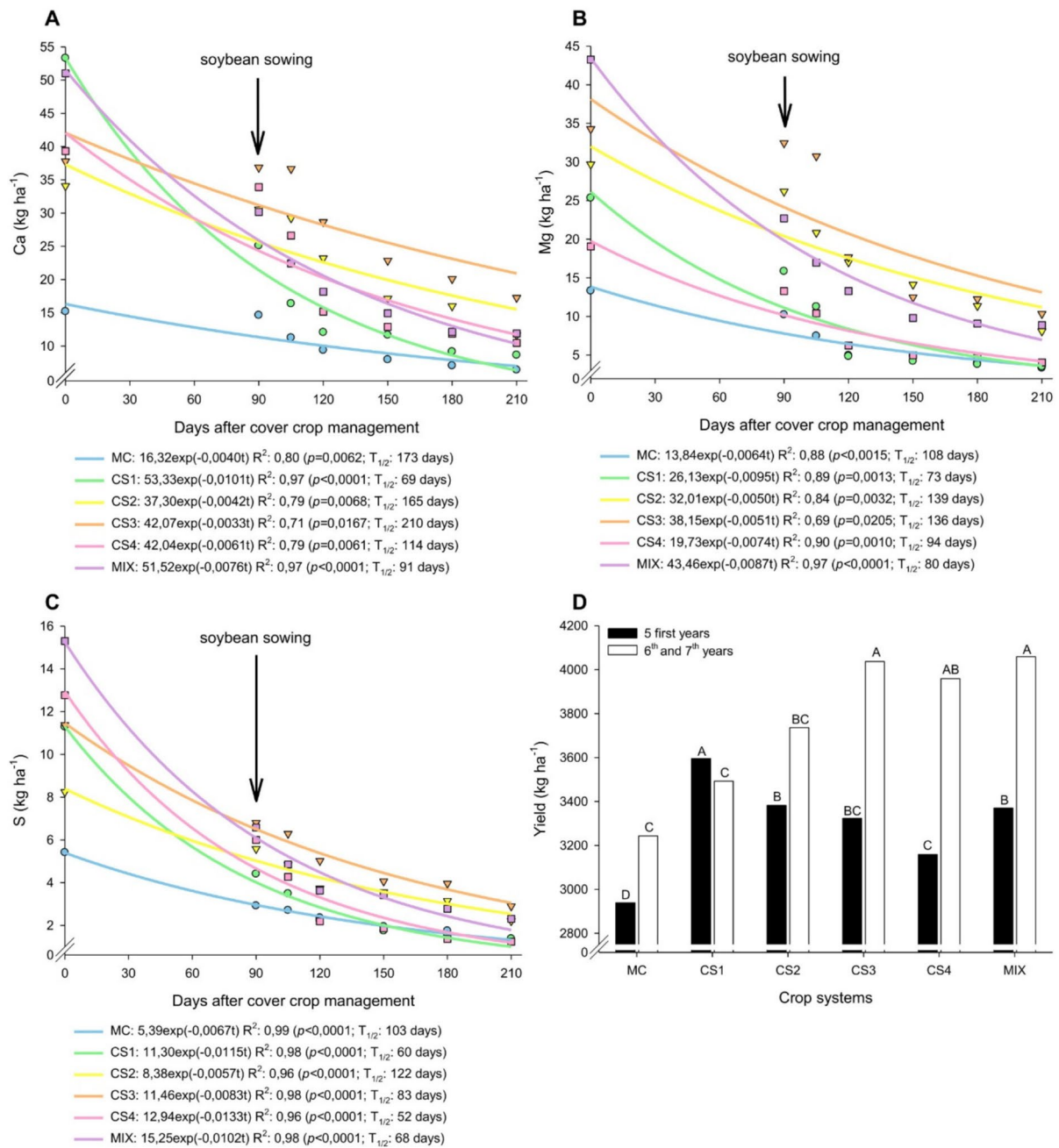


Fig. 4 Seven-year average (2014/15 to 2020/21) of **A** Ca, **B** Mg, and **C** S release after cover crop management (desiccation). **D** Soybean grain yield is shown as the average of the first five years, which corresponds to the stabilization phase of the NTS (black columns), and the average of the 6th and 7th years, after the stabilization phase (white columns). Black columns with different uppercase letters and white columns with differ-

ent lowercase letters are significantly different by Fisher's protected LSD test at $p\text{-value} \leq 0.10$. MC: monocropped (fallow under no-tillage); CS1: crop succession 1 (*Crotalaria spectabilis*); CS2: crop succession 2 (*Pennisetum glaucum*); CS3: crop succession 3 (*Urochloa ruziziensis*); CS4: crop succession 4 (*Cajanus cajan*); MIX (*C. spectabilis*+*P. glaucum*+*U. ruziziensis*+*C. cajan*). $T_{1/2}$: half-life

