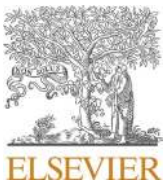
Field Crops Research 340 (2026) 110371



Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr



Limited variation in sorghum yield responses to diverse legume rotations under Sudano-Sahelian conditions

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ARTICLE INFO

Keywords:
Crop rotation
Residue management
Sorghum bicolor
Nitrogen cycling

ABSTRACT

Context: In Sudano-Sahelian West Africa, declining soil fertility due to land degradation, low fertilizer use, and shortened fallows threatens productivity. Legume-based rotations offer a sustainable solution by improving nitrogen availability and soil health, especially under low-input conditions.
Objectives: This study aimed to enhance sorghum-based cropping systems through one-year legume rotations. It sought to characterize a diversity of legume crops and evaluate the effect of returning their biomass (excluding grain) to the soil on subsequent sorghum crop's growth and yield.
Methods: Twenty crop precedents, comprising 17 legumes and 3 grasses, were evaluated across three randomized complete block design (RCBD) field trials under varying soil fertility conditions. Biological nitrogen fixation was quantified using the natural abundance ($\delta^{15}N$) method along with measurements of nitrogen content and total nitrogen accumulation in aboveground biomass. In the following season, sorghum was grown to assess rotational effects on yield and growth.
Results: The study revealed substantial and significant variability among legume species in biomass and nitrogen accumulation, with *Crotalaria juncea* and *Centrosema pascuorum* showing the highest values. However, these differences did not translate into significant yield gains for subsequent sorghum crops. While legumes outperformed grasses in improving sorghum yields, variation among legume species was minimal, suggesting nitrogen recycling inefficiencies under Sudano-Sahelian conditions.
Conclusions: Under Sudano-Sahelian conditions, non-nitrogen (non-N) effects appear to play a crucial role in the overall rotational benefits of legumes in cereal-based systems. Therefore, grain and fodder legumes should be preferred over green manure legumes because they provide high-protein food for humans and feed for animals, while enhancing the overall performance of crop rotations. Further diversification of legume crops is needed to optimize legume-nonlegume balance and manage trade-offs between food security and sustainable soil management.

1. Introduction

Addressing the intertwined challenges of food security, environmental sustainability, and soil health restoration requires integrated agricultural practices that boost productivity while minimizing environmental impacts. Diversified cropping systems and organic amendments have been shown to achieve these goals (Wang et al., 2025). In particular, cover crops enhance agroecosystem functioning by diversifying plant cover, improving soil fertility and structure, stimulating microbial carbon formation, contributing to climate regulation, and increasing Nitrogen Use Efficiency (NUE) when legumes are included (Qiu et al., 2024). Yet, adoption and effectiveness of these practices are limited by local biophysical and socio-economic constraints, highlighting the need to evaluate their relevance and performance in marginal Sudano-Sahelian environments.

In Sudano-Sahelian West Africa, soils are highly weathered and

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https://doi.org/10.1016/j.fcr.2026.110371
Received 8 September 2025; Received in revised form 26 January 2026; Accepted 26 January 2026
Available online 31 January 2026
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generally characterized by low inherent fertility, low soil organic carbon content, and poor water-holding capacity (Bationo et al., 1998). Deforestation, overgrazing, and agricultural expansion further degrade soil. At the same time, fertilizer use by small-scale farmers remains extremely low, at approximately 5 kg per hectare, insufficient to compensate for nutrient losses through crop harvests, resulting in ongoing soil depletion (Chianu et al., 2012). Traditional long fallow periods, which once allowed fields to replenish soil fertility, are no longer practiced due to rising land pressure driven by rapid growth of human and livestock populations. This soil management practice involved cultivating land continuously for a short period, typically two to five years, followed by an extended fallow period of up to 25 years. Although long fallows contribute to restoring soil physical, chemical, and biological properties through the natural regeneration of savanna vegetation and woodland, the overall productivity is low relative to the extensive land area left unproductive for extended periods (Tarawali et al., 1999). Furthermore, the frequent grazing and fire on fallow lands significantly delay the accumulation of soil fertility in the topsoil (Roose, 1993).

A key challenge is ensuring the long-term restoration of soil fertility, particularly through the enhancement of soil organic matter (Lal, 2004; Bationo et al., 2007), while simultaneously achieving short-term yield increases needed by farmers to enhance food security. Legume-based crop rotations can help tackle this challenge (Gan et al., 2015; He et al., 2025; Mudare et al., 2025). The inclusion of grain legumes in cereal-, root-, or tuber-based cropping systems has shown significant benefits in Sub-Saharan Africa (see Bado et al., 2022 - for millet-based cropping systems). Based on an analysis of 199 experiments, Franke et al. (2018) reported an average yield increase of 41 % in cereals grown in rotation with grain legumes, compared with continuous cereal cultivation. One of the key rotational effects of grain legumes is improving nitrogen (N) nutrition in subsequent crops. This is due to legumes' ability to fix atmospheric nitrogen (N_2) through symbiosis with rhizobia, thereby enhancing the overall nitrogen balance in the system (Dakora and Keya, 1997). The rotational benefits of legumes are more pronounced under low fertility conditions, particularly in Africa (Zhao et al., 2022). However, evidence that yield advantages persist even when high rates of mineral N are applied to the subsequent cereal crop suggests that non-N effects—such as improved soil structure, nutrient availability, and pest and weed suppression—also play a significant role (Peoples et al., 2009; Franke et al., 2018).

Herbaceous, shrub, or fodder legumes can be incorporated into crop rotations with non-leguminous species as green manure or cover crops during short-term fallow periods to improve soil fertility. Short-term improved fallows based on legumes—most commonly from genera such as *Sesbania*, *Tephrosia*, *Leucaena*, *Mucuna*, *Centrosema*, *Pueraria*, *Crotalaria*, *Cajanus*, *Indigofera*, and *Mimosa*—are increasingly being adopted by farmers in tropical regions (Sanchez, 1999). Improved fallows can accumulate large amounts of biomass and nitrogen (100–200 kg N ha^{-1}) in situ, which are returned to the soil as leaf and root litter (Giller et al., 1997). A significant portion of this N is derived from the atmosphere, though the exact amount varies with legume species and environmental conditions (Becker and Johnson, 1999). This nitrogen can either contribute directly to a positive nitrogen balance in the system or, at the very least, reduce nitrogen mining from the soil. Beyond nitrogen contributions, these legume rotations provide additional agronomic benefits, including weed suppression, reduction of *Striga* infestation, improved soil physical properties, and reduced soil erosion.

Numerous legume species have been evaluated for their potential as mulch in cropping systems in sub-Saharan Africa (Sanginga, 2003). These studies have primarily focused on maize-based systems in relatively humid environments, ranging from forest to Sudanian zones, with annual rainfall exceeding 1000 mm (Versteeg et al., 1998; Carsky et al., 1999; Sanginga, 2003; Eilittä et al., 2004; Baijukya et al., 2006; Snapp et al., 2010) and, to a lesser extent, upland rice (Becker and Johnson, 1998). Far fewer examples of such studies exist for sorghum- or millet-based cropping systems in the more arid conditions of the Sudano-Sahelian zone, which receives less than 800 mm of annual cumulative rainfall. It should be noted that green manuring is scarcely practiced by farmers in these areas, due to intense pressure on crop biomass, which is either harvested for fodder or consumed by free-grazing animals during the dry season (Kouyaté et al., 2000).

This study aimed to evaluate the potential to improve sorghum-based cropping systems by implementing a one-year legume rotation under semi-arid Sudano-Sahelian conditions in Burkina Faso. It focused on assessing the effects on subsequent sorghum yield of crop residue restitution from a range of preceding legume crops, including grain, fodder, and green manure types. The specific objectives of the study were to:

-Characterize these legume crops regarding cycle duration, ground cover capacity, growth behavior, nitrogen-fixing ability, biomass, and nitrogen accumulation.

-Quantify the carry-over effects of these legume crops on sorghum growth and yield performance in the following cropping season.

2. Materials and methods

2.1. Site and experimental conditions

The experiments were conducted in Gampela, 20 km east of Ouagadougou, in Burkina Faso (12°24' 54.427'' N, 1°23' 23.173''O). The area's climate is Sudano-Sahelian. It is characterized by a rainy season from June to October and a dry season from November to May. The average monthly temperature ranges from 23 to 33°C. The experimental station recorded cumulative rainfall of 818 mm, 913 mm, and 761 mm in 2021, 2022, and 2023, respectively (Fig. 1). Gampela's soils are of the leached tropical ferruginous type, derived from granitic parent rock (BUNASOL, 1988). The soils are predominantly silty-sandy in texture, with 6.86 % clay, 19.5 % silt, and 73.6 % sand. The soil is acidic (pH_{water}= 5.01) with low soil organic matter content (0.749 %) and low physicochemical fertility (N content = 0.039 %; P content = 108.6 mg.kg^{-1}; Plant-available P = 8077 mg.kg^{-1}).

