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The STICS intercrop model accurately reproduces interspecific interactions and yield in semi-arid West African cereal-legume intercropping systems

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ABSTRACT

Context: Cereal-legume intercropping offers potential for the sustainable intensification of annual cropping systems. Crop models can support the evaluation of agronomic and environmental benefits of intercropping. However, to be effective, they must capture interspecific interactions during the growing season, a challenging task in tropical systems where such models remain largely untested.
Objective: This study assessed the ability of the STICS model to simulate cereal-cowpea intercropping productivity and the final outcomes of interspecific interactions occurring over the cropping season under tropical semi-arid conditions.
Methods: Data from four experimental sites in West Africa, including sorghum, millet, and cowpea grown in sole cropping, were used for parameter calibration. STICS was evaluated using intercropping measurements. To analyse interspecific interactions in intercropping with contrasted sowing patterns, we adapted the partial Land

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Equivalent Ratio (pLER). Specifically, we corrected the pLER of each crop by dividing it by the ratio of the number of plants per m^2 in intercropping to the number of plants per m^2 in sole cropping ($pLER_{cor.dens}$). This adjustment allowed us to evaluate interactions at the plant level. Four situations were identified: i) cereal and legume $pLER_{cor.dens} < 1$, indicating that competition outweighed complementarity, compensation, and cooperation or facilitation effects, i.e., productivity of both crops was reduced in intercropping, ii) cereal $pLER_{cor.dens} > 1$ and legume $pLER_{cor.dens} < 1$, indicating that the cereal suppressed legume growth, iii) cereal $pLER_{cor.dens} < 1$ and legume $pLER_{cor.dens} > 1$, indicating that legume suppressed cereal growth and iv) cereal and legume $pLER_{cor.dens} > 1$, indicating that the productivity of both crops was enhanced by intercropping.

Results: STICS simulated cereal aboveground biomass and grain yield in intercropping with a higher model efficiency (Ef) than 0.48 and cowpea aboveground biomass with Ef = 0.31, but Ef < 0 for cowpea grain yield. The model simulated intercropping yields with low bias and was robust across agro-pedoclimatic conditions, but rRMSE was superior to 30%. In over 70% of irrigation × fertilisation × site combinations, STICS accurately simulated interspecific interactions, thanks to its accurate simulation of potential yields and water and N limitations. High observed soil moisture at the experimental sites limited the evaluation of model performance in simulating competition for water in intercropping.

Conclusion: Despite room for improvement, the STICS intercrop model accurately reproduced cereal-cowpea intercropping yields and interspecific interactions in semi-arid tropical conditions.

1. Introduction

In sub-Saharan Africa (SSA), significant yield gaps persist due to poor soil fertility, limited access to nutrient inputs and high interannual climate variability, particularly in the semi-arid regions (Tittonell and Giller, 2013). Maize water-limited yield gaps can reach 10 t ha^{-1} in the SSA regions (van Ittersum et al., 2016), highlighting the potential to intensify production through higher nutrient supply and to improve food security. However, under rainfed conditions, yield intensification through improved nutrient supply can also increase year-to-year yield variability, as crops become more responsive to interannual climate fluctuations when nutrient limitations are alleviated (Falconnier et al., 2020). Resilient strategies for intensification should account for this trade-off between increasing mean yield and maintaining yield stability under climate variability. By enhancing resource-use efficiency and making use of species complementarity, intercropping offers the prospect to buffer yield variability while improving overall productivity (Raseduzzaman and Jensen, 2017; Namatsheve et al., 2020). Evidence of the benefits for long weather series and contrasting nutrient supply of this widely practiced cropping system in SSA remains limited. Most empirical studies have been based on short-term trials (e.g., Traoré et al., 2022; Senghor et al., 2023) and long-term experiments are scarce in the region (exceptions are Diels et al., 2006 and Bado et al., 2022). Crop models able to simulate bispecific intercrops can complement field experiments by simulating the inter-annual performance of intercropping systems for a broader range of climate and soil conditions and crop management over multiple years. For this, intercrop models must accurately capture the dynamic interspecific interactions, particularly the aboveground interactions for light interception due to contrasting canopies, belowground competition and complementarity for water and nutrient uptake due to contrasts in rooting patterns and legume N_2 fixation.

Several crop models can simulate intercropping, including APSIM-Canopy/APSIM-Strip (Keating and Carberry, 1993; Gou et al., 2017), DayCent (Parton et al., 1998), DSSAT-Mixed/DSSAT-MPI (Jones et al., 2003; Pierre et al., 2023), LandscapeDNDC (Haas et al., 2012), LUCIA (Marohn et al., 2013), MONICA (Nendel et al., 2011), STICS (Brisson et al., 2004), SIMPLACE Lintul5-Intercrop (Demie et al., 2025), and WaNuLCAS (Van Noordwijk and Lusiana, 1998). Adam et al. (n.d.) showed that these models mainly differ by i) their complexity in terms of number of parameters, ii) the sowing patterns they can simulate (mixed within the row, alternate rows and strip intercropping), iii) the type of interspecific competitions they can simulate (light, water, and N), and iv) their capacity of computing detailed processes like N_2 fixation, plasticity effects or hydraulic lift. The STICS model is one of the most complex process-based models representing all the main processes governing light and water, C, and N cycles (Adam et al., n.d.). STICS includes formalisms allowing the simulation of bispecific intercrops by explicitly representing: i) competition for light between the two crops, ii) modified microclimate under the dominant canopy, and iii) competition for water and N root uptake in the soil (Brisson et al., 2004; Vezy et al., 2023).

The STICS model has been mostly calibrated and used for intercropping in temperate conditions (Corre-Hellou et al., 2009; Shili-Touzi et al., 2010; Justes et al., 2021b). Nevertheless, preliminary work on the STICS intercropping version in tropical environments (Traoré et al., 2022, 2023; Ganeme et al., 2024; Kwenda et al., 2025) and recent improvements in the intercropping version (Vezy et al., 2023) offer a unique opportunity to evaluate the level of robustness and accuracy of the model when simulating tropical intercrops.

This study aimed to evaluate the performance of the STICS crop model in simulating cereal-legume intercropping systems under contrasting tropical semi-arid conditions, with a focus on West Africa. The model parameters related to crop growth were calibrated on sole cropping observations and the model performance was evaluated against plant observations in intercropping systems. We hypothesized that the model is i) able to correctly reproduce intercropping yields thanks to accurate simulation of agronomic variables related to soil processes, crop growth, and grain formation, ii) accurate in accounting for the interactions between intercropped cereals and legumes, i.e., competition and complementarity for resource acquisition and iii) useful to understand how water and N stress impacted these interspecific interactions during the crop cycle and their consequences on the final yield.

2. Materials and methods

2.1. Experimental data used for calibration and evaluation of the model

2.1.1. Site description

Calibration data were obtained from three on-station experiments (N'Tarla-Mali, Saria-Burkina Faso, Bambey-Senegal), representative of climate and soil variability in semi-arid tropical warm conditions of West Africa (Table 1). Additional data from an on-farm trial in Sob-Senegal were also used for millet sole cropping calibration. Rainfall distribution is unimodal at all sites, with mean annual rainfall ranging from 511 mm y^{-1} in Sob-Senegal to 977 mm y^{-1} in N'Tarla-Mali (Table 1). The mean annual temperature was similar across sites (28.1–29.3°C). Soils were sandy-silt (N'Tarla-Mali, Saria-Burkina Faso, Bambey-Senegal) to sandy (Sob-Senegal) with soil organic N (SON) ranging from 0.011% to 0.030%. Soil water-holding capacity to maximum rooting depth ranged from 111 mm in Sob-Senegal to 208 mm in Bambey-Senegal (Table 1).