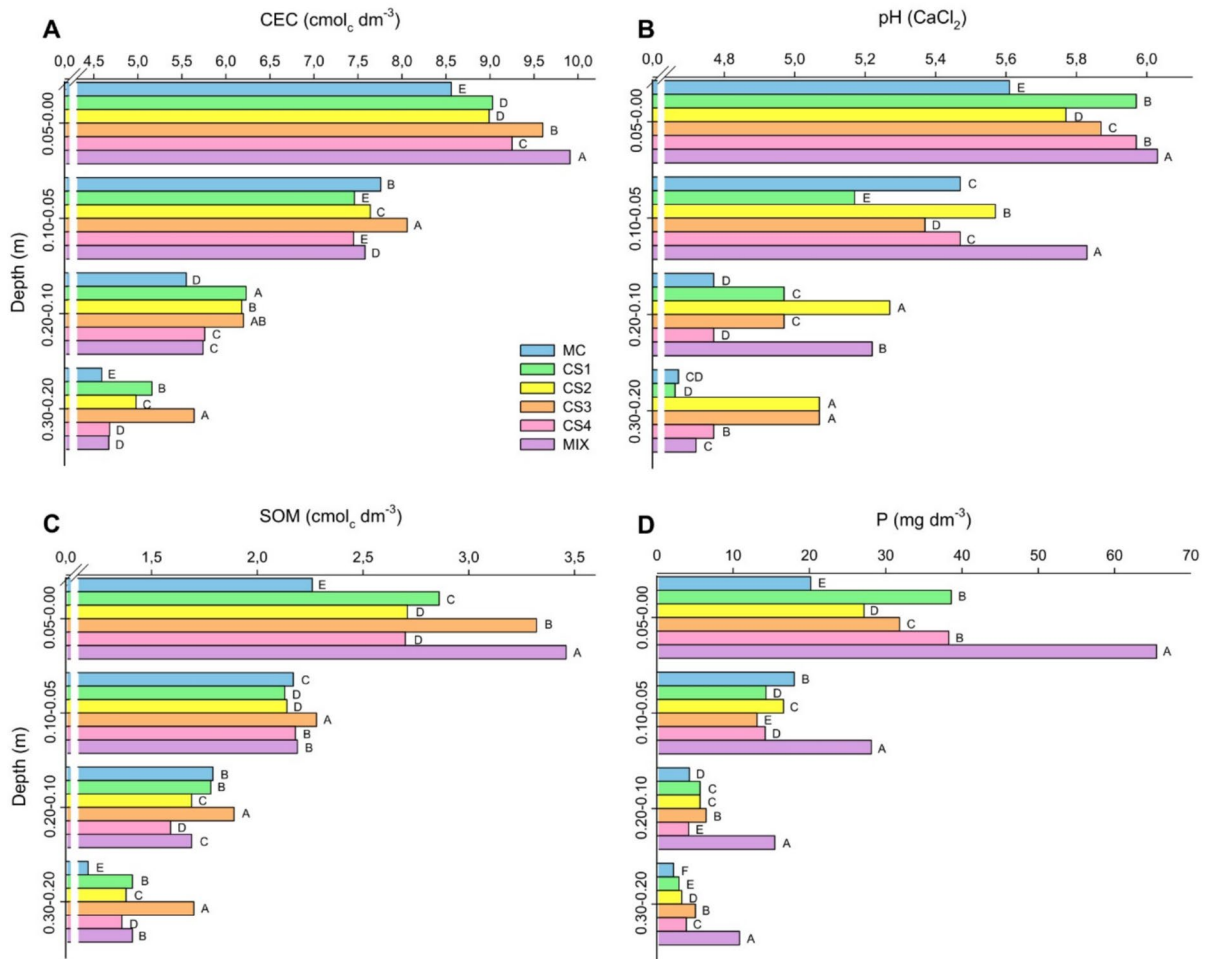


Fig. 5 Soil chemical properties and phosphorus concentrations in soil layers after the soybean harvest (crop season 2019/20) as a function of cover crop treatments. **A** Cation exchange capacity (CEC), **B** pH, **C** soil organic matter (SOM), and **D** phosphorus (P). MC: monocropped (fallow under no-tillage); CS1: crop succession 1 (*Crotalaria spectabilis*); CS2:

crop succession 2 (*Pennisetum glaucum*); CS3: crop succession 3 (*Urochloa ruziziensis*); CS4: crop succession 4 (*Cajanus cajan*); MIX (*C. spectabilis* + *P. glaucum* + *U. ruziziensis* + *C. cajan*). Columns for the same depth with different letters are significantly different by Fisher's protected LSD test at $p \leq 0.10$

addition, Pearson's correlation analysis (Fig. 8) demonstrated that nutrient accumulation in the aboveground biomass of the cover crops was positively correlated with soybean yield in the last two harvests.

Discussion

SDM accumulation improves agroecosystem performance

The greater accumulation of SDM and nutrients in MIX emphasizes the importance of incorporating

a diversity of crops with different phenological cycles in production systems (Clark 2012). Each cover crop has a specific function in the system that depends on its morphophysiological characteristics. *P. glaucum* has a short cycle and contributes to nutrient accumulation in the system in the initial phase of the second crop (Clark 2012). During the second crop, as water availability decreases, *P. glaucum* enters senescence, while vegetative growth and nutrient accumulation by the perennial species (*C. spectabilis*, *U. ruziziensis*, and *C. cajan*) used as soil cover plants continue. The greater quantity and