2.2. Plant material

Twenty plant species x cultivar combinations were selected for their good establishment and growth from a larger collection evaluated in 2019 and 2020 at the Gampela Research Station (Table 1, Fig. 2). Among them, 17 were legumes, representing 14 species and 17 cultivars in total. These legume species included grain legumes, fodder legumes, and legumes used as green manure (service plants). The main traditional grain legume crops of Burkina Faso—cowpea, bambara groundnut, and peanut—were included, along with diversification legumes such as mung bean, horse gram, jack bean, and pigeon pea. Three cowpea (*Vigna unguiculata*) cultivars were included, as it is the major indigenous grain legume crop in Burkina Faso. These were: Komcalle, an improved erect grain variety; Gourgou, an improved semi-erect dual-purpose variety (used for both grain and fodder); and Bengraaga, a traditional late-maturing, spreading variety. Two cultivars of velvet bean (*Mucuna pruriens*) with different growth cycle durations were also included. In addition to legumes, three grass species (Poaceae) were included for comparison: *Brachiaria ruziziensis*, a tropical forage grass; finger millet (*Eleusine coracana*), a major staple cereal in Eastern and Southern Africa; and sorghum (*Sorghum bicolor*), used here as a monoculture control. For sorghum, we selected the Kapelga variety, a traditional cultivar belonging to the Guinea type.

2.3. Experimental design

Twenty different crop precedents were evaluated across three field experiments, each conducted using a randomized complete block design

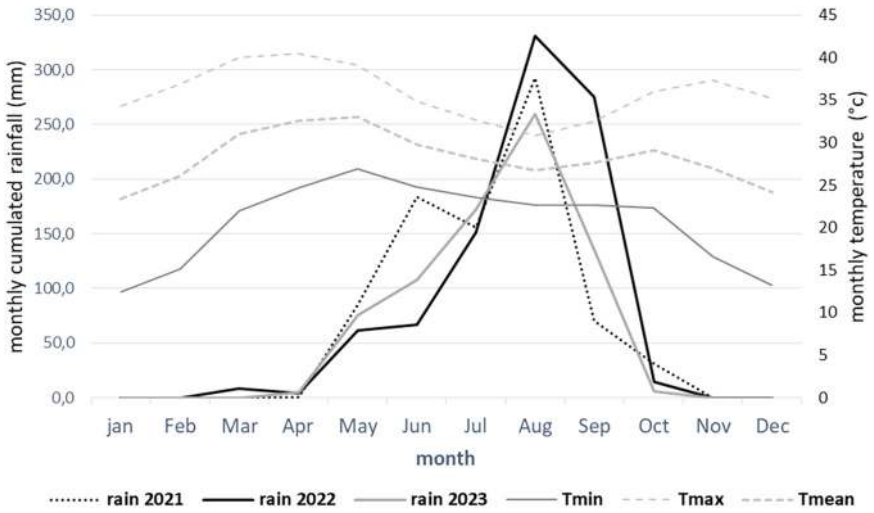


Fig. 1. Monthly rainfall recorded at the Gampela site for 2021, 2022, and 2023, along with the average monthly temperature calculated over the same three-year period.

Table 1
List of the 20 plant species × cultivar combinations used in this study, including their code name (as shown in the figures), crop type, and sowing protocol (intra-row spacing and number of seeds per hole).

Species	cultivar	code name	crop type	intra-row spacing (m)	nb seeds per hole
Sorghum bicolor	kapelga	sorghum	cereal grass	0.4	8
Eleusine coracana		finger_millet	cereal grass	0.1	8
Bracharia ruziziensis		brachiaria	forage grass	0.1	6
Arachis hypogaea	QH 243 C	peanut	grain legume	0.15	2
Cajanus cajan		pigeon_pea	grain legume	0.2	5
Canavalia ensiformis		jack_bean	green manure legume	0.4	2
Centrosema pascuorum		centrosema	forage legume	0.2	8
Crotalaria juncea		crotalaria_juncea	green manure legume	0.2	6
Crotalaria retusa		crotalaria_retusa	green manure legume	0.2	8
Crotalaria spectabilis		crotalaria_spectabilis	green manure legume	0.2	8
Macrotyloma uniflorum		horsegram	grain legume	0.2	6
Mucuna pruriens	deeringiana	velvet_bean_deeringiana	forage legume	0.4	2
Mucuna pruriens	rajada	velvet_bean_rajada	forage legume	0.4	2
Sesbania sesban		sesbania	green manure legume	0.2	8
Tephrosia bracteolata		tephrosia	green manure legume	0.2	8
Vigna radiata		mungbean	grain legume	0.2	5
Vigna subterranea	BFKVS 244	bambara_groundnut	grain legume	0.15	2
Vigna unguiculata	Bengraaga	cowpea_bengraaga	grain legume	0.4	3
Vigna unguiculata	Gourgou	cowpea_gourgou	grain legume	0.4	3
Vigna unguiculata	Komcalle	cowpea_komcalle	grain legume	0.4	3

(RCBD) with four replications. Two experiments were conducted in 2021 under contrasting fertility conditions: one under low fertility (LF21) and the other under high fertility (HF21). A third experiment was conducted in 2022 under low fertility conditions (LF22). In 2021, each elementary plot measured 19.44 m^2 (5.4 m × 3.6 m) and comprised nine cultivated rows spaced at 0.6 m intervals. In 2022, the elementary plot size was slightly reduced to 17.28 m^2 (4.8 m × 3.6 m), with eight cultivated rows also spaced at 0.6 m. Within-row spacing between seed holes was adjusted according to the crop species evaluated (Table 1). In the following season of each experiment, the same plots were used to cultivate sorghum as a test crop to assess carry-over effects. Sorghum was sown with an intra-row spacing of 0.4 m, resulting in nine seed holes per row. The same improved sorghum variety, Sariaso 16, was used across all trials. Sariaso 16 is a caudatum-type variety released by INERA (Institut de l'Environnement et des Recherches Agricoles) in 2008, and is well-adapted to the agroecological conditions of the study area.

2.4. Crop management

Experiment HF21 (high-fertility conditions) was established on a plot under long-term fallow and cleared in 2019. In contrast, experiments LF21 and LF22 (low-fertility conditions) were conducted on land that had undergone continuous cultivation over several years, resulting in considerably lower soil fertility than HF21. Before establishing the experiments, the preceding crop was sorghum in all plots. In all cases, primary tillage was performed using a tractor, followed by manual secondary tillage to prepare seedbeds. Each experiment involved 20 different preceding crop treatments. Seeds were sown manually using a daba (traditional planting tool), with the number of seeds per hole adjusted according to each crop's grain size (Table 1). Experiments HF21 and LF21 were sown on 6 July 2021, while LF22 was sown on 7 July 2022. Seeds produced in each plot were harvested and removed (exported), while the remaining plant biomass (stems and leaves) was left on the soil surface as mulch to support soil restoration until ploughing eight months later, in June of the following season, prior to the subsequent sorghum crop. The Gampela experimental station is fully fenced and protected against grazing animals. Sorghum was sown on 22

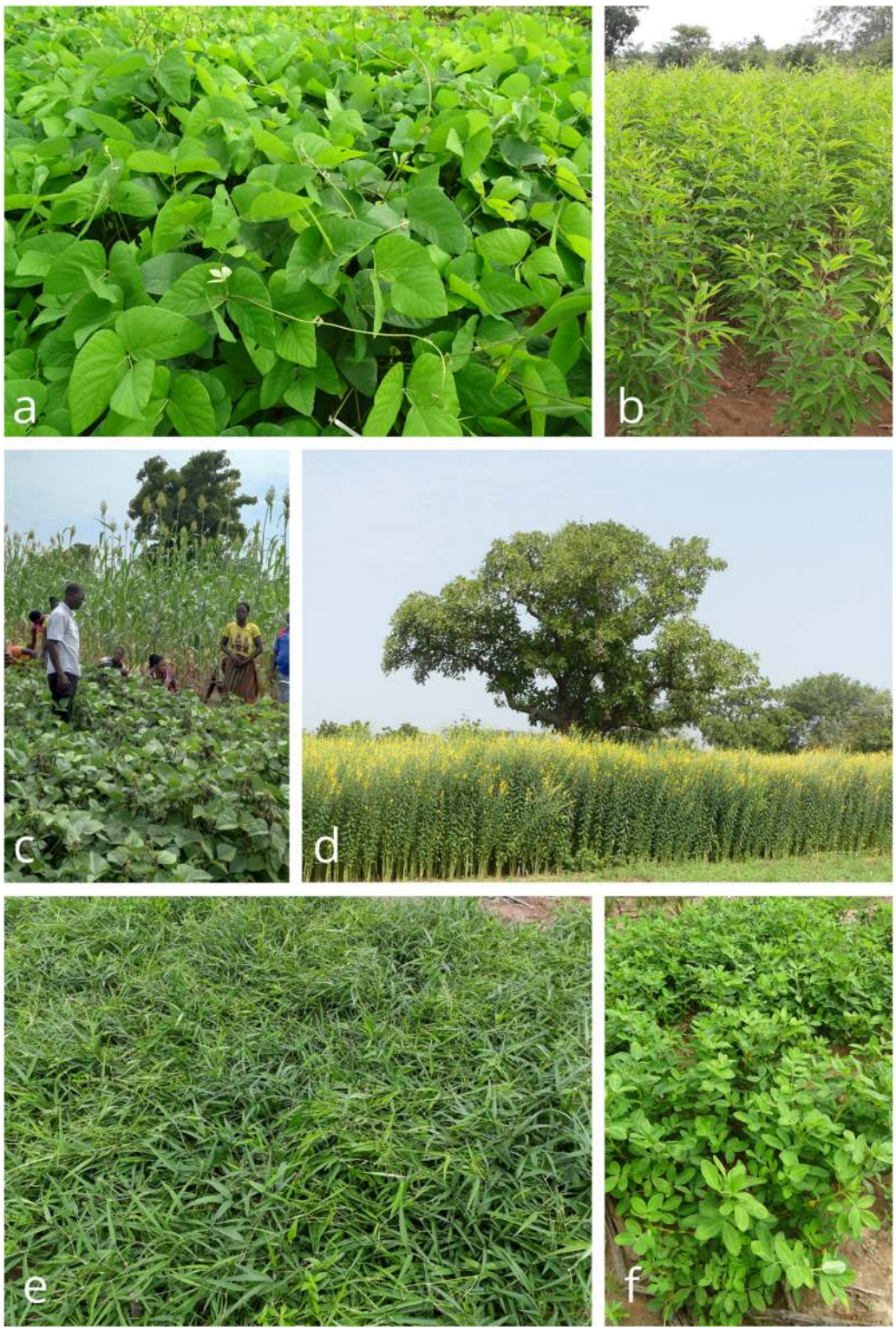


Fig. 2. Photographs of *Mucuna pruriens* or velvet bean (a), *Cajanus cajan* or pigeon pea (b), *Vigna radiata* or mungbean(c), *Crotalaria juncea* (d), *Centrosema pascuarum* (e), *Arachis hypogeae or peanut* (f), taken in Gampela station, Burkina Faso.