2.1.2. Experimental designs and measurements

Intercrops and the corresponding sole crops were grown over two consecutive growing seasons at each site, under controlled conditions where pests and weeds were managed to suppress their influence on crop performance. At N'Tarla-Mali and Bambey-Senegal, additive intercropping was implemented. Additive intercropping is when the number of plants per square meter increases in intercropping compared to sole cropping. In this intercropping design, the density of the principal crop, in our experiments, the cereal, is sown at its sole crop density (6.25 plants per m^{-2} for sorghum at N'Tarla and 1.2 plants per m^{-2} for millet at Bambey, Table 2), and the secondary crop, in our experiments, the cowpea, is added to the cereal plot. If the secondary crop is sown at its sole crop density, the design is a full additive design (6.25 plants per m^{-2} of cowpea at N'Tarla); if it is sown at a reduced density, it is a partial additive design (4.9 plants per m^{-2} in sole cropping and 0.6 plants per m^{-2} in intercropping at Bambey, Table 2). In contrast, substitutive intercropping was implemented at Saria-Burkina Faso. Substitutive intercropping is when the secondary crop, the cowpea, replaces a share of the number of plants of the principal crop, the cereal, resulting in an equal number of plants per square meter in intercropping as in cereal sole cropping. The spatial arrangement differed between sites. At N'Tarla-Mali, cowpea was planted in alternating rows with sorghum. At Bambey-Senegal, cowpea was planted within the rows of millet. At Saria-Burkina Faso, two sowing patterns were tested: (i) alternating rows of sorghum and cowpea, each planted at 50% of their respective sole crop densities (3.1 plants per m^{-2}), and (ii) within-row intercropping, where cowpea was planted at 17% of the sole crop density (1.0 plants per m^{-2}) and sorghum was planted at 83% of the sole crop density (5.2 plants per m^{-2}, Table 2 and Fig. S1). Hill planting was implemented in both sorghum and cowpea sole cropping and intercropping in N'Tarla, where two seeds of the same crop were sown in the same planting hole. At Saria, hill planting was implemented in the within-row arrangement, where most planting holes contained two sorghum seeds and a third of them contained one cowpea and one sorghum seed. At all sites, cowpea was sown two weeks after the cereal sowing date. In Saria-Burkina Faso, a single mineral N input rate was applied (37 kg N ha^{-1}), while in N'Tarla-Mali, and Bambey-Senegal, two treatments were implemented, with 0 kg N ha^{-1} and a fertilized treatment at the recommended rate in Bambey (68.5 kg N ha^{-1}) and only the second year in N'Tarla (38 kg N ha^{-1}). The first year, a rate of 8 kg N ha^{-1} was applied in N'Tarla. All experiments were rainfed, except in Bambey-Senegal where an irrigated treatment was added. Improved cultivars were sown at all sites, with a comparison to local landraces conducted in Bambey-Senegal and Saria-Burkina Faso. Cultivars differed in cycle duration, sensitivity to photoperiod (sorghum only), growing profile, maximum grain number and weight, and maximum harvest index (Table S1).

In-season soil water was monitored at all sites except Saria-Burkina Faso (Table S2). Plant measurements included phenological stages (emergence, flowering, and maturity), in-season leaf area index (LAI, except in Saria-Burkina Faso), in-season and end-of-season (measured at plant maturity or harvest) plant N content (except in Saria-Burkina Faso), in-season and end-of-season aboveground biomass, number of grains, and grain yield (Table S2). The agronomic variables were averaged over three replicates at the Saria-Burkina Faso and Sob-Senegal trials. In N'Tarla-Mali and Bambey-Senegal, where soil water content was specifically measured in one replicate, all agronomic variables measured on this replicate were used.

More details on the experiments and measurement protocols are provided in Traoré et al. (2022) for Mali, Ganeme et al. (2024) for Burkina Faso, Senghor et al. (2023) for Bambey-Senegal, and Sow et al. (2024) for Sob-Senegal.

2.2. STICS model brief description

2.2.1. Overview of the STICS model

The STICS model (Simulateur mulTIdisciplinaire pour les Cultures Standard) is a daily time-step soil-crop model (Brisson et al., 2003; Beaudoin et al., 2023). This model simulates the effect of climate, soil, and crop management on crop growth, yield formation, and environmental outputs. The soil is represented by a succession of horizontal layers with varying properties, but is assumed to be horizontally homogeneous.

STICS simulates crop development in response to a thermal time scale (degree days) and, if necessary, to photoperiod sensitivity. Crop growth is driven by the radiation interception of the canopy and its conversion into aboveground biomass using radiation use efficiency coefficients specific to the juvenile, vegetative, and reproductive phases. Aboveground biomass accumulated during a specific number of days before grain filling (crop parameter *nbjgrain*) is used to compute the number of grains. A dynamic harvest index that increases linearly with time is used to compute grain yield (Spaeth and Sinclair, 1985; Beaudoin et al., 2023).

The model simulates crop water needs based on potential transpiration and computes actual transpiration based on soil supply (Beaudoin et al., 2023). Water stress is modeled using different stress indices, calculated as ratios of soil water content above the wilting point to specific thresholds that influence physiological processes. N budgets are calculated thanks to the computation of N leaching, organic matter mineralisation, nitrification, ammonia volatilization, plant N uptake, and N_2 fixation. Plant N uptake is computed based on the crop critical dilution curve (Justes et al., 1994; Lemaire and Gastal, 1997). N availability in the soil limits plant uptake. N stresses are computed based on the ratio of actual plant N content to the plant N demand, i.e., the N nutrition index. N stresses impact all processes, with effects depending on the physiological process (Beaudoin et al., 2023). The combined effect of water and N stresses on LAI is calculated as the stress produced by the most limiting factor. In contrast, the combined effect of stresses on

Table 1
Description of pedoclimatic characteristics of each site, including mean annual temperature (T_{MEAN}), mean cumulative annual rainfall (Rainfall), mean cumulative global solar radiation (SRAD), maximal soil rooting depth, clay content, pH, soil organic carbon (SOC) and nitrogen (SON) and plant available water capacity (PAWC).

Site	Latitude (decimals)	Longitude (decimals)	T_{MEAN} (°C)	Rainfall (mm y^{-1})	SRAD (MJ m^{-2} y^{-1})	Soil type	Maximal soil rooting depth (cm)	Clay %	pH	SOC %	SON %	PAWC (mm)
N'Tarla-Mali, Traoré et al. (2022)	12.6	−5.7	29.3	977	7237	Lixisol	145	10.7	5.8	0.13	0.011	186
Saria-Burkina Faso, Ganeme et al. (2024)	12.3	−2.15	28.1	843	7618	Lixisol	120	9.8	4.9	0.30	0.025	177
Bambey- Senegal, Senghor et al. (2023)	14.7	−16.5	28.3	568	7334	Fluvisol	160	6.2	8.2	0.36	0.030	208
Sob-Senegal, Sow et al. (2024)	14.5	−16.45	28.5	511	6741	Arenosol	160	5.0	6.5	0.22	0.018	111

Table 2
Description of treatments tested at the four calibration and evaluation sites in West Africa.

Sites	Experimental years	Crops	N fertilisation (kg ha^{-1})	Local and/or Improved varieties	Number of sowing dates tested	Irrigation (mm)	Sowing density (plants per m^{-2})	Design of intercropping
N'Tarla-Mali, Traoré et al. (2022)	2017–2018	Cowpea	0	Improved	1	0	6.25	
		Sorghum	0, 8 or 38	Local and improved	2	0	6.25	
		Cowpea Intercropping	0	Local and improved	1	0	6.25	Additive[*]
		Sorghum Intercropping	0, 8 or 38	Improved	2	0	6.25	Additive[*]
Saria-Burkina Faso, Ganeme et al. (2024)	2017–2018	Cowpea	37	Local and improved	1	0	6.25	
		Sorghum	37	Local and improved	1	0	6.25	
		Cowpea Intercropping	37	Local and improved	1	0	3.1 in alternating rows and 1.0 in within-row mixture[***]	Substitutive[**]
		Sorghum Intercropping	37	Local and improved	1	0	3.1 in alternating rows and 5.2 in within-row mixture[***]	Substitutive[**]
Bambey-Senegal, Senghor et al. (2023)	2018–2019	Cowpea	0 or 9	Local and improved	2	0	4.9	
		Millet	0 or 68.5	Local and improved	1	0–53	1.2	
		Cowpea Intercropping	0	Local and improved	1	0–53	0.6	Additive[*]
		Millet Intercropping	0 or 68.5	Local and improved	1	0–53	1.2	Additive[*]
Sob-Senegal, Sow et al. (2024)	2018–2021	Millet	0	Improved	1	0	1.2	

[*] Intercropping design where the legume was added to a full-density cereal crop

[**] Intercropping design where both crops had reduced densities compared to sole crops

[***] In Saria-Burkina Faso, two spatial arrangements were tested: alternating rows and within-row sorghum-cowpea intercropping

biomass growth is calculated as the product of stresses (Beaudoin et al., 2023).