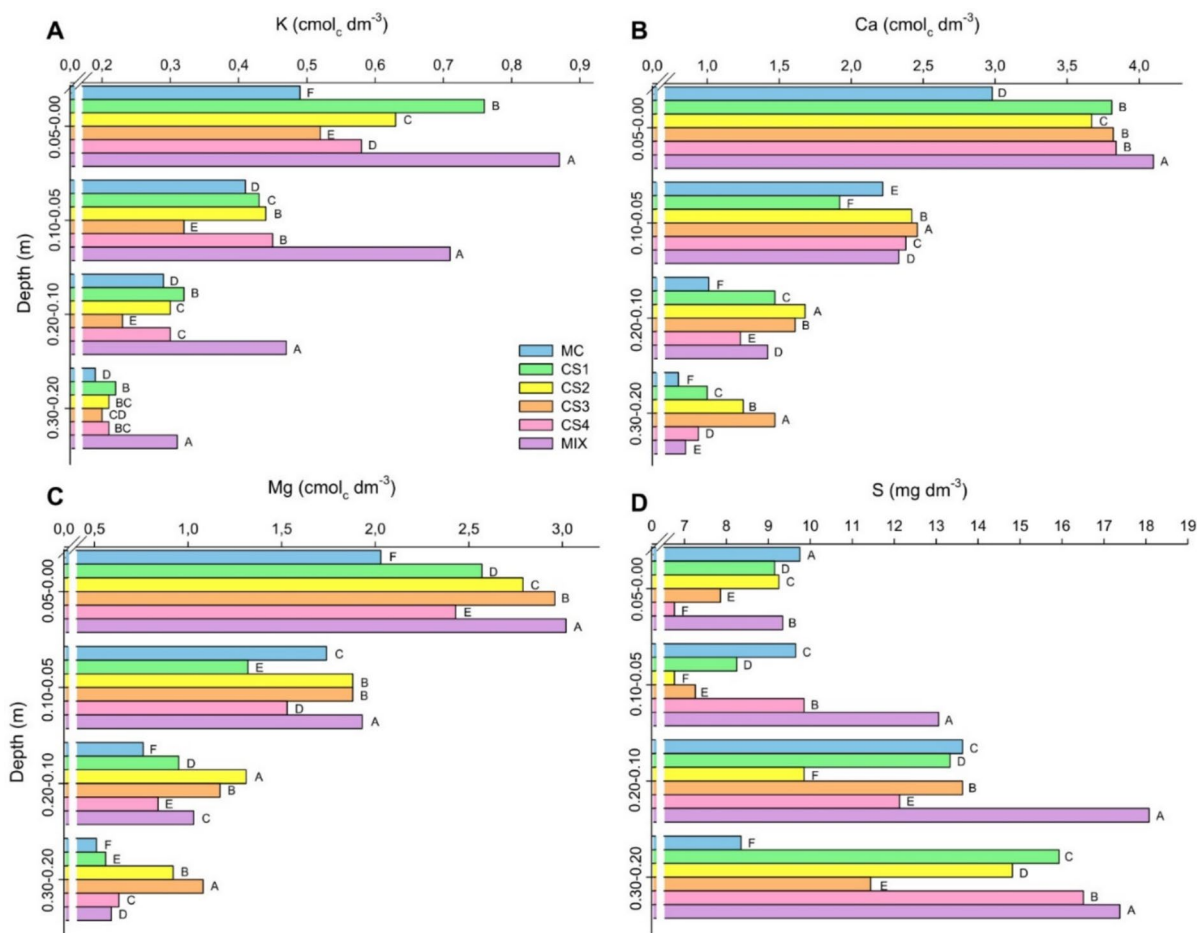


Fig. 6 Soil nutrients in soil layers after the soybean harvest (crop season 2019/20) as a function of cover crop treatment: **A** K, **B** Ca, **C** Mg, and **D** S. MC: monocropped (fallow under no-tillage); CS1: crop succession 1 (*Crotalaria spectabilis*); CS2: crop succession 2 (*Pennisetum glaucum*); CS3: crop suc-

sion 3 (*Urochloa ruziziensis*); CS4: crop succession 4 (*Cajanus cajan*); MIX (*C. spectabilis* + *P. glaucum* + *U. ruziziensis* + *C. cajan*). Columns for the same depth with different letters are significantly different by Fisher's protected LSD test at $p \leq 0.10$

quality of organic residues benefit the succeeding soybean crop (Carvalho 2022).

Oliveira Jr et al. (2014) found that *U. ruziziensis* and *P. glaucum* have beneficial allelopathic potential, as they observed chemical inhibitory effects of these cover crops on weed species such as *Euphorbia heterophylla* and *Bidens pilosa*. In addition to covering the soil, the species in the MIX system may have engaged in interactions that increased the exudation of a greater diversity of secondary metabolites and quantity of carboxylic compounds and complex organic matter derived from the grasses. Moreover, the high lignin content of grasses favors increased soil microbial biomass, as observed by Brandani and Santos

(2016) and Moreira and Siqueira (2006), due to the addition of SOM and proteins that reduce resistance to root growth along the soil profile. These inputs are positively reflected in the ability of the system to absorb and allocate nutrients in the organic fraction of SDM under NTS.