June 2022 for HF21 and LF21, and on 28 June 2023 for LF22. Weed control was performed manually, with two weeding operations approximately 20 and 50 days after sowing. In HF21, a fertilizer dose of 75 kg ha^{-1} of NPK (14−23−14) was applied after the first weeding, both on the 20 preceding crops, in 2021, and on the subsequent sorghum crop, in 2022. In contrast, no fertilizer was applied in the LF21 and LF22 experiments. Sorghum seeds were treated with Calthio C, a combination of 25 % endosulfan (insecticide) and 25 % thiram (fungicide), at a rate of 2.5 g kg^{-1} of seed, to protect against early-season pests and diseases.

2.5. Measurements

On the twenty preceding crops:
Canopeo, an Android-based mobile application, was used to estimate

plant canopy cover (CANOPEO42; Table 2) 42 days after sowing (Patrignani and Ochsner, 2015). Additionally, canopy development rate was assessed by monitoring changes in canopy cover between 35 and 55 days after sowing, expressed as CANOPEO_SPEED. Flowering date was recorded at the 50 % flowering stage (FLO50). At this stage, considered as the stage of maximum vegetative development, we measured canopy height (CANOPY) and above-ground plant biomass. Two rows (out of 9 in LF21 and HF21, or 8 in LF22) were harvested in the middle of each elementary plot and weighed to assess fresh biomass. One representative plant sample per elementary plot was collected and oven-dried at 60°C for 72 h to determine its moisture content. It was then used to estimate dry plant biomass per hectare (BIOM_ha). The total harvested biomass was left on the ground to be returned to the soil.

Biological N_2 fixation in crops was determined using aboveground plant tissues (stems + leaves) collected from harvested biomass samples at the flowering stage. The plant material subsamples were analyzed for Nitrogen content (N), Carbon to Nitrogen ratio (C:N), and $\delta^{15}N$ isotopic composition at Catholic University of Leuven, Belgium, using an EA1110 elemental analyzer with a Delta V Isotope Ratio Mass Spectrometer via a ConFlo IV universal continuous flow interface (Thermo Fischer Scientific, Waltham, Massachusetts, USA). The proportion of nitrogen derived from the atmosphere (NDFA) was estimated using the ^{15}N-natural abundance method (Unkovich et al., 2008). The $\delta^{15}N$ of non-N_2-fixing reference plants ($\delta^{15}N$_ref) was obtained from sorghum plots (corresponding to the highest $\delta^{15}N$ values obtained). The $\delta^{15}N$ of legume crops was then used in the following equation to calculate NDFA:

$$NDFA = \frac{\delta 15Nref - \delta 15Nleg}{\delta 15Nref - B} \times 100$$

where δ_{15}Nref was the $\delta^{15}N$ value for sorghum (3.48 ‰ and 5.05 ‰ in 2021, mean of the four replications of experiment LF21 and HF21 respectively, and 5.99 ‰ in 2022, mean of the four replications of experiment LF22). δ^{15}Nleg is $\delta^{15}N$ of evaluated crops. B is the δ^{1} ^{5}N value of the legume when it completely depends on atmospheric nitrogen for its nitrogen nutrition (no nitrogen in the soil). B-values were sourced from published literature: −1.00 for *Canavalia*, −1.82 for *Mucuna*, −1.10 for *Crotalaria* spp., −1.76 for *Sesbania sesban*, −1.83 for *Macrotyloma*, −2.60 for *Arachis hypogaea*, −2.05 for *Vigna radiata*, −1.40 for *Vigna subterranea*, −1.76 for *Vigna unguiculata*, −1.65 for *Centrosema*, −0.66 for *Tephrosia*, and −1.12 for *Cajanus cajan* (Gathumbi et al., 2002; Makoi et al., 2009; Nyemba and Dakora, 2010; Ojiem et al., 2007; Okito et al., 2004; Unkovich et al., 2008). Total N in biomass per hectare (NTOT_ha) was calculated as the product of N content and biomass. Total N fixed per hectare (NFIX_ha) was then determined as the product of NDFA and NTOT_ha.

All plots were harvested for grain yield using the remaining rows after two rows per plot had been used for biomass estimation. This corresponds to seven rows in LF21 and HF21, and six rows in LF22. Pods or panicles were sun-dried for several days before being threshed, winnowed, and weighed to determine grain yield (GY). Seed total phosphorus (P_seed) and potassium (K_seed) contents were analyzed using Inductively Coupled Plasma Atomic Emission Spectroscopy (ICP-AES). Seed total nitrogen (N-seed) content was measured using dry combustion (Dumas method). These analyses were conducted by the CIRAD Laboratory for Water, Soil, and Plant Analysis (US Analyses, CIRAD, Montpellier, France). Based on these data, we estimated nitrogen, phosphorus, and potassium export per hectare (N_EXP_ha, P_EXP_ha, and K_EXP_ha, respectively). For nitrogen, we further estimated the amount available for return to the subsequent sorghum crop by subtracting the nitrogen exported in the seeds from the total nitrogen per hectare accumulated in biomass at the flowering stage (NTOT_delta_ha).

On sorghum:

Yield squares were defined within each elementary plot by excluding the first and the last rows of each plot as well as the first and the last hills of each row. They consisted of seven rows of six sorghum hills (13.44 m^2) in LF21 and HF21 and six rows of six sorghum hills (10.08 m^2) in LF22. All sorghum panicles were harvested. Panicles were sun-dried for several days before threshing, winnowing, and weighing of grains to determine sorghum grain yield (GY_so). Sorghum stems were harvested and weighed to get the total fresh weight per yield square. Fresh samples representative of the overall plot biomass were taken, weighed, and then oven-dried for 72 h at 60°C to determine the dry weight and thus the sorghum straw yield (SY_so).

Table 2
Description of the 19 traits measured in this study on preceding crops and sorghum rotation.

Crop	Trait_code	Trait description	unit
Preceding crop	FLO50	Number of days to 50 % flowering	days
Preceding crop	CANOPY	Canopy height (cm)	cm
Preceding crop	BIOM_ha	Above ground plant biomass per ha at 50 % flowering	t.ha^{-1}
Preceding crop	GY	Grain yield	t.ha^{-1}
Preceding crop	HGW	Hundred grain weight	g
Preceding crop	CANOPEO42	Canopeo 42 days after sowing	%
Preceding crop	CANOPEO_SPEED	Canopeo speed between 35 and 55 days	% per day
Preceding crop	N	Nitrogen content of biomass	%
Preceding crop	C:N	Carbon to nitrogen ratio	-
Preceding crop	NDFA	Natural determination of fixed atmospheric nitrogen	% of total N
Preceding crop	NTOT_ha	Total nitrogen in biomass per ha	kg.ha-1
Preceding crop	NFIX_ha	Fixed nitrogen in biomass per ha	kg.ha-1
Preceding crop	N_seed	Nitrogen content of seeds	%
Preceding crop	P_seed	Phosphorus content of seeds	%
Preceding crop	K_seed	Potassium content of seeds	%
Preceding crop	N_EXP_ha	N exportation per ha	kg.ha-1
Preceding crop	NTOT_delta_ha	Total nitrogen of biomass restituted per ha	kg.ha-1
Sorghum	GY_so	Grain yield	kg.ha-1
Sorghum	SY_so	Straw yield	kg.ha-1

2.6. Statistical analysis

Path analysis, such as PLS-SEM, was not considered because the available data did not support the specification of meaningful causal paths involving at least three variables. Instead, we used a linear mixed-effects model, which allowed us to account for the experimental design and its control factors, as well as potential spatial correlations among residuals.

Modelling the spatial trend of errors to enhance the species comparison

The experimental design in complete blocks requires an analysis with blocks as a control factor, thus estimating a block effect, possibly random. However, not all natural variability can be controlled with blocks. When plots are numerous enough, one can try to further control for natural variability by taking advantage of the similarity of the fertility of neighbouring plots. This can be achieved by treating the linear model errors as spatially correlated, then simultaneously adjusting the block and species effects, along with an error spatial variation model.

Several algorithms have been developed to this end, allowing the adjustment of various spatial variation models. Among these, separable

AR(1) × AR(1) gaussian process (Gleeson and Cullis, 1987) and 2D-splines (Wood, 2025) have been chosen as candidates and tested against the independent errors model. This was carried out using R statistical software with the lme4 package for the independent errors model, with the asreml-R commercial package (Butler et al., 2017) for the AR(1) × AR(1) process, and with the gamm4 package for the 2D-splines.