2.2.2. Interspecific interactions in the STICS intercrop version

The STICS model was adapted to simulate bispecific row intercropping (see Brisson et al., 2004 and Vezy et al., 2023 for detailed equations description). Aboveground competition for light between crops with vertically divided canopies is computed with a radiative transfer approach. The bispecific canopy is divided into three sub-systems: i) dominant canopy, ii) dominated shaded canopy, and iii) dominated sunlit canopy. The amount of radiation the dominated canopy intercepts depends on the share of radiation transmitted by the dominant canopy. A geometric representation of the canopy is used to calculate this radiative transfer and relies on a series of model parameters (Brisson et al., 2004). This includes, e.g., the canopy shape of each crop (rectangle or triangle, the *form* parameter), the ratio of thickness to width of the crop shape (*rapform* parameter), the extinction coefficient of photosynthetic active radiation through the dominant species (*ktrou* parameter), and the distance between the dominant and the dominated crop (*interrang* parameter). Evapotranspiration simulation is based on the resistive model of Shuttleworth and Wallace (1985), adapted to calculate evapotranspiration in each of the three sub-systems, and requiring the minimum stomatal resistance of each crop's leaves (*rsmin* parameter). The unequal interception of light by the sub-systems leads to differences in aboveground biomass accumulation, height, and leaf growth among species, and therefore different water and N requirements (Brisson et al., 2004).

The competition for water and N is simulated as a function of soil conditions, namely water and N availability and temperature, which affect root length and spatial distribution of both crops (Brisson et al., 2004). This competition results from the water and N uptake by both species in the same soil volume, with daily sequential access starting from the dominant crop. The competitiveness of each crop for resource acquisition is based on root density in each 1 cm soil layer (Vezy et al., 2023).

A novel version of the STICS intercrop was recently published, including novel equations aiming at improving the simulation of bispecific row intercropping (Vezy et al., 2023). This updated version was used in this work.

2.3. Model inputs, calibration, and evaluation

Weather records, measured soil properties (see Table 1 for data source and Appendix 1), and crop management (Table 2) were used as direct inputs to the model. A combination of measured plant growth variables (Table S2), choice of model formalisms for crops simulation (Table S3), and values of crop and cultivar (both improved and local) parameters from the literature (Table S4 and S5) were used to parameterise plant files. Both sole crops and intercrops were simulated using the radiative approach and the water resistive model options, which are suitable for both sole cropping and intercropping systems involving crops with contrasting canopy heights.

The recent works of Wallach et al. (2023); Wallach et al. (2024); Wallach et al. (2025) were used as a basis to define the calibration protocol. Recommendations given by Vezy et al. (2023) for simulating intercrops with the STICS soil-crop model were also followed. Calibration was cultivar-specific (across all the sites where the cultivar was cropped, see Table S1) and focused on sole crop treatments, meaning that no specific parameter was optimised on intercrops. Easy-to-measure parameters were set either based on available observations of cultivar-specific variables (e.g., maximum number of grains) or based on literature references for well-studied parameters (e.g., radiation use efficiency). Other parameters that could not be directly derived from field observations or measurements were either fine-tuned manually or mathematically optimised to minimise ordinary least squares between simulations and observations of plant variables (Tables S4 and S5). We used the R package "CroptimizR" (Buis et al., 2023) that was recommended by Wallach et al. (2023); Wallach et al. (2024); Wallach et al.

(2025) and made a manual trial-and-error correction, when necessary, based on the fit of simulations with observations. This parameter calibration followed three steps.

The first step was the calibration of model parameters under non-limiting conditions at all sites, to ensure that the model correctly simulated potential growth of all crop cultivars (meaning growth driven by solar radiation, temperature, and CO2 concentration, see the description of model parameter value assignment and calibration procedure in Appendix 2). We mathematically optimized crop cycle duration based on observations of plant phenology and LAI dynamics. Then, we fine-tuned parameters defining cultivar potential growth: *dlaimaxbrut*, i.e., the maximum rate of the setting up of LAI, *durvieF,* i.e., the maximal lifespan of an adult leaf; *cgrain,* i.e., the slope of the relationship between grain number and growth rate and *vitircarb,* i.e., the rate of increase of the C harvest index vs time. The experimental dataset did not contain treatments under non-limiting conditions (ensuring the absence of water and N stresses) for all crop cultivars. Indeed, no site except Bambey-Senegal had irrigated treatments and N fertilisation treatments above 40 kg N ha^{-1}. Therefore, we made simulations without activating water and N stress effects in the model and fine-tuned these parameters based on the maximum observed values of LAI, aboveground biomass, number of grains, and grain yield per cultivar in the datasets, as well as cultivar potential yields from the literature (Table S6 and S7).

The second step was the calibration of model parameters to improve simulations of N cycling. The parameter *finert*, i.e., the initial fraction of soil organic N inactive for mineralisation, was set at each site to reach the observed plant N uptake of the unfertilised cereal, used as a proxy for mineral N supplied by soil organic matter mineralisation. Parameter values related to N_2 fixation by cowpea were set according to the literature. Parameters related to N absorption (*Vmax2*, the maximum specific N uptake rate with the high-affinity transport system and *Kmabs2*, the affinity constant of N uptake by roots for the low uptake system) were mathematically optimised to improve the fit between simulated and observed plant N uptake (Tables S4 and S5). Soil water holding capacity was also set based on soil water measured along the season at each site. The elongation rate of cowpea's root apex (*croirac*) was set based on the dataset of Latati et al. (2014) to ensure an accurate representation of water balance dynamics (see Appendix 4).

Finally, the third step was the calibration of crop- or cultivar-specific parameters linked to water and N stress sensitivity (see Appendix 5). These parameters were mathematically optimised against dynamic measurements of LAI and aboveground biomass. Simulation units that did not show strong water stress (soil water content above 65% of plant available water capacity) were used to optimise parameters governing N stress effects. Parameters related to water stress effects were optimised on measurements of LAI and aboveground biomass of fertilised treatments.

Calibration was performed only with sole crop observations, while evaluation was carried out on intercrop simulation units, providing an independent evaluation of the relevance of STICS intercrop to simulate interspecific interactions. Intercropping sowing patterns in the field were adapted in STICS using adjusted row spacing and number of plants per m^2 (Fig. S1).

2.4. Model evaluation for simulating land productivity of intercrops

The Land Equivalent Ratio (LER) is an indicator measuring the land area required with two sole crops to produce the same yield as when these two crops are grown in intercropping (Willey, 1979, see Eq. 1).

$$LER = pLER_C + pLER_L \tag{1}$$

With $pLER_c$ and $pLER_L$ being the partial LER (pLER, see Eq. 2) of the cereal or legume crop respectively, calculated by dividing the yield of a crop in intercropping by its yield in sole cropping.

$$pLER_i = \frac{Yield_{IC,i}}{Yield_{SC,i}} \tag{2}$$

with $\mathrm{Yield}_{SC,i}$ and $\mathrm{Yield}_{IC,i}$ the sole crop yield and intercrop yield of the ith crop in the bispecific mixture.

LER can be interpreted as a measure of the land productivity of intercropping compared to sole cropping. An LER greater than 1 indicates that intercropping is more productive than sole cropping per given land surface in a particular environment, whereas an LER less than 1 indicates the opposite.

As advised by Mead and Willey (1980), we have calculated LERs based on sole cropping and intercropping yields obtained in the same site, same season, with the same irrigation and fertilisation status, when possible. STICS does not directly simulate LER. Thus, we compared the results of LER and pLER calculated with the measured and simulated aboveground biomass and grain yield for the same situations. In what follows, we refer to observed and simulated LER and pLERs.