Nutrient cycling

The N content of SDM was higher in CS4, where only *C. cajan* was cultivated, than in CS1, CS2, and CS3 (Fig. 2). Approximately 70 kg ha⁻¹ more N per year was accumulated in SDM in CS4, highlighting the importance of this legume in N cycling under

NTS through biological N fixation. *C. cajan* also increased N cycling when multiple cover crops were intercropped in the MIX system, possibly by releasing metabolites that increased N fixation. These observations are supported by the results of Ferreira et al. (2017) and Carvalho et al. (2022), who found that *Crotalaria* sp. and *C. cajan* increased the community of diazotrophic microorganisms responsible for the conversion of N_2 into inorganic forms that can be assimilated by plants (NO_3^-/NH_4^+) and improved the lignin:N ratio, which was associated with an increase in soil particulate organic C. Osterholz et al. (2018) emphasized that diversified legumes reduce the risk of N loss through gross ammonification, i.e., the gross flux of NH_4^+ produced by microbial mineralization of organic N compounds during grain crop growth.

According to Teodoro et al. (2011), in addition to N accumulation, the deep and branched root systems of *C. spectabilis* and *C. cajan* also enhance Ca and P availability in the Cerrado by exuding organic compounds that promote nutrient release. We observed greater Ca accumulation in SDM in CS1. This accumulation can be attributed to the root morphology (i.e., taproot) and root physiology of *C. spectabilis*, which favor the absorption of Ca from the soil during the second crop season.

In this sense, Koefender et al. (2017) found Ca accumulation values of 71.1 kg ha^{-1} in *Crotalaria juncea* biomass and 56.6 kg ha^{-1} in millet. In agreement with the results obtained in the present experiment, Pacheco et al. (2013) reported Ca half-life values of 67 days for cover crop species similar to those evaluated in this study, in addition to Ca accumulation of approximately 90 kg ha^{-1} in the species *U. brizantha* and *U. ruziziensis* + *C. cajan* at the time of desiccation, with a reduction to approximately 10 kg ha^{-1} after 120 days of desiccation, evidencing the high cycling of this nutrient under tropical conditions.

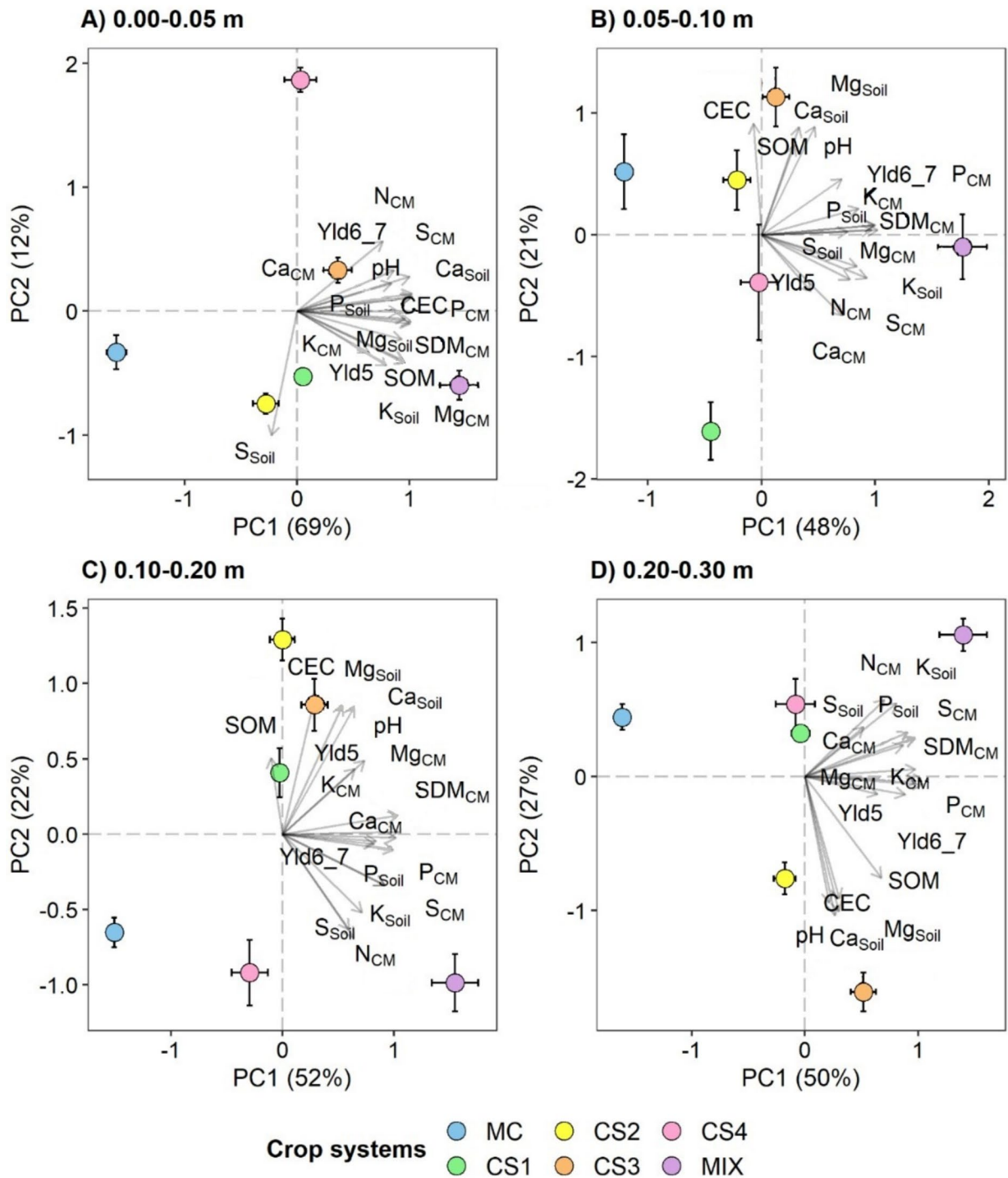
Studies conducted during the winter with *Raphanus sativus* also reported significant Ca accumulation in plant biomass, of approximately 140 kg ha^{-1} (Koefender et al. 2017). In the same experiment, other cover crops showed Ca accumulation within a quantitative range similar to that obtained in the present study, around 50 kg ha^{-1} . Even more pronounced, the cultivation of the cover crops *Canavalia ensiformis* and *Crotalaria* sp. during the summer resulted in Ca accumulations of