The four statistical models we used are now presented for a single experiment. For the series of three experiments, the corresponding mod
els are presented in the supplementary material (ModelS1).

Model 1: linear mixed model with independent errors

$$Y_{jkl} = m + b_j + c_{jk} + D_l + E_{jkl}$$

where:

- b_j are the fixed effects of genotype families j, $j = 1 \ldots J$
- c_{jk} are the fixed effects of genotypes k within families j, $k = 1 \ldots K$
- D_l are the gaussian random effects of blocks l
- E_{jkl} are the random error terms, assumed gaussian and independent from one another and from the block effects

Model 2: linear mixed model with AR(1) × AR(1) spatially correlated errors

$$Y_{jkl} = m + b_j + c_{jk} + D_l + E_{jkl}$$

Where, in addition to model 1:

let r and c be the row and column of the plot where genotype (j,k) was randomly assigned in block l and similarly r' and c' for the genotype (j',k') in block l'.

E_{jkl} are random error terms, assumed gaussian and spatially correlated: $\mathbb{E}\left[E_{jkl}\right] = 0$, $\mathbb{V}\left[E_{jkl}\right] = \sigma_E^2$ and the covariance between two errors is:

$$\mathrm{Cov}\left(E_{jkl}, E_{j'k'l'}\right) = \rho_{row}^{(r'-r)}\rho_{col}^{(c'-c)}$$

where ρ_{row} is the correlation between errors on two neighbouring plots in the same column (thus in adjacent rows)

and ρ_{col} is the correlation between errors on two neighbouring plots in the same row (thus in adjacent columns)

With model 2, correlation between errors in the same column decreases exponentially with distance, as $\rho_{row}^{(r'-r)} = e^{(r'-r)\log(\rho_{row})}$. This is also true for correlation between errors in the same row.

Model 3: linear mixed model with AR(1) × AR(1) errors + independent errors

According to model 3, a first part of the error is spatially independent as in model 1, and a second part follows the gaussian process of model 2 (though with different parameters). The two parts of the error are independent. Thus:

$$Y_{jkl} = m + b_j + c_{jk} + D_l + E_{jkl} + E'_{jkl}$$

with E_{jkl} as in model 1 and E'_{jkl} as in model 2.

Model 4: linear mixed model with 2-D splines and independent errors

$$Y_{jkl} = m + b_j + c_{jk} + D_l + s(r,c) + E_{jkl}$$

where in addition to model 1:

let r and c be the row and column of the plot where genotype (j,k) was randomly assigned in block l. $s(r,c)$ is a 2D spline, i.e. a smooth piecewise polynomial function of r and c, and E_{jkl} is a spatially independent error.

Model choice

For each variable, the best model was selected according to the BIC criterion, and the species means were estimated using the chosen model.

Species means comparison

The genotypes are of two families: leguminous and grass. We tested differences between the two families and within each family (thus 3 F-tests). Some of the variables had to be transformed to stabilize their error variances. Confidence intervals were computed for species means and species differences. For transformed variables, the species' mean confidence intervals were back-transformed to make them more readable. With model 1, when no data is missing, the estimated species means are equal to the ordinary means. Conversely, means adjusted using spatial variations predicted with models 2, 3, or 4 usually differ from ordinary means.

Heatmap

A heatmap was generated with the pheatmap package in R. Data were scaled by column to enable comparison between features of different magnitudes. Hierarchical clustering was performed using the complete linkage method, and samples were grouped into three clusters.

3. Results

3.1. Characterization of the different plant species × cultivar combinations used as preceding crops for sorghum cultivation

Analysis of variance and cultivar means estimations

The estimated means for the traits measured across twenty plant species × cultivar combinations used as preceding crops in sorghum rotation, are presented in Table 3. The plant family effect (legumes versus grasses), averaged across the three experiments, is highly significant on all traits, except preceding crops biomass yield (BIOM_ha). On this biomass yield, plant family effects are significant in each individual experiment (Table S1), but their pattern varies across experiments, as indicated by a highly significant experiment × family interaction (Table 3). On the other traits, the averaged effect of families was significant, and of a different pattern for each experiment except for the number of days to 50 % flowering and the hundred grain weight. On the same other traits, the averaged effect of crop within families is likewise significant and of a different pattern for each experiment except for the total and fixed N per hectare.iven the extensive phenotypic variability observed in the panel of plants, we have chosen to represent them by their mean values across the three experiments for concision. However, detailed results for each individual experiment are provided in Table S1.

Heatmap and cultivar clustering

The different plant species × cultivar combinations are structured into three distinct groups: the non-leguminous group or grasses, the grain legume group, and the biomass legume group (Fig. 3). The biomass legume group includes both forage legumes, whose biomass can potentially be used for animal feed, and green manure legumes, whose biomass is typically returned to the soil to improve fertility. Grasses are distinct from the legume groups because they do not fix nitrogen (low NDFA), contain low levels of nitrogen (N), and, as a consequence, accumulate lower quantities of nitrogen in their biomass (NFIX_ha and NTOT_ha). They also tend to have a higher carbon-to-nitrogen ratio (C:N). The two legume functional groups are primarily distinguished by their biomass yield (BIOM_ha) and the total nitrogen content accumulated in aboveground biomass per hectare (NTOT_ha). Compared to grain legumes, biomass legumes generally exhibit slower early development, as indicated by lower canopy cover at 42 days after sowing (CANOPEO42), but sustain vegetative growth for a longer period, as reflected by higher canopy expansion rates (CANOPEO_SPEED) between 35 and 55 days after sowing. Ultimately, they develop a greater canopy (CANOPY) — with the notable exception of *Centrosema* — and flower later.

One discrepancy concerns the rajada cultivar of velvet bean, which is classified as a grain legume (Fig. 3; Table 3). Although it produces relatively low biomass (2.86 t ha^{-1}) and a comparatively high grain yield (1.02 t ha^{-1}), it is more accurately considered a forage legume, as its grains are not easily consumable due to toxicity issues. In contrast, deeringiana, the other evaluated velvet bean cultivar, flowers later (64

Table 3
Trait means of the 20 different plant species x cultivar combinations and P-values of the variance components, as estimated by the optimal linear mixed models across the three experiments.

		TRAITS														
		CANOPY	CANOPEO42	CANOPEO_SPEED	Flo_50	BIOM_ha	N	NTOT_ha	NDFA	NFIX_ha	GY	HGW	C:N	N_seed	P_seed	K_seed
	unit	cm	%	% per day	days	t ha^{-1}	%	kg ha^{-1}	% total N	kg ha^{-1}	t ha^{-1}	g	-	%	%	%
	estimated means															
Sorghum precedent	peanut	42	47	2.26	33.6	2.53	2.41	60	47.2	25.8	0.59	33.77	15.8	4.67	0.30	0.80
	brachiaria	83	29	2.13	122.0	5.57	1.10	62	0.0	0.0	0.01	0.45	38.6	1.79	0.35	0.34
	jack_bean	90	47	1.66	61.1	2.35	2.28	54	4.7	1.8	0.94	106.22	18.1	4.10	0.32	1.31
	centrosema	45	33	2.54	85.8	5.68	2.55	142	61.2	79.9	0.23	2.20	16.9	5.39	0.39	0.93
	crotalaria_juncea	242	58	1.80	67.3	7.45	2.70	201	48.8	65.9	0.25	4.08	15.4	6.92	0.55	1.54
	crotalaria_retusa	84	21	2.34	95.7	4.37	2.83	122	45.9	47.4	0.02	1.90	14.8	4.63	0.34	1.15
	crotalaria_spectabilis	128	34	2.15	67.2	3.89	2.98	112	61.8	65.9	0.42	1.70	13.6	5.66	0.38	1.31
	finger_millet	80	11	0.72	78.9	1.70	1.61	27	0.0	0.0	0.03	0.26	24.6	1.73	0.31	0.56
	horsegram	43	63	1.51	36.8	1.81	2.61	48	58.0	29.1	0.48	3.32	13.9	4.31	0.31	1.27
	velvet_bean_deeringiana	64	36	1.96	87.7	4.27	2.77	116	60.1	56.2	0.10	58.74	16.2	5.08	0.44	1.25
	velvet_bean_rajada	52	51	2.00	67.0	2.86	3.31	96	59.6	55.1	1.02	54.35	13.2	4.18	0.28	1.10
	mungbean	69	63	1.59	45.8	2.41	2.51	63	67.8	42.4	1.12	3.37	16.1	4.23	0.35	1.37
	cowpea_bengraaga	27	59	2.00	61.9	2.45	3.32	83	50.1	33.7	0.49	13.40	12.3	3.99	0.40	1.33
	cowpea_gourgou	39	69	2.05	55.0	2.76	3.02	82	53.3	30.5	0.34	18.55	13.7	4.48	0.49	1.37
	cowpea_komcalle	32	59	1.07	46.0	2.25	2.90	63	35.5	18.6	0.62	15.82	13.7	4.04	0.38	1.12
	pigeon_pea	168	36	2.20	148.0	5.46	2.53	141	51.4	60.3	0.04	5.50	18.0	4.83	0.55	2.03
	bambara_groundnut	22	29	1.48	38.1	1.66	2.57	41	57.3	21.1	0.68	60.52	13.1	3.42	0.25	1.29
	sesbania	192	52	2.61	54.3	3.41	3.44	114	32.2	29.9	0.87	2.52	12.8	6.12	0.35	0.98
	sorghum	286	34	1.41	71.2	3.42	1.86	63	0.0	0.0	0.80	2.73	22.8	1.68	0.23	0.38
	tephrosia	169	28	2.28	78.1	4.29	2.50	105	55.4	53.3	0.50	1.01	18.0	7.21	0.60	1.54
	Analysis of variance															
	transformation applied	log()	-	-	-	log()	log()	log()	-	log (+10)	log (+0.05)	log()	log()	-	-	-
	model retained	1	1	3	1	2	1	2	1	1	1	1	1	-	-	-
	experiment	4.5E-03	1.1E-02	3.6E-02	2.6E-02	2.3E-03	5.9E-04	4.9E-04	2.3E-01	1.7E-01	8.6E-02	3.8E-05	5.5E-05	-	-	-
	family	**< 1E-16**	**1.1E-16**	**1.0E-02**	**< 1E-16**	*2.6E-01*	**< 1E-16**	**6.7E-16**	**-**	**-**	**< 1E-16**	**< 1E-16**	**< 1E-16**	**-**	**-**	**-**
	family:crop	**< 1E-16**	**< 1E-16**	**1.9E-13**	**< 1E-16**	**< 1E-16**	**< 1E-16**	**< 1E-16**	**< 1E-16**	**< 1E-16**	**< 1E-16**	**< 1E-16**	**< 1E-16**	**-**	**-**	**-**
	experiment:family	1.0E-04	1.7E-03	2.5E-08	*7.1E-02*	8.2E-09	8.8E-06	*2.1E-04*	-	-	7.1E-13	*9.6E-01*	5.5E-06	-	-	-
	experiment:family:crop	2.1E-02	3.9E-09	6.2E-05	2.7E-14	6.6E-04	4.9E-06	4.0E-03	*7.6E-02*	7.0E-02	< 1E-16	1.1E-02	3.4E-05	-	-	-