2.5. Model evaluation for simulating interspecific interactions in intercropping

The 4 C concept proposed by Justes et al. (2021) uses the partial LER (pLER - see Section 2.4) to analyze the outcome of dynamic plant-plant interactions in intercropping, namely competition, complementarity, facilitation (or cooperation), and compensation. The concept was developed with situations related to substitutive intercropping designs, where each species was sown at half its sole crop density (i.e., the number of plants per m^2). The computed pLER is compared to a value of 0.5, corresponding to the relative density in intercropping compared to sole cropping. This is used to assess the performance of one plant in the bispecific mixture compared with one plant in the monospecific canopy. We adapted this indicator for contrasting relative plant densities in intercropping compared to sole cropping (see Eq. 3).

$$\mathrm{pLER}_{\mathrm{cor.dens}} = \frac{\mathrm{Yield}_{\mathrm{IC,i}}}{\mathrm{Yield}_{\mathrm{SC,i}}} \times \frac{\mathrm{d}_{\mathrm{SC,i}}}{\mathrm{d}_{\mathrm{IC,i}}} \tag{3}$$

Where $\mathrm{pLER}_{\mathrm{cor.dens}}$ is the partial Land Equivalent Ratio corrected for density and $\mathrm{d}_{\mathrm{SC,i}}$ and $\mathrm{d}_{\mathrm{IC,i}}$, are the densities for sole crops and intercrops of the ith crop, respectively.

When $\mathrm{pLER}_{\mathrm{cor.dens}}$ is below 1, interspecific competition effects exceed beneficial complementarity, compensation or facilitation effects. When $\mathrm{pLER}_{\mathrm{cor.dens}}$ is above 1, complementarity, compensation, and facilitation effects outweigh interspecific competition. Plotting cereal and legume $\mathrm{pLER}_{\mathrm{cor.dens}}$ help distinguish four situations (Fig. 1). The first situation is when cereal and legume $\mathrm{pLER}_{\mathrm{cor.dens}} < 1$, indicating that competition outweighs complementarity, compensation, and facilitation effects for both crops. The productivity of both crops is reduced in intercropping. The second situation is when cereal $\mathrm{pLER}_{\mathrm{cor.dens}} > 1$ and legume $\mathrm{pLER}_{\mathrm{cor.dens}} < 1$, indicating that the cereal benefits from complementarity, compensation, and facilitation effects but imposes competition effects that outweigh beneficial effects to the legume. The cereal suppresses the legume. The third situation is when cereal $\mathrm{pLER}_{\mathrm{cor.dens}} < 1$ and legume $\mathrm{pLER}_{\mathrm{cor.dens}} > 1$, indicating that the legume suppresses the cereal. Finally, when cereal and legume $\mathrm{pLER}_{\mathrm{cor.dens}} > 1$, it means that the productivity of both crops is enhanced by intercropping.

We calculated cereal and legume $\mathrm{pLER}_{\mathrm{cor.dens}}$ using either measured or simulated aboveground biomass and grain yield for the same cropping situations. This allowed us to assess the model's ability to account for final outcomes of interspecific interactions occurring over the cropping season. In what follows we refer to interspecific interactions and we use the $\mathrm{pLER}_{\mathrm{cor.dens}}$ of a crop as an estimate of the interspecific interactions that this crop experiences in intercropping compared to sole cropping.

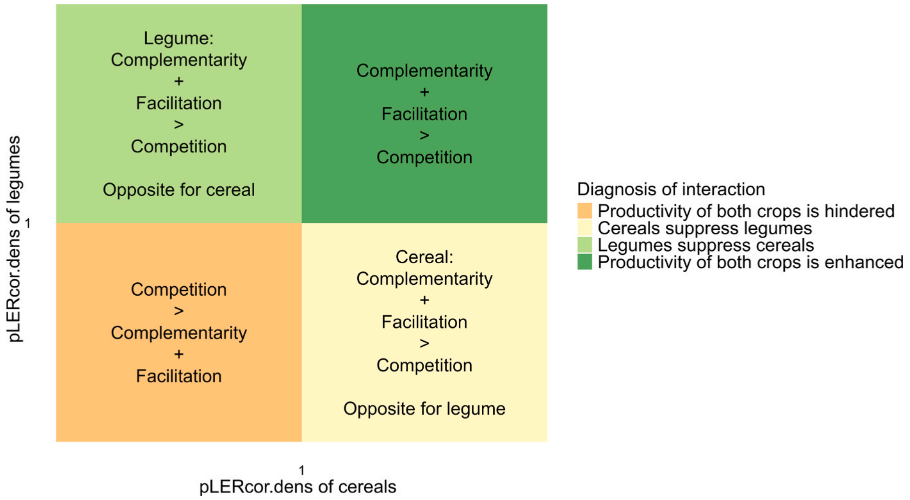

Fig. 1. Two-dimensional representation of partial Land Equivalent Ratio corrected by density ($pLER_{cor.dens}$) of cereal and legume, displaying four possible outcomes in terms of interspecific cereal-legume interactions (adapted from Justes et al., 2021).

2.6. Model performance assessment: accuracy, precision and robustness

Model performance assessment consisted in evaluating model accuracy, precision, and robustness on variables like cycle duration, maximum LAI, total aboveground biomass at maturity, plant N uptake at maturity, number of grains, and grain yield. Two statistical indicators applied to these variables were used to measure model accuracy and precision, namely relative root mean square (rRMSE, %, see Eq. 4) and mean bias error (bias, see Eq. 5).

$$rRMSE = \sqrt{MSE} \times \frac{1}{\bar{O}} \times 100 = \sqrt{\sum_{i}^{n} \frac{(S_i - O_i)^2}{n}} \times \frac{1}{\bar{O}} \times 100 \tag{4}$$

$$bias = \frac{\sum_{i}^{n}(S_i - O_i)}{n} \tag{5}$$

Where S_i is the simulated values, O_i is the observed value of the ith measurement, n is the number of observations, and $\bar{O}$ is the average of the observed values.

Bias is a measure of model accuracy. rRMSE gives the magnitude of the model error and captures both accuracy (measured by bias) and precision (measured by variance of errors), since MSE = Var(S_i-O_i) + bias^2 (Kobayashi and Salam, 2000).

Model efficiency (Ef) was also computed to compare the predictive performance of the model with the mean of observations (see Eq. 6).

$$Ef = 1 - \frac{\sum_{i}^{n}(S_i - O_i)^2}{\sum_{i}^{n}(O_i - \bar{O})^2} \tag{6}$$

Ef ranges from −∞ to 1. When Ef = 1, there is no difference between observations and simulations; when Ef = 0, the model has the same predictive ability as the mean of observations and when Ef < 0, the model is less predictive than the mean of observations.

The rRMSE, bias and Ef were calculated for the calibration dataset (sole crops) and for evaluating the STICS model in intercropping, as an independent assessment.

Robustness is the quality of a model that has homogeneous errors over a wide range of tested conditions (Confalonieri et al., 2010; Coucheney et al., 2015). The robustness of STICS was assessed across the four West African sites on both calibration (sole crops) and evaluation (intercrops) datasets by applying a method developed by Coucheney et al. (2015). We compared the observed variations in agronomic variables due to contrasting agro-pedoclimatic conditions to their simulations. We selected variables describing the pedoclimatic conditions adapted to the semi-arid context. Soil properties were defined by clay content (Clay %), soil organic nitrogen content (SON %), plant available water capacity (PAWC in mm), and mean daily soil water content during the vegetative and reproductive stages (percent of PAWC). Agroclimatic properties of growing seasons (from sowing to harvest) were defined by cumulative global solar radiation (SRAD in MJ.m^{-2}day^{-1}), mean seasonal temperature (T_{MEAN} in °C), cumulative seasonal water supply (rainfall and irrigation, in mm), and N fertiliser rate (N kg ha^{-1}). Observed values for the agro-pedoclimatic indicators were classified in three categories, including either low, moderate or high values relative to the rest of the dataset, see Table S8 for ranges of values. Each class contained the same number of observations. We assessed how precise and accurate was the model in reproducing changes in plant growth variables for different classes of agro-pedoclimatic indicators using bias and rRMSE.

2.7. Understanding model sensitivity to water and N stresses on simulated interspecific interactions

The sole cropping and intercropping situations were simulated by successively activating stress options to understand the relative contribution of water and N stress on model simulations of interspecific interactions (see Section 2.5). Situations were simulated i) without water and N stresses (deactivation of water and N stress in the model), ii) with water stress only (deactivation of N stress and activation of water stress in the model), iii) with N stress only (deactivation of water stress and activation of N stress in the model), and iv) with water and N stress (activation of water and N stress), corresponding to real conditions.