670 kg ha^{-1} and 340 kg ha^{-1} , respectively (Pereira et al. 2017). Thus, there are indications that the calcium cycle is occurring effectively, contributing to its availability to subsequent crops due to the dynamics of element cycling following the initial input from liming and gypsum application at the beginning of the long-term experiment.

Our results confirm those of Araújo et al. (2021), who found that incorporating *C. spectabilis* increased soil pH from 5.0 to 5.3 and thus enhanced soil Ca^{2+} and Mg^{2+} levels. These changes also increased the accumulation of Ca^{2+} and Mg^{2+} in plant tissues, demonstrating that this cover crop can cycle nutrients, increase CEC and BS, and reduce Al content and potential acidity.

According to Baptistella et al. (2021), Teutscherova et al. (2019), and Louw-Gaume et al. (2017), *U. ruziziensis* specialized to grow in environments with low available P by developing a more widespread root system with intense colonization of mycorrhizal fungi and by exuding acid phosphatases and organic acids (OAs), such as nicotinic, glycolic, malic, pyruvic, succinic, and fumaric acids. When *U. ruziziensis* was grown as a single cover crop in CS3, P cycling was stimulated possibly due to the abundance of P near the root, given its low mobility in the soil profile, associated with mechanisms previously described in the literature, such as root exudation of enzymes and OAs capable of solubilizing poorly labile P fractions (Baptistella et al. 2021; Louw-Gaume et al. 2017). Almeida et al. (2020) and Louw-Gaume et al. (2017) found that the shoots or root surface of *U. ruziziensis* exude several OAs, mainly citric, oxalic, and malic acids, that can solubilize P and increase its availability to the grass. These OAs make P available to plants due to their high affinity for specific minerals: oxalate releases P associated with Ca, and citrate and malate release P bound to Fe and Al oxides. Since OAs are highly energetic molecules produced by *U. ruziziensis* that are used in microbial metabolism, their production and decomposition form a continuous stimulation cycle. Thus, the solubilization of P by OAs increases P bioavailability in the soil solution or P bound to SOM, such as phytates (Almeida et al. 2018). This P is protected from losses to the environment but is generally not available to plants.

The results highlight the positive effects of cover crop mixtures and nutrient accumulation on soil and illustrate the synergistic relationship between P and



Ca dynamics (Fig. 8). Cover crop diversity was correlated with increased P and Ca concentrations, particularly in the surface soil layers (Fig. 5 and 6), along with greater availability of these nutrients 90 days after desiccation, promoted by the decomposition

of SDM before soybean planting (Figs. 3 and 4). According to Rosolem and Marcello (1998), low P availability can restrict root development and impair the uptake of other nutrients. Because the mobility of P in soil is low, nutrient-root contact via a broad,

◀**Fig. 7** PCA of shoot dry mass (SDM) production, nutrient accumulation at cover crop management (desiccation, CM), and soybean yield in the first five years of the experiment and the last two years (6th and 7th) in the **A** 0.00–0.05 m layer, **B** 0.05–0.10 m layer, **C** 0.10–0.20 m layer, and **D** 0.20–0.30 m layer after harvesting the 2019/20 soybean crop. The following variables were measured at CM: shoot dry mass (SDM_{CM}), nitrogen (N_{CM}), phosphorus (P_{CM}), potassium (K_{CM}), calcium (Ca_{CM}), magnesium (Mg_{CM}), and sulfur (S_{CM}). Yld5, soybean yield in the first five years of the experiment; Yld6_7, soybean yield in the 6th and 7th years of the experiment, SOM, soil organic matter; CEC, cation exchange capacity; N_{soil} , soil nitrogen content; P_{soil} , soil phosphorus content; K_{soil} , soil potassium content; Ca_{soil} , soil calcium content; Mg_{soil} , soil magnesium content; S_{soil} , soil sulfur content. MC: monocropped (fallow under no-tillage); CS1: crop succession 1 (*Crotalaria spectabilis*); CS2: crop succession 2 (*Pennisetum glaucum*); CS3: crop succession 3 (*Urochloa ruziziensis*); CS4: crop succession 4 (*Cajanus cajan*); MIX (*C. spectabilis* + *P. glaucum* + *U. ruziziensis* + *C. cajan*)

well-developed root system is essential to access available P (Ernani et al. 2000). Low soil Ca availability also negatively affects root growth, reducing the volume of soil explored by roots, and these effects are exacerbated by P deficiency (Rosolem and Marcello 1998).

Our results indicate that diversified cover cropping improves soil fertility by increasing nutrient retention and reducing potential leaching losses (Fig. 5 and 6). However, management strategies are needed to enhance the availability and plant accessibility of nutrients that may be fixed or stored in deeper soil layers, thereby improving nutrient cycling. Overall, all analyzed nutrients were highest in MIX, suggesting that greater cover crop diversity increased nutrient availability and uptake by the subsequent crop. Thus, MIX may reduce fertilizer use and could be an interesting strategy to enhance soybean productivity.