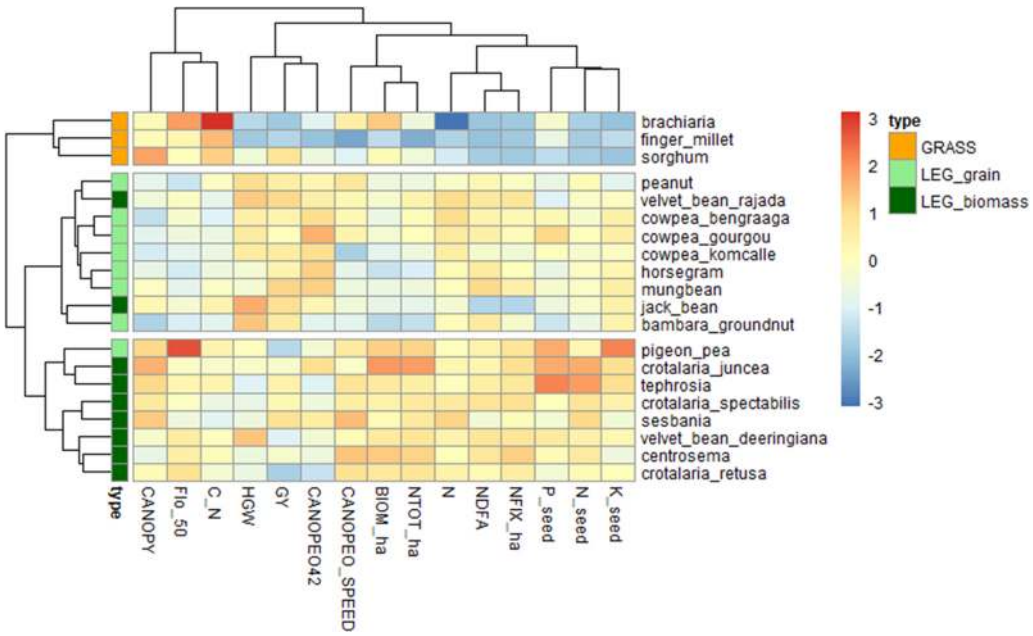


Fig. 3. Heatmap representing agronomic trait values measured across different plant species × ultivar combinations. Rows correspond to plant species × cultivar combinations, while columns represent the measured traits. Trait values were standardized by column and clustered using complete linkage hierarchical clustering. Color intensity reflects relative trait values, with warm colors indicating higher values and cool colors indicating lower values. Row annotations (right) indicate plant types: *NOLEG* (non leguminous; orange), *LEG_grain* (grain legumes; light green), and *LEG_biomass* (gathering forage legumes and green manure legumes; dark green).

days compared to 52 days for Rajada), produces more biomass (4.27 t ha^{-1}), yields fewer grains, and is appropriately classified among the biomass legumes (Fig. 3). A second discrepancy involves jack bean, which is also classified among the grain legumes. Although this species produces very long pods with large seeds (hundred-grain weight, HGW = 106 g), it is primarily used as green manure or for soil fertility improvement, rather than for grain, since the seeds contain toxic compounds that can pose health risks to humans and animals if not properly processed. Under our experimental conditions, jack bean appeared to be very inefficient at fixing nitrogen (NDFA = 4.7 %), and no nodules were observed on its roots. It produced relatively low biomass (2.35 t ha^{-1}) but a high grain yield (0.94 t ha^{-1}). The third discrepancy concerns pigeon pea, which is typically regarded as a grain legume that also provides biomass suitable for animal feed. However, the cultivar used in our study behaved more like a biomass forage legume, producing a large amount of biomass (5.46 t ha^{-1}) but very little grain (0.004 t ha^{-1}), due to its very late flowering (148 days).

The relationship between nitrogen accumulation in biomass (NTOT_ha) and biomass yield (BIOM_ha) was plotted for the 20 evaluated plant species × cultivar combinations (Fig. 4). A very strong correlation was observed between NTOT_ha and BIOM_ha ($R = 0.96$, $p = 5.7 \times 10^{-10}$ for legumes only, $R = 0.85$, $p = 0.36$ for grasses only, and $R = 0.85$,

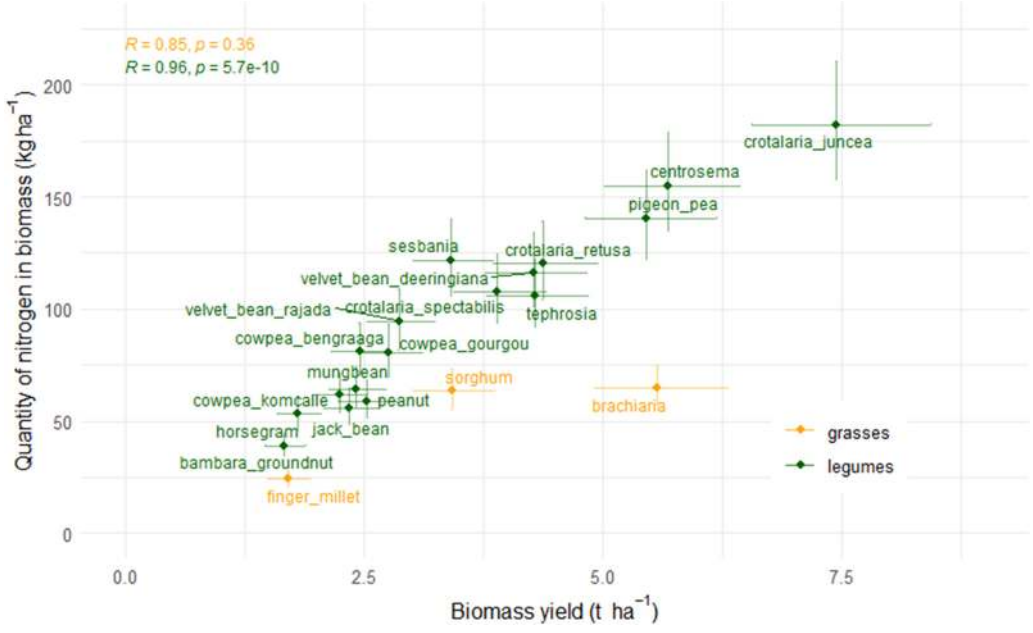


Fig. 4. Relationship between the quantity of nitrogen accumulated in the biomass (NTOT_ha) and the biomass yield (BIOM_ha) of the 20 preceding plant species × cultivar combinations across all three experimentations.

$p = 2.3 \times 10^{-6}$ for all plant together). Non-leguminous species (grasses) were consistently positioned below the general trend defined by legumes, indicating a lower nitrogen accumulation per unit of biomass. The graph also reveals a considerable variability in biomass yield (BIOM_ha) among the twenty plant species × cultivar combinations, ranging from 1.66 t ha^{-1} for bambara groundnut to 7.45 t ha^{-1} for Crotalaria juncea. Similarly, there was a large variability in total nitrogen accumulation in biomass (NTOT_ha), from 27 kg ha^{-1} for finger millet to 201 kg ha^{-1} for Crotalaria juncea. The three best-performing species in terms of both biomass yield and nitrogen accumulation were *Crotalaria juncea*, *Centrosema*, and pigeon pea. *Crotalaria juncea* is a green manure legume, and *Centrosema* is a forage legume. Pigeon pea is typically a grain legume, but the cultivar used in this study behaved more like a forage-type biomass legume, as previously discussed.