The $\Delta pLER_{cor.dens}$, i.e., the difference between $pLER_{cor.dens}$ simulated with each combination of stresses and $pLER_{cor.dens}$ simulated in non-limiting conditions, was calculated to assess the impact of either water stress, nitrogen stress, or their combined effects on the simulation of interspecific interactions in intercropping. We also computed the difference between $pLER_{cor.dens}$ calculated from observed yields and from simulated yields under non-limiting conditions, hereafter referred to as observed $\Delta pLER_{cor.dens}$, to quantify the deviation of observed interspecific interactions from interspecific interactions simulated with potential growth. Comparing this observed $\Delta pLER_{cor.dens}$ with $\Delta pLER_{cor.dens}$ simulated under water stress, nitrogen stress, or their combined effects enabled us to disentangle the respective contributions of each abiotic stress to this deviation.

3. Results

3.1. Model performance for cereal and cowpea yields in sole cropping across all sites

After calibration of sole crops, the STICS model simulated the aboveground biomass of cereals with an Ef of 0.15 and an rRMSE of 33% (Fig. 2a). Cereal grain yield was simulated with an Ef of 0.29 and an rRMSE of 40%. A slight positive bias was simulated for both variables, but without a large significant deviation, showing correct accuracy of the model according to the large variability observed in the experiments (Fig. 2a, b). Cereal calibration resulted in the simulation of realistic in-season and end-of-season agronomic variables under observed and non-limiting conditions (Tables S6 and S9), with well-captured contrasts between crops and cultivars, which highlighted the relevance of the model in West African conditions.

The model simulated cowpea aboveground biomass and grain yield with Ef of 0.58 and 0.70, respectively, and rRMSE of 38% in both cases (Fig. 3a, b). This calibration led to accurate simulation of most in-season and end-of-season agronomic variables for all crops, except for the number of grains (Table S9), and realistic simulation of aboveground biomass, grain weights, and grain yields under non-limiting conditions (Table S7).

3.2. Model performance for cereal and cowpea yields in intercropping across all sites

STICS simulated cereal growth in intercropping with an Ef value close to 0.50 for both aboveground biomass and grain yield (Fig. 2c, d). The model simulated aboveground biomass in intercropping with an rRMSE of 30%, similar to the one in sole cropping. However, the model accuracy slightly decreased (bias = −0.8) in intercropping, mainly because of the underestimated maximum aboveground biomass observations of sorghum and millet. The simulations of grain yield were very accurate (bias = 0 t ha^{-1}) and the rRMSE was close to the one in sole cropping (rRMSE=37%), but maximum millet grain yields were underestimated.

The model simulated cowpea in intercropping with lower performance for aboveground biomass compared to sole cropping (rRMSE = 76%) but with a positive Ef of 0.31. The model was nearly as efficient at simulating cowpea grain yields as the mean of the observations (Ef close to 0, Fig. 3d). Cowpea yields in intercropping were very small on average across all sites: 1.1 t ha^{-1} of aboveground biomass and 0.21 t ha^{-1} of grain yield in intercropping compared to 4.0 t ha^{-1} and 0.75 t ha^{-1} in sole cropping, respectively. The model correctly captured these low yields with low positive bias. The simulations of the highest cowpea aboveground biomasses and grain yields were also well captured, whereas the lowest yields for each site were overestimated (Fig. 3c, d).

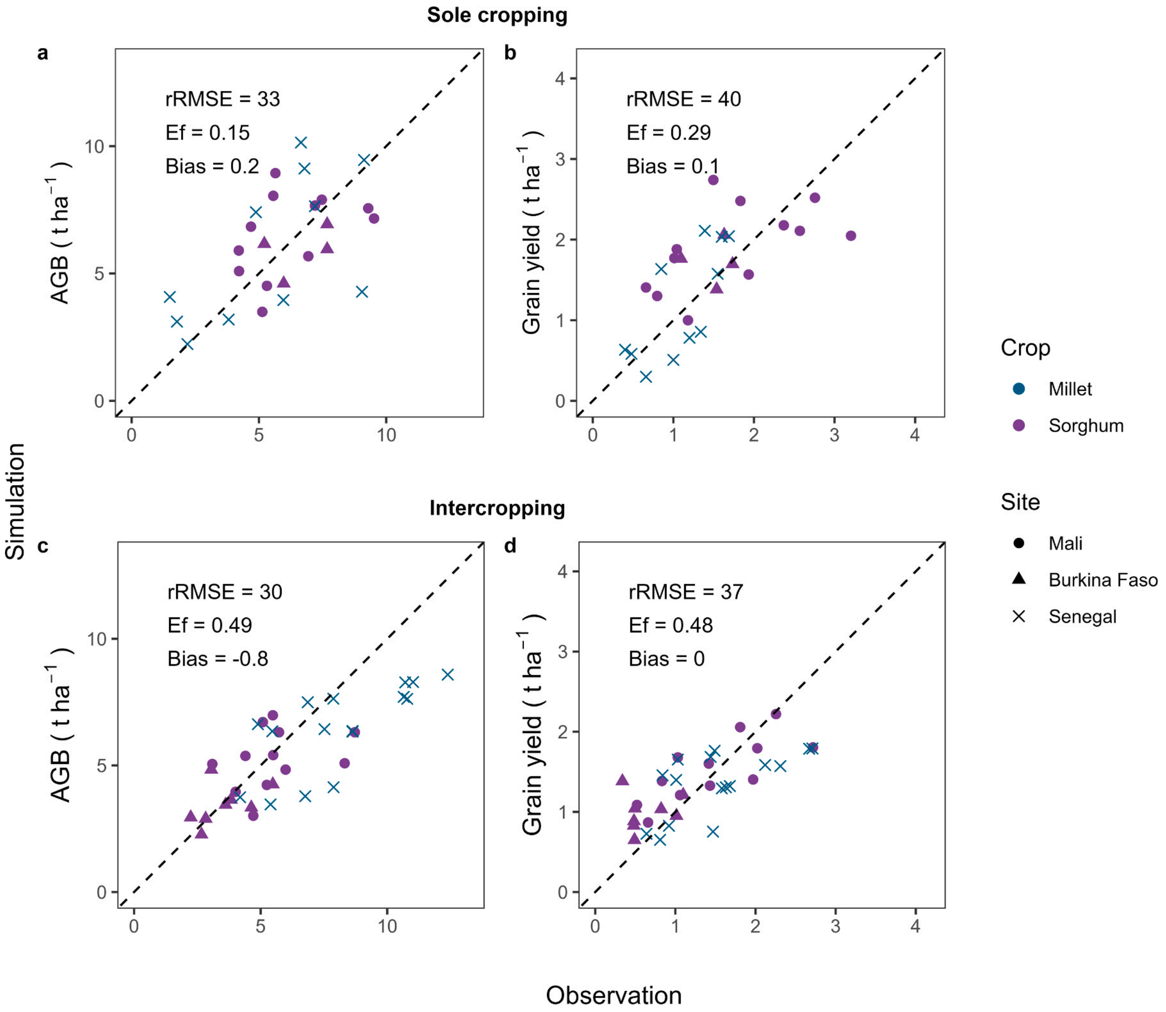

Fig. 2. Comparison of observed and simulated cereal (millet and sorghum) aboveground biomass at maturity (AGB, a, c), and grain yield (b, d) in sole cropping (a, b) and intercropping (c, d) in four West African sites (millet was calibrated in sole cropping in Bambey and Sob and evaluated in intercropping only in Bambey). Sole cropping situations were used as calibration datasets and intercropping situations as evaluation datasets. Statistical description of model performance is displayed: rRMSE in %, bias in t ha^{-1}, and efficiency (Ef) has no unit.