Cover crop mixtures enhance SDM decomposition, nutrient release, and soybean yield

The intermediate half-life of SDM decomposition and nutrient release in MIX reflects the diversity of plants in this system (Fig. 3A) and their decomposition rates. Significantly, half of this SDM remained on the soil when soybean was sown. The presence of *U. ruziziensis*, whether as a single cover crop (CS3) or intercropped (MIX), was important for increasing the quantity of SDM on the soil surface under NTS, as a long residue half-life of 210 days was observed in

CS3. Pacheco et al. (2017) reported superior development of *U. ruziziensis* when intercropped with corn compared with oversowing with soybean; the accumulated SDM reached 18,000 kg ha⁻¹, confirming the quantitative importance of *U. ruziziensis* for soil protection in the Cerrado. Rosolem et al. (2012) also observed high persistence of SDM from *U. ruziziensis* on the soil surface and found that its root system decomposed by only 10% at 45 days after desiccation.

Our current results confirm that MIX provides adequate quantitative maintenance of phytomass on the soil surface under NTS and more efficient nutrient cycling during the second crop season. Nutrient release improves soil nutrient dynamics and nutrient availability for subsequent crops. MIX was among the systems with the highest rates of nutrient release to the soil, primarily due to the inclusion of two legumes (*C. spectabilis* and *C. cajan*), which favor organic residues enriched with N. The treatments with single *C. spectabilis* (CS1) and *C. cajan* (CS4) also showed high rates of nutrient release (N, S, and Ca). Rosa et al. (2017) observed an increase in low-molecular-weight C compounds, such as OAs and sugars, after the cultivation of *Mucuna deeringiana*, *C. cajan*, *Crotalaria juncea*, *Brassica napus*, *Crambe abyssinica*, and *Raphanus sativus*, indicating the high lability of legume-derived residues. Rosa et al. (2017) also noted that continued cover crop insertion contributed to the accumulation of stable organic matter fractions, favoring SOM persistence and improving soil properties, which in turn enhanced the development and activity of subsequent crops and soil microorganisms.

Soybean grain yield in the last two agricultural years (Yld6_7) is the most appropriate indicator of the effects of nutrient cycling promoted by cover crops, while the first five years of the NTS represent an initial “system establishment” phase. The crop diversity provided by MIX led to high soybean yields, demonstrating that interactive nutrient cycling occurred between the crop species over time and provided a more suitable environment for soybean development in succession. The enhanced soybean yield in succession to single *U. ruziziensis* (CS3) can be attributed to greater soil coverage, weed suppression through allelopathic effects, and enhanced P cycling under NTS, as reported by Baptistella et al. (2021), Almeida et al. (2020), and Almeida et al. (2018). The effect of diversity over the seasons was clear in CS4, in which *Stylosanthes* (2014) was followed by