3.2. Effect of the different preceding crops on the growth and yield of sorghum cultivated in rotation

3.2.1. Analysis of variance

The analysis of variance is presented separately for each of the three experiments, to highlight the specific response of sorghum to crop precedents across the different experiments and fertility conditions (Table 4). The effect of the family of the preceding crop (legumes vs. grasses) was significant in all three experiments for both sorghum straw yield (SY_so) and grain yield (GY_so). Leguminous precedents consistently led to higher sorghum grain yields than non-leguminous ones (grasses). Under low fertility conditions, sorghum grain yield (GY_so) was 1.19 t ha^{-1} and 0.98 t ha^{-1} following a leguminous crop, compared to 0.95 t ha^{-1} and 0.71 t ha^{-1} after a non-leguminous crop in LF21 and LF22, respectively. In the high fertility experiment (HF21), sorghum grain yield was 2.59 t ha^{-1} after a leguminous crop, versus 2.09 t ha^{-1} - after a non-leguminous crop. Overall, sorghum grain yield under high fertility (HF21) was approximately double that observed under low fertility (LF21 and LF22). A similar pattern was observed for sorghum straw yield (SY_so), which reached 3.16 t ha^{-1} and 3.89 t ha^{-1} following a leguminous crop, compared to 2.29 t ha^{-1} and 2.92 t ha^{-1} after a non-leguminous crop in LF21 and LF22, respectively. In HF21, sorghum straw yield was 6.32 t ha^{-1} after a leguminous crop, versus 4.79 t ha^{-1} after a non-leguminous crop. Significant variation among the 17 tested leguminous species × cultivar combinations was observed only for sorghum straw yield under high fertility conditions (HF21). In contrast, greater variation was seen among the non-legumes (grasses), with significant differences in sorghum grain yield (GY_so) in LF22 and HF21, and in sorghum straw yield (SY_so) in HF21.

3.2.2. Correlation between traits of preceding legumes and sorghum growth and yield in rotation

Only preceding legume crops were considered in this analysis, while non-leguminous species (grasses) were excluded. As described in the previous paragraph, the family of the preceding crop (legumes vs. grasses) had a highly significant effect. Including grass species would have disproportionately influenced the correlation structure, due to their distinct behavior compared to legumes. The study examined various legume traits that could affect sorghum performance through nutrient carry-over from one year to the next, with a particular emphasis on nitrogen-related parameters. The variables analyzed included aboveground biomass yield per hectare (BIOM_ha), total nitrogen accumulated in the biomass per hectare (NTOT_ha), nitrogen exported in the harvested grain per hectare (N_EXP_ha), total nitrogen potentially returned to the system after accounting for grain export (NTOT_delta), atmospheric nitrogen fixed and accumulated in the biomass per hectare (NFIX_ha), as well as phosphorus and potassium exported in the grain (P_EXP_ha and K_EXP_ha, respectively). The nitrogen concentration in the biomass (N) and the carbon-to-nitrogen ratio of the biomass (C:N) were also analyzed.

In the low-fertility experiment LF21, several significant correlations were observed between the traits of the preceding legume crops and the performance of the subsequent sorghum crop. (Table 5). Sorghum grain yield (GY_so) was positively correlated with BIOM_ha ($R = 0.61$, $p = 0.0086$), NTOT_ha ($R = 0.59$, $p = 0.012$), and NTOT_delta ($R = 0.51$, $p = 0.036$). A significant negative correlation was observed with N_EXP_ha ($R = -0.56$, $p = 0.018$). Sorghum straw yield (SY_so) in LF21 also showed significant correlations with preceding legume traits. It was positively correlated with NFIX_ha ($R = 0.51$, $p = 0.037$) and negatively correlated with N_EXP_ha ($R = -0.59$, $p = 0.013$). However, in the second low-fertility experiment (LF22), no significant correlations were detected between the characteristics of the preceding legume crops and either sorghum grain or straw yield. In HF 21, a significant positive correlation was detected between GY_so and N ($R = 0.49$, $p = 0.046$) and a negative one with C:N ($R = -0.49$, $p = 0.044$). Similarly, SY_so was positively correlated with N ($R = 0.55$, $p = 0.021$) and negatively correlated with C:N ($R = -0.58$, $p = 0.014$).

Although statistically significant, the positive correlation between the amount of nitrogen accumulated in the biomass (NTOT_ha) and the subsequent sorghum grain yield in LF21 translated into only a modest agronomic response (Fig. 5): A fivefold increase in NTOT_ha resulted in just a 1.5-fold increase in grain yield. Moreover, this relationship was not observed in LF22 or HF21 (Fig. 5). Consequently, it is not surprising that no significant effect of legume species on subsequent sorghum grain yield was found in any of the experiments (Table 4). Finally, a negative relationship was observed between sorghum grain yield and carbon-to-nitrogen (C:N) ratio of the preceding legume crop under high fertility conditions (Fig. 6). Including grasses in the analysis did not alter the observed negative correlation between the C:N ratio of preceding crops and sorghum grain yield (Fig. 6). As expected, grasses, due to their typically higher C:N ratio, were associated with lower sorghum grain yields. Consequently, a highly significant overall negative correlation between sorghum grain yield and the C:N ratio of the preceding crop was observed in this experiment ($R = -0.76$, $p = 9.4\ 10^{-5}$).

Table 4
P-values of the effects of family (leguminous vs. grasses) and crop within families. on sorghum straw and grain yields in each experimentation.

sorghum trait			grain yield (GY_so)						straw yield (SY_so)					
unit			t ha-1						t ha-1					
trial	LF21		LF22		HF21		LF21		LF22		HF21			
analysis of variance														
transformation applied	LOG(GY_so)		LOG(GY_so)		LOG(GY_so)		LOG(SY_so)		LOG(SY_so)		LOG(SY_so)			
model retained	2		2		1		2		2		2			
family	**0.03092**	*	**0.00031**	***	**0.00000**	***	**0.00119**	**	**0.00023**	***	**0.00000**	***		
within legumes	0.34164		0.50559		0.18490		0.05736		0.08283		**0.00419**	**		
within grasses	0.11218		**0.00200**	***	**0.00202**	***	0.09326		0.05288		**0.01161**	*		
estimated means														
Legumes	**1.19**		**0.98**		**2.59**		**3.16**		**3.89**		**6.32**			
grasses	**0.95**		**0.71**		**2.09**		**2.29**		**2.92**		**4.79**			

Table 5
Analysis of Pearson correlations between sorghum grain yield and straw yield and various characteristics of the preceding legume crop.

trial	LF21		LF22		HF21	
statistic	r pearson	pval pearson	r pearson	pval pearson	r pearson	pval pearson
Sorghum grain yield (GY_so) in year + 1						
BIOM_ha	**0.61**	**0.0086**	-0.19	0.46	-0.29	0.26
NTOT_ha	**0.59**	**0.012**	-0.21	0.42	-0.073	0.78
N_EXP_ha	**-0.56**	**0.018**	0.097	0.71	-0.19	0.47
NTOT_delta	**0.51**	**0.036**	-0.3	0.25	0.13	0.63
NFIX_ha	0.44	0.078	0.0016	1	0.16	0.55
P_EXP_ha	-0.43	0.086	0.021	0.42	-0.071	0.79
K_EXP_ha	-0.46	0.062	0.25	0.33	-0.21	0.41
N	0.11	0.68	-0.067	0.8	**0.49**	**0.046**
C:N	0.061	0.82	-0.15	0.58	**-0.49**	**0.044**
Sorghum straw yield (SY_so) in year + 1						
BIOM_ha	0.36	0.15	-0.079	0.76	-0.27	0.29
NTOT_ha	0.43	0.083	-0.14	0.61	-0.022	0.93
N_EXP_ha	**-0.59**	**0.013**	0.014	0.96	-0.093	0.72
NTOT_delta	0.31	0.22	-0.23	0.37	0.12	0.65
NFIX_ha	**0.51**	**0.037**	0.06	0.82	0.16	0.54
P_EXP_ha	-0.47	0.058	0.079	0.76	-0.071	0.79
K_EXP_ha	-0.48	0.05	0.11	0.68	-0.065	0.81
N	0.22	0.41	-0.15	0.58	**0.55**	**0.021**
C:N	-0.064	0.81	-0.16	0.55	**-0.58**	**0.014**

4. Discussion

The selected panel of legume diversity evaluated in this study exhibited a wide and highly significant variability across all traits. Notably, the panel showed substantial variation in biomass production, which was positively correlated with nitrogen accumulation in plant biomass. A clear phenotypic segregation was observed along this continuum between legume species selected for high biomass production and those cultivated primarily for grain yield intended for human consumption. The latter group includes traditional legume crops of the Sudano-Sahelian zone, such as cowpea (*Vigna unguiculata*), peanut (*Arachis hypogaea*), and Bambara groundnut (*Vigna subterranea*). Nitrogen accumulation in the biomass ranged from 41 to 201 kg N ha^{-1}, while the proportion of nitrogen derived from the atmosphere (NDFA) varied between 4.7 % and 67.8 %. This variability is consistent with that reported in a study of 21 legume species by Becker and Johnson (1998). The average level of atmospheric nitrogen fixation observed in our panel (NDFA = 50 %) is also comparable to the value they measured at their Guiana savanna site (NDFA = 52 %). However, other studies have reported higher average NDFA values. For instance, in a pot experiment involving 12 legume species in the Guinea savanna of Nigeria, Sanginga et al. (1996) reported an average nitrogen fixation rate of about 80 %. Field studies have shown more variable results: Kermah et al. (2018) found contrasting levels of nitrogen fixation among grain legumes (cowpea, soybean, and groundnut), ranging from 73 to 88 % in the northern Guinea savanna to 41–69 % in the southern Guinea savanna. Overall, the amounts of nitrogen fixed by grain legumes in Africa can be substantial but vary significantly among species and locations. These differences are influenced by soil characteristics, native or introduced Rhizobium populations, legume genotypes, and management of the cropping system (Dakora and Keya, 1997). Under our Sudano-Sahelian conditions, two plant species stood out regarding biomass and nitrogen accumulation: *Crotalaria juncea* and *Centrosema pascuorum*. *Crotalaria juncea* is a green manure/cover crop legume that is easy to establish and grows vigorously from the outset, adapting well to local conditions. *Centrosema pascuorum* is a fodder legume that grows slowly during the early stages, but once established, it produces a high quantity of biomass. Both species readily produce large amounts of seeds, enhancing their potential for dissemination and adoption by farmers.