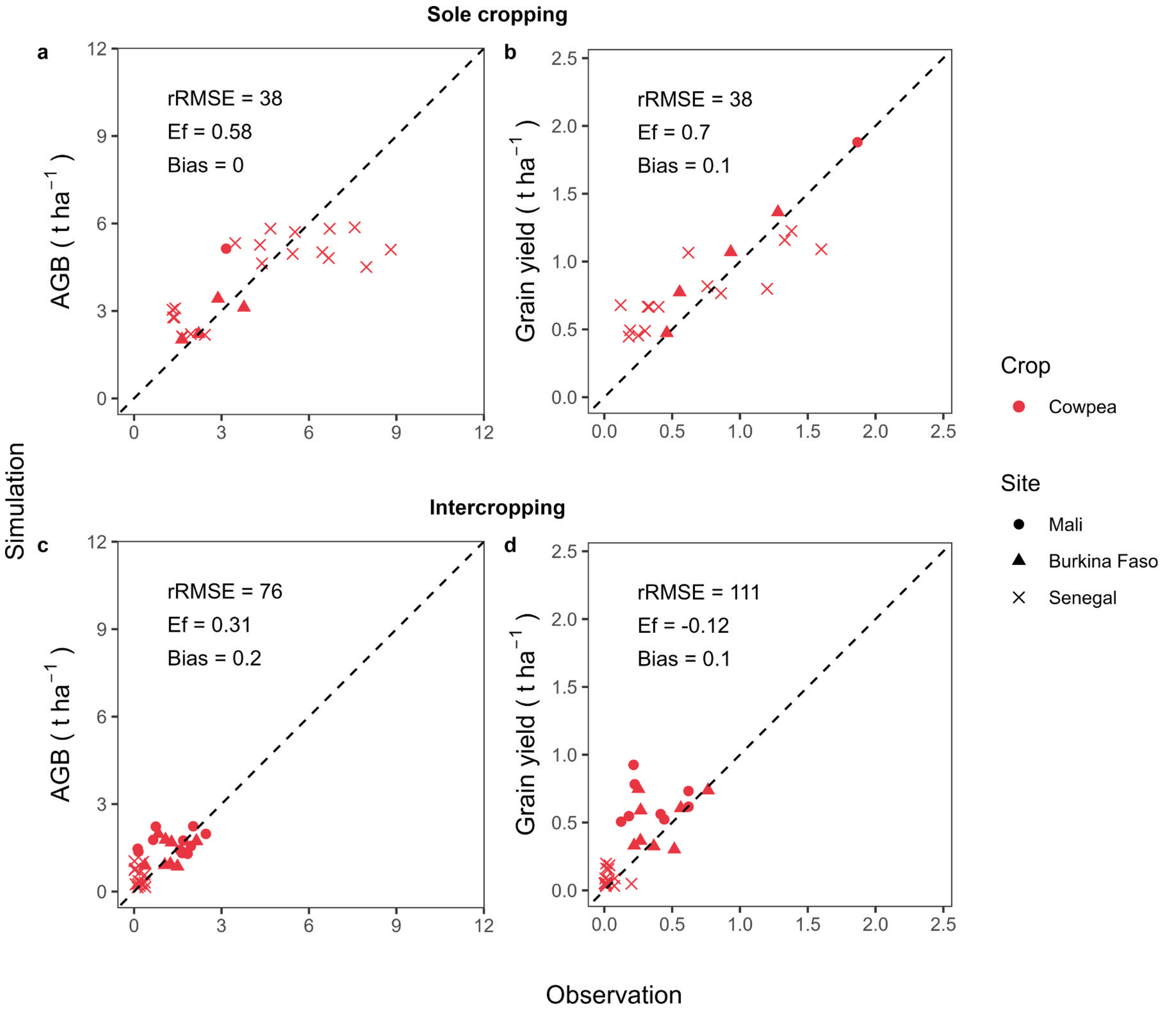

Fig. 3. Comparison of observed and simulated cowpea aboveground biomass at maturity (AGB, a, c), and grain yield (b, d) in sole cropping (a, b) and intercropping (c, d) in three West African sites (the Senegalese site is Bambey). Sole cropping situations were used as calibration datasets and intercropping situations as evaluation datasets. Statistical description of model performance is displayed: rRMSE in %, bias in t ha^{-1}, and efficiency (Ef) has no unit.

3.3. Robustness of sole cropping and intercropping simulations

The STICS intercrop model allowed robust simulation of plant variables (cycle duration, LAI, aboveground biomass at maturity, plant N uptake at maturity, number of grains and grain yield) across a range of soil, climate, and management conditions (Fig. 4). The model was able to reproduce the observed variations in crop growth induced by variations in agro-pedoclimatic conditions with good accuracy (low bias) and low rRMSEs. Bias was zero across plant variables and agro-pedoclimatic indicators and rRMSEs were inferior to 11% for variables like crop cycle duration, aboveground biomass at maturity and grain yield (Fig. 4 and S2). Plant N uptake and number of grains were simulated with slightly increased rRMSEs, never exceeding 19%.

3.4. Land productivity of intercropping compared to sole cropping

Simulated pLER for aboveground biomass and grain yield matched observed pLER, with Ef above 0.6, rRMSE under 50% and no bias, suggesting the relevance of the model to simulate land productivity of each intercrop. Overall, contrasts between crops were well captured as well as the distinction between situations with high or low pLER computed for aboveground biomass as well as grain yield (Fig. 5a, c).

The model did not reproduce the variability in observed LER (Ef < 0) (Fig. 5b, d) but simulated LER had good accuracy (low bias). The model simulated LER with a slight negative bias for aboveground biomass (bias = −0.1 t ha^{-1}) and a slight positive bias for grain yield (bias = 0.1 t ha^{-1}), with rRMSE below 40%.

Majority of the observed LER were greater than 1, which indicates higher overall land productivity in intercropping compared to sole cropping.

3.5. Interspecific interactions simulated in cereal-legume intercropping

The model successfully simulated interspecific interactions (i.e., observations and simulations fall into the same quadrant of the two-dimensional representation of $\mathrm{pLER}_{\mathrm{cor.dens}}$, Fig. 1) in intercropping for 53% of the 34 observed aboveground biomass values, and 56% of the 25 observed grain yield values (Fig. 6 and Fig. S3). Most failures in simulating interspecific interactions (i.e., observations and simulations do not fall into the same quadrant of the two-dimensional representation of $\mathrm{pLER}_{\mathrm{cor.dens}}$) happened in millet-cowpea intercropping in Senegal, especially under rainfed treatments. For sorghum-cowpea intercropping, the model successfully simulated interspecific interactions in 70% and 75% of the situations for aboveground biomass and grain yield, respectively.

3.6. Sensitivity analysis of interspecific interactions simulated in intercrops for water and N stresses situations

The difference between observed $\mathrm{pLER}_{\mathrm{cor.dens}}$ and $\mathrm{pLER}_{\mathrm{cor.dens}}$