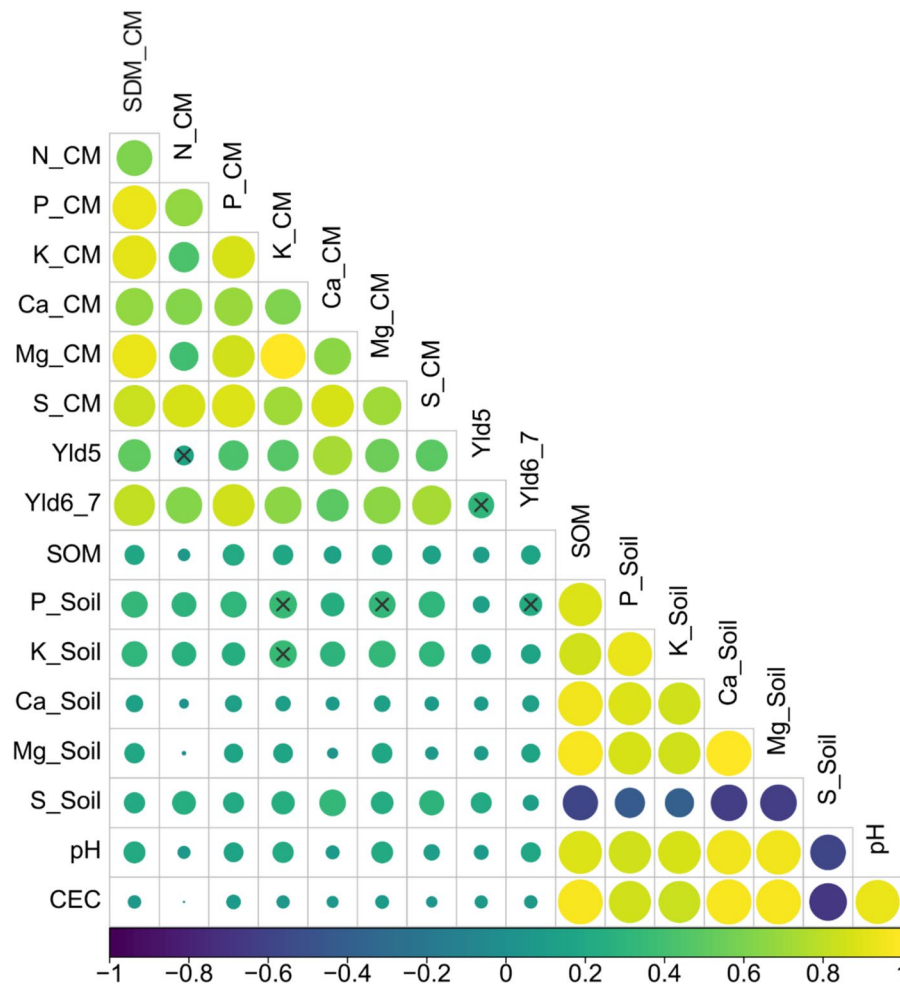


Fig. 8 Heatmap of Pearson's correlation analysis of shoot dry mass (SDM) production, nutrient accumulation at cover crop desiccation, soybean yield in the first five years of the experiment and the last two years (6th and 7th), and soil chemical properties at the experimental site. The following variables were measured at cover crop management (desiccation, CM): shoot dry mass (SDM_{CM}), nitrogen (N_{CM}), phosphorus (P_{CM}), potassium (K_{CM}), calcium (Ca_{CM}), magnesium (Mg_{CM}), and sulfur (S_{CM}). Yld5, soybean yield in the first five years of the

experiment; Yld6_7, soybean yield in the 6th and 7th years of the experiment, SOM, soil organic matter; CEC, cation exchange capacity; N_{soil}, soil nitrogen content; P_{soil}, soil phosphorus content; K_{soil}, soil potassium content; Ca_{soil}, soil calcium content; Mg_{soil}, soil magnesium content; S_{soil}, soil sulfur content. Correlations above zero are positive and below zero are negative. Correlations with an "X" are not significant, and the circle size is proportional to significance

V. unguiculata (2015 and 2016) and *C. cajan* (2017 to 2020).

Soil chemical properties correlated with soybean yield

Among soil chemical properties (Figs. 5, 6), MIX efficiently increased SOM content and CEC, mainly in the top soil layers. These increases can be attributed

to the quantitative effect of the SDM of *U. ruziziensis* intercropped with other cover crops, as similar effects were observed for the single grass (CS3) up to a depth of 0.20–0.30 m. *U. ruziziensis* has an abundant, fasciculate root system, which intensifies the contribution of organic residues to the soil, as corroborated by Carvalho et al. (2022), who reported greater accumulation of SOM under cover crops, and by Rosolem et al. (2019, 2012), who observed persistent roots and

high C/N ratios that influenced nutrient cycling and residue decomposition.

In addition, by promoting the accumulation of C and N in the soil, *U. ruziziensis* likely increases the microbial synthesis of SOM fractions and C stabilization in the soil, enhancing C sequestration (Eberhardt et al. 2021; Nishigaki et al. 2020; Yao et al. 2019; Schmatz et al. 2017). The increases in SOM and CEC in deeper soil layers in CS3 are likely attributable to the lack of interspecific competition. The diversity of cover crops in MIX also provided a better soil pH buffering effect up to a depth of 0.10–0.20 m. Weakly acidic functional groups in SOM, such as carboxylic and phenolic acids, form a buffer system through protonation and deprotonation, as observed by Xu et al. (2012), Latifah et al. (2017), and Shi et al. (2019). This increased buffering can reduce limestone use over time and prevent drastic changes in soil properties that can negatively affect crops and microbiota.

The patterns of soil nutrient content confirmed that shoot residues in MIX promoted the cycling of nutrients, particularly P, K, Ca, Mg, and S. However, it is important to emphasize that while MIX was not fertilized, the previously planted sunflower was fertilized annually for three years with 100 kg ha⁻¹ of MAP, KCl, and urea. The MIX treatment was fertilized during the 2015/16 to 2017/18 crop years, when sunflower was used as the second crop to support the growth and root expansion of *U. ruziziensis* for nutrient uptake and cycling. Since the second crops were not harvested (Fig. 1), the fertilizer remained in the system. The decomposition of desiccated sunflower + *U. ruziziensis* tissues contributed to nutrient mineralization and availability for the succeeding crops, which included soybean/*C. spectabilis* + *P. glaucum* + *U. ruziziensis* + *C. cajan* from 2018/19 to 2020/21. This may have contributed to the high soybean yield and the positive effects on soil properties.

In tropical soils, which are highly weathered and dominated by Fe and Al oxides, CEC is highly variable and depends on pH. The liming and gypsum application events likely increased pH throughout the 7 years and created additional negative charges on soil colloids, enhancing the retention of basic cations, as well as representing an important input of Ca into the system. However, under no-till conditions, the absence of mechanical mixing limits cation redistribution, favoring nutrient accumulation near the surface (Crusciol et al. 2011). Therefore, the long-term

improvement in surface fertility cannot be attributed solely to liming but rather to the continuous contribution of the cover crop systems.

The decomposition of crop residues over the years increased SOM content, which plays a central role in nutrient retention and availability in tropical soils with low permanent charge. The higher SOM levels contributed to an increase in pH and CEC, favoring Ca²⁺ and Mg²⁺ retention and reducing their leaching potential and losses (Crusciol et al. 2015, 2023). In addition, SOM complexes exchangeable Al³⁺, mitigating acidity and enhancing BS. The slow release of nutrients from residue mineralization prevents rapid nutrient losses and promotes the gradual accumulation of exchangeable bases in the uppermost layers (Crusciol et al. 2015, 2023). These effects are among the long-term benefits of cover crop diversity, which were evident from the increases in soybean yield in the sixth and seventh years compared with the first five years. During the system stabilization period, environmental conditions and variations in management practices influence nutrient accumulation and decomposition rates, altering system performance. The lower yields in the first 5 years of this study indicate that the benefits of MIX materialize only after multiple growing seasons.