Across the three experiments, almost no significant differences were observed among the tested legume species × cultivar combinations in their effects on subsequent sorghum grain and straw yields. A significant variation among legumes was detected in subsequent straw yield only under high-fertility conditions. However, the difference between legumes and grasses was statistically significant in all experiments, with legumes leading to higher subsequent sorghum yields than grasses Sorghum, Eleusine, or Brachiaria). These findings reveal a surprisingly low impact of legume diversity on overall system performance under our Sudano-Sahelian conditions, characterized by a very long dry season. This is despite the large differences observed in biomass production and total nitrogen accumulation among the studied species. Nevertheless, they confirm the positive rotational effect of legumes revealed in Zhao et al. (2022) global meta-analysis, which showed a particularly strong increase in crop yields following legumes on the African continent. The superiority of legume-cereal rotations over continuous cereal cultivation was also highlighted in a literature review encompassing 44 different studies from Sub-Saharan Africa by Franke et al. (2018) and, more specifically, for sorghum under Sudano-Sahelian conditions by Kouyaté et al. (2000), Bagayoko et al. (2000), Bado et al. (2006), and Ncube et al. (2007). The absence of significant differences between the tested legume species × cultivar combinations in their effects on the subsequent sorghum crop observed in our study is consistent with findings from other studies conducted under similar sub-Sahelian conditions. For example, Sauerborn et al. (2000) also found no significant differences among groundnut, cowpea, and soybean in their effects on the subsequent cereal crop—whether maize or sorghum—in northern Ghana. Similarly, in northern Nigeria, Carsky et al. (1999) reported only minor differences in maize grain yield following the cultivation of contrasted legumes (Mucuna, Lablab, Crotalaria, and cowpea), despite large variations in biomass production and nitrogen accumulation. In Kouyaté et al. (2000), over an eight-year experiment, a slight and similar advantage was observed from incorporating green manure from Lablab or Sesbania compared to cowpea, in terms of yield of the subsequent cereal crop. However, in the case of cowpea, all biomass (grain and fodder) had been removed from the fields. These results do not indicate a yield benefit from including green manure legumes in cereal rotations compared to using grain legumes. The loss of grain production every other year, due to dedicating land solely to green manure cultivation, is not compensated for. This was an apparent reason for the rejection of Crotalaria rotations by farmers involved in a participatory experiment to co-design legume-based agroecological cropping systems in North-Sudanian Burkina Faso, not to mention the risk of biomass being consumed by livestock during the dry season if plots are not adequately fenced (Bagagnan et al., in press). Trade-offs between farmers' food security constraints and soil fertility improvement objectives have to be taken into account.

It is widely emphasized that legumes benefit subsequent crops in

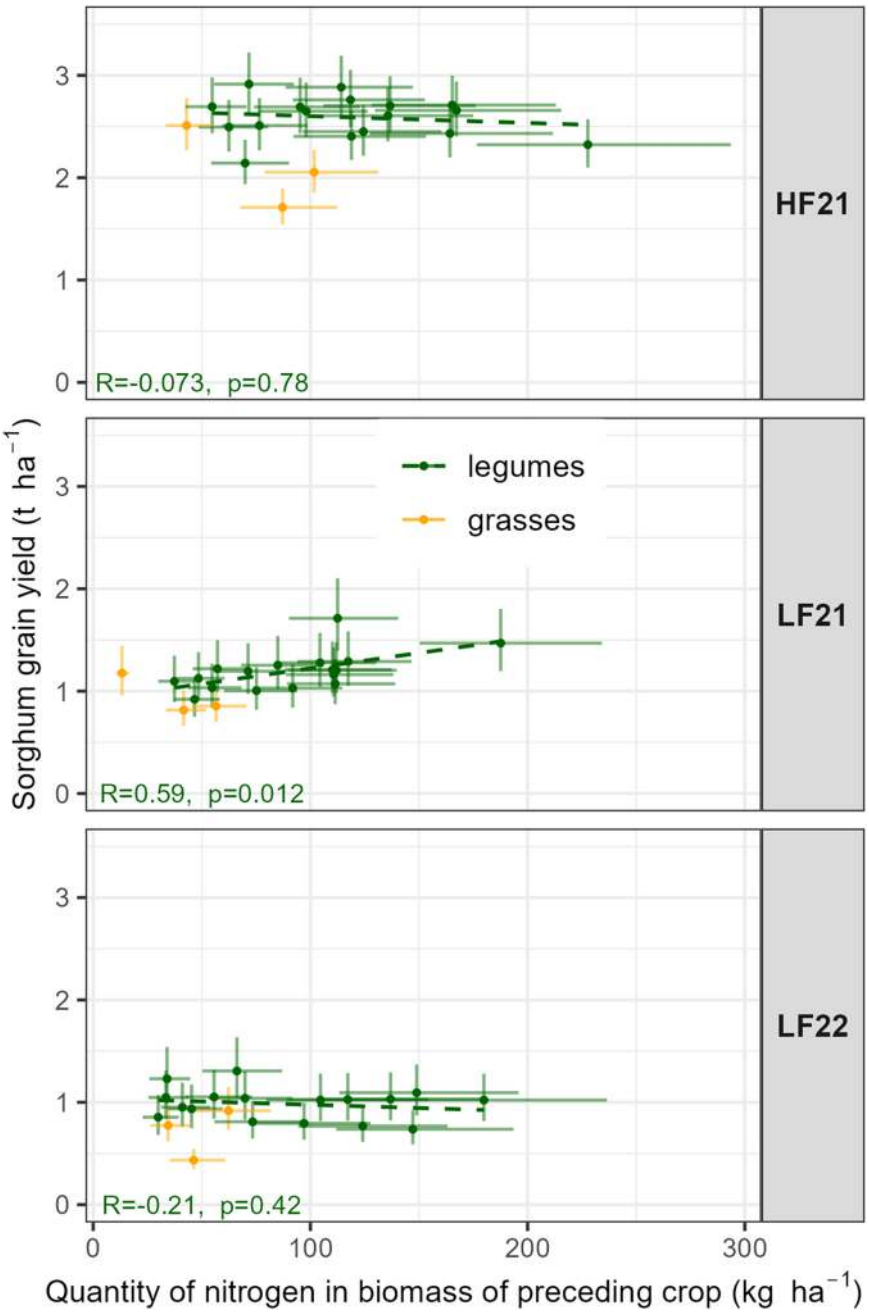


Fig. 5. Relationship between the quantity of nitrogen accumulated in the biomass of the preceding crop (NTOT_ha) and the subsequent grain yield of sorghum (GY_so) for each of the three experimentations.

rotations by fixing atmospheric nitrogen, thereby enhancing nitrogen availability for following non-legume crops and potentially reducing fertilizer requirements (Franke et al., 2018). However, under the Sudano-Sahelian conditions characterized by a prolonged dry season, our findings revealed little relationship between nitrogen in the legume crop and the yield performance of the subsequent sorghum crop. This held regardless of whether we considered total nitrogen, nitrogen potentially returned after accounting for seed export, or the proportion of nitrogen biologically fixed from the atmosphere. These results suggest that most of the nitrogen returned through legume residue is not available for the subsequent sorghum crop. A likely explanation lies in the poor synchrony between nitrogen mineralization and crop nitrogen demand (Chen et al., 2014), compounded by nitrogen losses through various pathways, including volatilisation, and possibly leaching and denitrification triggered by sporadic wet conditions following the long dry season at the start of the next cropping cycle. Under Sudano-Sahelian conditions, rapid turnover of organic matter occurs due to high soil temperatures and intense faunal activity, especially by termites (Bationo et al., 2007), leading to rapid mineralization and a transient accumulation of ammonium in surface soils. This process is especially pronounced for legume residues, which typically have low C: N ratios and are readily degradable. Under these conditions, NH_3 volatilization may be the major nitrogen loss pathway in dryland agro-ecosystems (Liu et al., 2020). For instance, Ncube et al. (2007) observed little correlation among legume species, between the total nitrogen accumulated during the legume phase and the grain yield of the subsequent sorghum crop, once data from continuous sorghum plots were excluded. Likewise, Becker et al. (1998) found no significant relationship between legume N accumulation and rice grain yield in their two contrasted savanna sites considered separately. When data