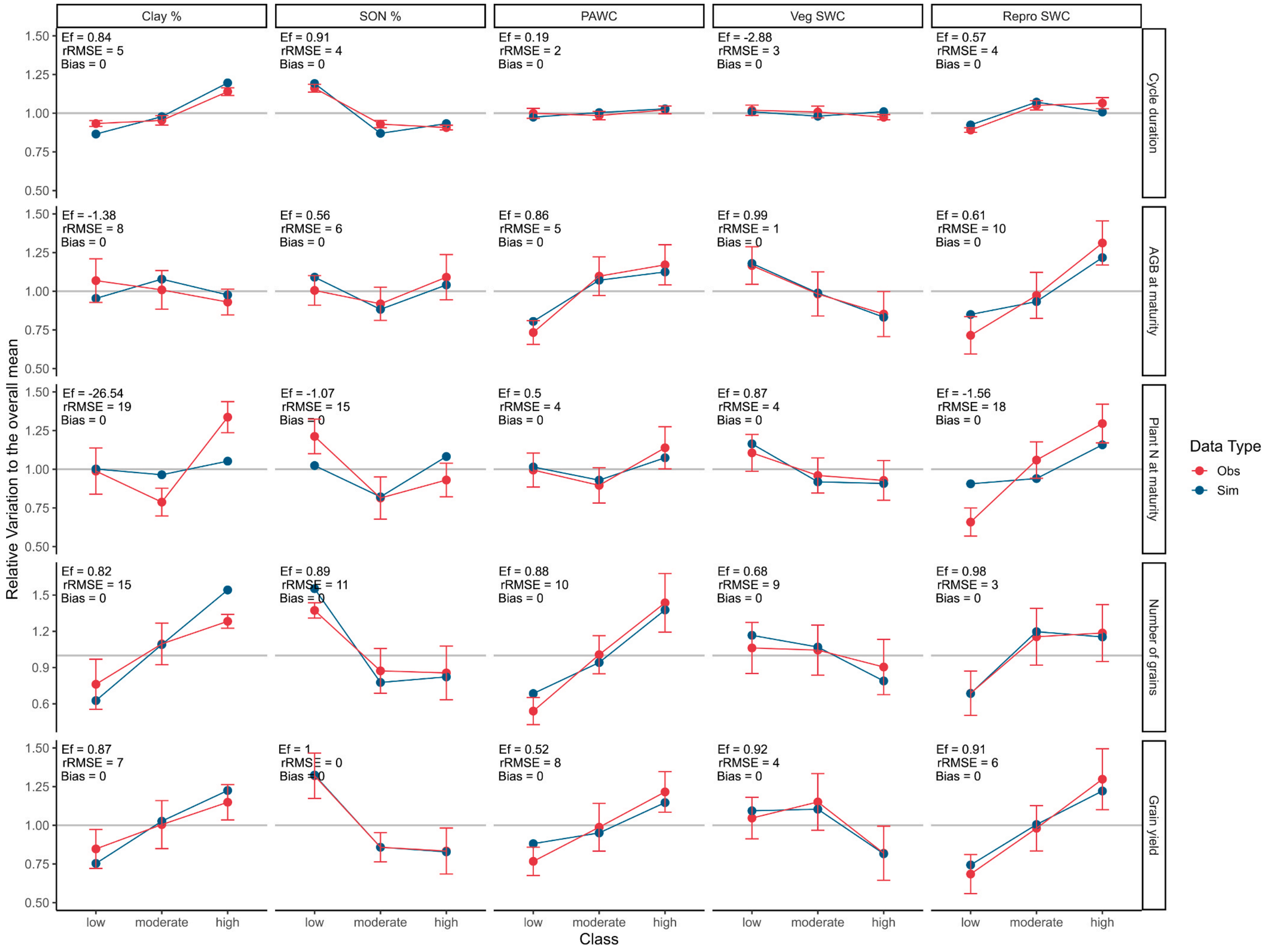

Fig. 4. Reproduction by the model of general observed trends for contrasted pedological conditions over both calibration (sole crops) and evaluation (intercrops) datasets in four West African sites. Relative variations of simulated and observed plant variables between classes of soil indicators, including clay content (Clay %), soil organic N content (SON %), plant available water capacity (PAWC in mm), daily mean soil water content during vegetative (Veg SWC, expressed as percent of PAWC) and reproductive stage (Repro SWC expressed as percent of PAWC). Each point represents the ratio of the mean value of a given class to the mean overall value of the same agronomic variable. Standard error relative to the mean global value of observed agronomic variables are displayed to indicate the uncertainty on the relative mean. Statistical description of model performance is displayed and calculated on the relative mean variations between classes: rRMSE in %, bias in days for cycle duration, t ha^{-1} for aboveground biomass at maturity (AGB) and grain yield, N kg ha^{-1} for Plant N Uptake and number of grains per m^2 for number of grains, and efficiency (Ef) has no unit.

simulated in non-limiting conditions (the distance between the red dashed line and the solid line in Fig. 7 and S4), which quantifies the deviation between observed interspecific interactions and interspecific interactions simulated in non-limiting conditions, was substantial for aboveground biomass and grain yield of cereal and cowpea in the three study sites. Activation of water stress (first boxplot) had a limited impact on the simulation of interspecific interactions, except in Burkina Faso, where it led to increased simulated complementarity effect (Fig. 7 and S4). Water stress simulation helped reduce the difference between simulated and observed $\Delta pLER_{cor.dens}$ of cowpea in Burkina Faso, meaning that the model performance was increased for simulating interspecific interactions affecting cowpea in intercropping compared to sole cropping in Burkina Faso. There was no effect of water stress on interspecific interactions in Mali and Senegal. However, water stress was simulated in both cropping systems according to Fig. S5, meaning that water stress had the same effect on sole cropping and intercropping.

N stress played a greater role compared to water stress in simulating interspecific interactions affecting cereal growth in intercropping (Fig. 7 and S4). Activating N stress helped reduce the distance between simulated and observed $\Delta pLER_{cor.dens}$ of cereal aboveground biomass and grain yield at all sites, increasing the model performance. In Senegal and Mali, N stress clearly increased the $\Delta pLER_{cor.dens}$ of millet and sorghum, meaning that simulated N stress was associated with an increase in simulated complementarity effects compared to competition effects affecting the cereal in intercropping. In Burkina Faso, on the contrary, activating N stress slightly reduced $\Delta pLER_{cor.dens}$ of cereals. The model simulated interspecific interactions in intercropping with a success rate increased by 12% point for aboveground biomass, thanks to activation of N stress (Table S10). The success rate of the model mainly increased in Senegal, by 29 and 11% point for aboveground biomass and grain yield, respectively.

4. Discussion

4.1. Simulation of yields in contrasted intercropping systems

The approach chosen in this paper was to calibrate the STICS intercrop model (Vezy et al., 2023) on sole crop observations and to evaluate the relevance of the model to simulate intercropping. In line with our first hypothesis, the model satisfactorily simulated cereal and legume

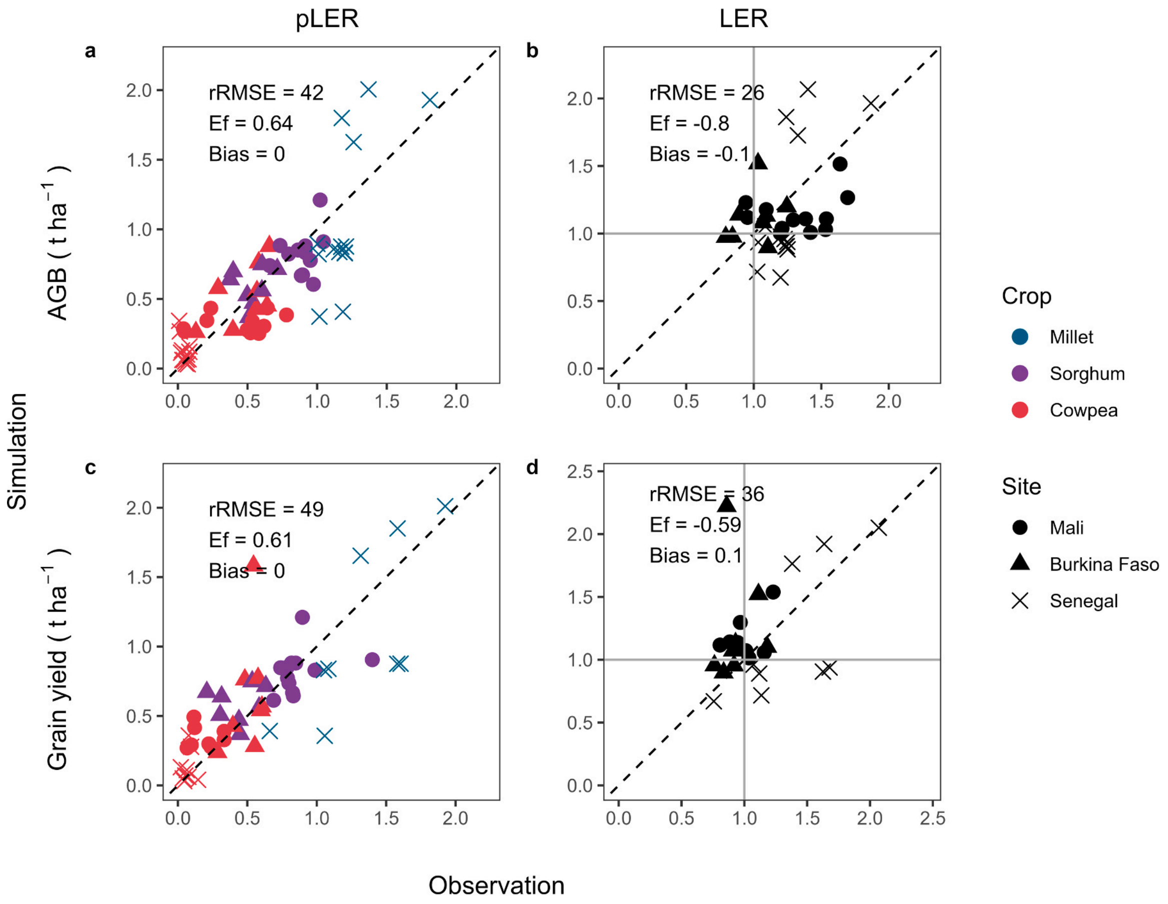

Fig. 5. Comparison of observed and simulated partial Land Equivalent Ratio (pLER: a, c) and LER (b, d) for aboveground biomass at maturity (a, b) and grain yield (c, d) in three West African sites (the Senegalese site in Bambey). Statistical description of model performance is displayed: rRMSE in %, bias and efficiency (Ef) have no unit.