Among the cover crop species used, *U. ruziziensis* plays a particularly important role in nutrient cycling. Its deep root system enables the uptake of Ca and Mg from deeper soil layers and their subsequent return to the surface via litter deposition. This biological recycling mechanism explains the consistent increase in these cations in surface layers. While K is more mobile in the soil than Ca and Mg, the high biomass production and litter return also contribute to its retention in the surface layer along with the accumulation of SOM, improvements in CEC, and enhanced soil structure, all of which favor nutrient conservation. Thus, the synergy between SOM enrichment, the nutrient recycling capacity of *U. ruziziensis*, and the ability of variable-charge minerals to buffer pH and retain nutrients, help to explain the sustained increases in Ca, Mg, and K in the surface soil layers throughout the duration of the experiment (Crusciol et al. 2015, 2023).

The interaction among cover crop species proved to be a decisive factor in nutrient cycling, with each playing specific roles but together acting synergistically to increase nutrient use efficiency. This synergy

was greatest for P, K, and S cycling. S is easily leached to depths below 0.30 m, as demonstrated by Bossolani et al. (2021b), Crusciol et al. (2019), and Da Costa et al. (2018), and MIX enhanced S cycling by promoting S absorption by roots at greater depths, allocation in organic residues, and subsequent release to the soil. The effects of *U. ruziziensis* on Ca and Mg cycling at greater soil depths were also evident in CS3, as Ca and P stimulate the root growth of soybean in succession (Crusciol et al. 2021b; Bossolani et al. 2021a, 2021b; Dos Reis et al. 2018). These effects explain the high grain yields of soybean in succession to *U. ruziziensis*, whether in MIX or CS3.

The PCA summarizes the main findings and contrasts the positive impact of the MIX treatment on nutrient cycling, soil properties, and soybean yield with the negative effects observed in MC (fallow). It also illustrates the intermediate effects of CS1 and CS4, where the species used in MIX were grown separately. Despite the benefits of MIX, some variables in Fig. 7, such as soil S content at 0.00–0.05 m, SOM, CEC, and soil Mg and Ca, were more positively influenced by specific crop successions, particularly CS1, CS2, and CS3. Similarly, SOM, CEC, pH, and soil Mg and Ca at depths of 0.05–0.10 m and 0.20–0.30 m were notably improved in CS2 and CS3. The high similarity of the data for shoot nutrients, soil fertility variables, and soybean yield between PC1 and PC2 confirmed the effects of nutrient cycling. In addition, the high similarity of these variables between MIX and single *U. ruziziensis* (CS3) confirms the benefits of these systems for nutrient cycling and soybean yield in succession.

Pearson's correlation analyses demonstrated that nutrient accumulation in the aboveground biomass of cover crops is an important indicator of the potential of cover crop systems to promote nutrient cycling and increase soybean yield under NTS. The variability in nutrient release rates as a function of cover crops underscores the importance of choosing the best cover crop to ensure the availability of adequate nutrients to meet the demands of crops of economic interest.

Conclusions

The use of cover crops alone or as a mixture promoted nutrient cycling and enhanced soybean yield

in the Brazilian Cerrado, as evidenced by improvements in SOM, CEC, pH, and nutrient concentrations at soil depths of 0.00–0.05 m and 0.05–0.10 m. Each cover crop species played a specific role in the second-crop systems, which was potentially driven by differences in root development, N fixation, nutrient cycling, soil coverage, and stimulation of enzymes involved in organic residue decomposition, but all contributed to C accumulation under no-tillage conditions. By contrast, MC is not recommended, as it did not improve soil physical or biochemical properties or support soybean yield under Cerrado conditions.

Diversified systems with a mixture of cover crops can provide long-term improvements in soil chemical properties, nutrient cycling, and crop yields. Single cover crops such as *U. ruziziensis*, *C. cajan*, and *C. spectabilis* also provide these effects because they are adapted to the edaphoclimatic conditions of the Brazilian Cerrado. In addition, the nutrient cycling provided by these crops in MIX system increases soybean yield in succession. Thus, diverse cover crop systems may be a strategy for complementing or even reducing the use of chemical fertilizers, thereby increasing the sustainability of production systems.

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Author Contribution A.S.D.C., C.A.C.C., and L.P.P. were responsible for the conceptualization of the study. A.S.D.C., C.A.C.C., L.P.P., K.S.M., and T.R.M.G. developed the methodology. A.S.D.C., E.R.B., V.H.L.R., I.M.P., J.W.B., K.S.M., and T.R.M.G. performed the formal analysis and investigation. A.S.D.C. prepared the original draft of the manuscript. A.S.D.C., C.A.C.C., L.P.P., F.A.P., E.D.S., J.F.N., J.P.G.R., and B.M.T. reviewed and edited the manuscript. C.A.C.C. and L.P.P. acquired the funding and managed the resources. C.A.C.C. and L.P.P. also supervised the study.

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Data Availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

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