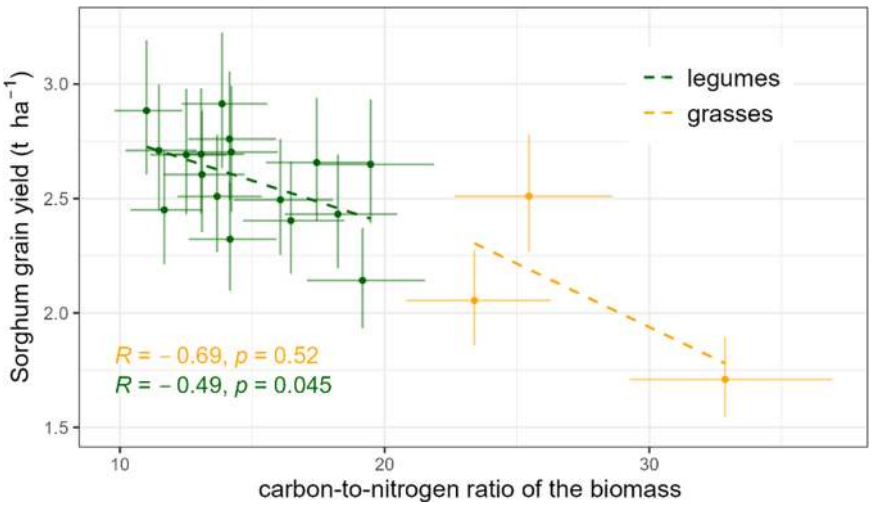


Fig. 6. Relationship between the Carbon-to-nitrogen ratio of the preceding crop (C:N) and the subsequent grain yield of sorghum (GY_so) in the high fertility experiment HF21.

from both sites were combined, an artefactual correlation was revealed. Supporting this, Sauerborn et al. (2000) found that sunflower, cotton, and legume crops performed equally well—and better than cereals—in improving the yield of subsequent maize or sorghum crops in Northern Ghana. They also found that rotating cereals with crops that are neither cereals nor legumes had a more positive impact on yields than rotations involving cereal-legume intercrops. Avoiding species recurrence in successive cropping seasons on the same field—even through intercropping—can help maximize rotational benefits. Biomass quality can also modulate nitrogen availability to the subsequent crop. In our experiment, a negative relationship between the C:N ratio of the preceding crop biomass and the yield of the subsequent sorghum crop was observed, but only under high-fertility conditions. Low-quality biomass with low N concentrations, high C:N ratio, or high lignin:N ratio exhibit slower N mineralisation rates and may contribute to nitrogen immobilization, thereby reducing plant-available nitrogen (Chen et al., 2014). In Sudano-Sahelian conditions, non-N effects play a crucial role in the overall rotational benefits of legumes in cereal-based systems. These effects include biotic factors such as pests, weeds, and diseases. Poor seedling emergence and crop establishment on continuous sorghum plots may also be caused by allelopathy (Kouyate et al., 2000). Non-N effects also include abiotic factors like changes in water or nutrient availability (excluding nitrogen), soil pH, organic matter, and soil structure (Franke et al., 2018). In particular, rotation effects on phosphorus (P) availability may be particularly important, as P is often the most growth-limiting factor. Some legumes mobilize less-labile P through the exudation of low-molecular-weight organic acids and phosphatases, thereby increasing plant-available P (Dai et al., 2025). Beyond these rhizosphere processes, legume-based rotations can enhance P cycling by promoting P-solubilizing microorganisms and increasing phosphatase activity (Chen et al., 2025). In addition, preceding legumes can increase cereal P uptake through higher arbuscular mycorrhizal colonization (Alvey et al., 2001), thereby improving P-use efficiency in subsequent cereal crops. Many of these changes, however, occur slowly and may only become evident over the long term.

In the Sudano-Sahelian regions, crop diversification with grain legumes can help increase yields, lessen market risks, and create new agronomic and economic opportunities for smallholder farmers. Among the grain legumes evaluated in this paper, Mung bean is well-suited to semi-arid conditions and showed promise in these Sudano-Sahelian conditions (Raboin et al., 2023). Among the fodder legumes, *Centrosema pascuorum* emerged as a valuable option for fodder production and crop-livestock integration, combining high biomass yield with high protein content in our experiments. The cultivar Rajada of velvet bean (*Mucuna pruriens*) is rather a fodder legume, but it also produces high grain yields, making it a potentially interesting protein source. However, its widespread adoption would require disseminating farmer-friendly detoxification methods for mucuna seeds (Versteeg et al., 1998) or establishing technological value chains for the valorization of these proteins (Sowdhanya et al., 2024). Among all the legumes evaluated in this paper, *Crotalaria juncea* stood out as particularly well adapted, with the highest biomass and nitrogen accumulation. Although this did not translate into yield improvements in the subsequent sorghum crop, it could still serve as a valuable service crop, provided its biomass is recycled through composting for vegetable production (where higher economic returns may justify labor costs) or returned more efficiently to the system though an accelerated rotation supplemented with irrigation. In addition, *Crotalaria* has been shown to have benefits for nematode management (Wang et al., 2002). Under Sudano-Sahelian conditions, our research has shown that nitrogen recycling from biomass residues between cropping seasons is highly inefficient. As a result, cover crops, service crops, or green manure legumes are unlikely to be adopted by farmers, as they offer limited immediate agronomic benefits and do not produce a marketable yield compared to grain or fodder legumes. Moreover, residues left in the field often requires fencing to protect it from freely grazing animals (Carsky, 1999). In contrast, grain and fodder legumes are particularly valuable because they provide high-protein food for humans and animal feed, while enhancing the overall performance of crop rotations. The supplementary nitrogen fixed from the atmosphere by legumes is more effectively utilized when it is harvested as grain or fodder and partially returned to the field as manure after being processed through livestock (Laub et al., 2023). Crop rotation between cereals and legumes is the most effective farming system for maintaining or improving the long-term productivity and resilience of smallholder farms. In a 25-year-long-term trial in Niger, cereal-legume rotation proved to be even more beneficial than cereal-legume intercropping in this regard (Bado et al., 2022). The same experiment also highlighted the positive effects of applying small doses of fertilizers and returning cereal residues to the field as mulch. Clearly, biological nitrogen fixation alone cannot meet the crop nitrogen requirements, and essential nutrients like phosphorus and potassium must be continually replenished through external inputs. Sustainable intensification in the region requires the appropriate use of mineral fertilizers and organic amendments to restore and maintain soil fertility (Bationo et al., 2007; Falconnier et al., 2023) and optimize crop rotations. Nonetheless, legumes play a key role in smallholder farming systems in sub-Saharan Africa (SSA), contributing significantly to food and nutrition security and supporting household income (Vanlauwe et al., 2019). Diversifying

cropping systems with legumes offers major agronomic, economic, and ecological advantages (Foyer et al., 2016). There is a need to increase and diversify legume use to improve food and nutrition security and reduce overreliance on major cereal crops.

Our results indicate that, in the Sudano-Sahelian context, the agronomic value of legumes in cereal-based systems arises from multiple ecosystem services rather than the maximization of a single function. Although legume species differed widely in biomass production and nitrogen accumulation, their effects on subsequent sorghum yields were remarkably similar, reflecting strong environmental constraints on N recycling during the long dry season. These findings confirm that legume–cereal rotations consistently outperform continuous cereal cropping in smallholder systems, emphasizing the overall benefit of introducing legumes. Under these conditions, short-term nitrogen transfer is unlikely to drive legume contributions, as recycling efficiency is low and nitrogen losses are high. Positive effects appear to rely more on non-nitrogen mechanisms, including crop diversification, improved soil cover and water conservation, enhanced phosphorus cycling, biological regulation, and the avoidance of species recurrence. From a management and policy perspective, these results support regionally differentiated recommendations for legume species. In the Sudano-Sahelian context, grain and fodder legumes emerge as the most robust and adoptable options, whereas green-manure or service legumes have limited potential due to low recycling efficiency, residue losses to grazing, and opportunity costs for farmers. Nitrogen fixed from the atmosphere is more effectively valorized when stored in grains or fodder and recycled through livestock, rather than via direct residue transfer between seasons. Diversifying legume options provides greater flexibility to balance legumes and non-legumes at the farm scale, aligning with farmers' priorities—particularly household food security—while supporting long-term soil fertility. Beyond simple rotations, further research should explore how legumes can be better mobilized under Sahelian conditions by optimizing spatiotemporal diversification, for instance through the combined use of rotation and intercropping to improve productivity and resource-use efficiency (Chi and Dong, 2024; Lv et al., 2025), as well as through the evaluation of legume genetic resources to support this diversification.

CRediT authorship contribution statement

Louis-Marie Raboin: Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Oumarou Diallo:** Writing – review & editing, Investigation. **Eric Gozé:** Writing – review & editing, Supervision, Methodology, Formal analysis. **Benoit Joseph Batieno:** Writing – review & editing, Resources, Methodology. **Guelika Kafando:** Writing – review & editing, Investigation. **Julie Dusserre:** Writing – review & editing, Supervision, Methodology, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) used ChatGPT in order to improve english formulation. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

Funding

This study was financially supported by the McKnight Foundation's Global Collaboration for Resilient Food Systems (CRFS) program as part of the project "Feeding the soil and feeding the cow to feed the people: co-designing agro-sylvo-pastoral systems in Sudano-Sahelian Burkina Faso" (3F2), grant number 21-522.

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.

Acknowledgements

We are grateful to the CIRAD Laboratory of Water, Soil and Plant Analysis (US Analyses, CIRAD, Montpellier, France) for carrying out the plant analyses. The authors extend their gratitude to David Boundaogo for his invaluable assistance in establishing and overseeing the field experiments at the Gampela station.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fcr.2026.110371.

Data availability

Data will be made available on request.

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