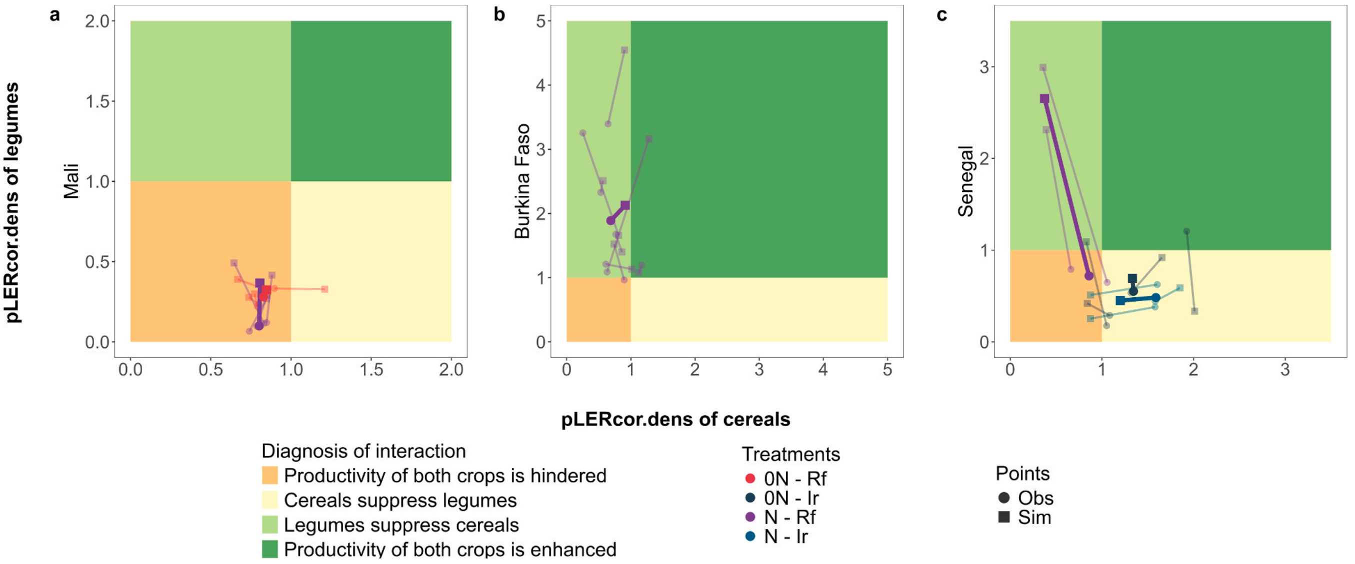

Fig. 6. Observed (round point) and simulated (square point) outcome (linked by a line for same situation) in terms of final interactions calculated on grain yield when intercropping a cereal and a legume in three West African sites (the Senegalese site is Bambey). All situations are displayed, and their average per level of irrigation and fertilisation for each site (across all other factors) is shown with bigger points and no transparency. Treatments: 0 N = not fertilised (or <10 N kg ha^{-1} for sorghum in Mali), N = fertilised, Rf = rainfed, Ir = irrigated.

growth in intercropping systems, after a calibration on sole crops and without any re-calibration of parameters for the intercropping situations. In comparison, Vezy et al. (2023) tested STICS on four cereal-legume and sunflower–soybean intercrops and reported a bias of 0.22 t ha^{-1}, an rRMSE of 18% and an efficiency of 0.87 for grain yield. Compared to this calibration obtained in temperate environments, the

STICS model in our study obtained similar accuracy (bias=0.1 t ha^{-1}), high efficiency (Ef=0.74) but lower precision with an rRMSE of 49% (statistics calculated for all crops in intercropping, results not shown). The lower precision in our study is explained by the high rRMSE of intercropped cowpea simulations, partly due to very low observed yields that are challenging to simulate. In our simulations, the underestimation of some cereal aboveground biomasses might have imposed less competition on cowpea in intercropping. This could indicate that the potential biomass and yield of cereals were still slightly underestimated in the model simulations, likely because their yield potential was derived from literature rather than from direct field measurements. Overall simulations under non-limiting conditions remained very close to yield potentials found in the literature and to the maximum values observed for LAI, aboveground biomass, number of grains and grain yield in our dataset (Table S6 and S7).

Few studies have assessed model performance under tropical or subtropical climates. APSIM simulated intercropping and obtained rRMSEs of 7% for sorghum and 31% for cowpea grain yields in a humid subtropical climate (Chimonyo et al., 2016) and rRMSEs of 37% for millet and 58% for cowpea grain yields in sole cropping and intercropping in a semi-arid tropical climate (Nelson et al., 2022). The present study obtained similar rRMSEs of 38% for cereals and 61% for cowpea in sole cropping and intercropping, with a bias of 0.1 t ha^{-1} in both cases in semi-arid conditions of West Africa (statistics calculated on both cropping systems together, results not shown). With a biogeochemical model system, LandscapeDNDC, Fuchs et al. (2024) simulated maize grain yield in sole cropping and intercropping with an rRMSE of 50% across SSA. They also simulated cowpea grain yield in sole cropping and intercropping with an rRMSE of 65%.

Because MSE = $\text{bias}^2 + \text{Var}(S_i\text{-}O_i)$ (Kobayashi and Salam., 2000), the rRMSE above 30% combined with biases close to zero indicates that most of the error comes from the variance of the errors. This suggests that the simulations are accurate (low systematic error) but not precise (high variability around observations). Most rRMSE values obtained may seem high from a strict model performance evaluation perspective. However, the expected magnitude of yield increase with sustainable intensification will largely exceed our model error (e.g., up to +150% for calorie production and +450% for protein production, Traoré et al., 2023). A hypothesis we might consider is that moderate model accuracy (rRMSEs for yields from 30% to 40%) will probably not compromise the ability of the STICS model to support analyses of intensification pathways and climate adaptation strategies in sub-Saharan Africa.

STICS had accurate (low bias) LER simulations for contrasting intercropping sowing patterns and pedoclimatic conditions in West Africa. These results are very encouraging, given the challenge involved in simulating ratios of yields in sole cropping and intercropping. Most errors in simulating LER occurred in Senegal, where millet aboveground biomass was underestimated in intercropping, leading to overestimations in cowpea yields. Only few studies reporting on model evaluation for land productivity using LER and its decomposition in the pLER of cereal and legume are available to put our results into perspective. We simulated pLER with an rRMSE of 42 and 49% for aboveground biomass and grain yield, respectively. Using the STICS intercrop model, Vezy et al. (2023) obtained an rRMSE of 21% for pLER of 5 different intercropping combinations based on 6 crop species, in temperate conditions. Fuchs et al. (2024) simulated maize–cowpea intercropping systems under tropical conditions with both observed and simulated grain yield LER values consistently greater than 1. However, a slight positive bias was reported in Fuchs et al. (2024), mainly attributable to an overestimation of the cowpea pLER, similarly to our study. However, in our case, this mainly occurred when cereal pLER was underestimated, whereas in Fuchs et al. (2024), maize pLER was well captured, suggesting a less accurate representation of light competition in their study. In addition, their dataset lacked observations covering contrasted LER values. In comparison, our study included observed LER values both greater and lower than 1. While extreme contrasts were not always precisely reproduced, simulated LER values generally captured the observed trends, with a low overall bias of approximately 0.1. Additionally, the study of Fuchs et al. (2024) focused on maize, a crop that was more intensively calibrated and tested compared to sorghum and millet. The STICS model does not explicitly simulate facilitation processes when one species modifies the environment of another species, enhancing its growth. Yet, STICS accurately simulated millet pLER values greater than 1 for the driest of the experimental years in Senegal. This result is not attributable to facilitation processes but to higher organic matter mineralisation in the intercropped plots, due to differences in nitrogen organic content and clay content of the soils in the field experiment. The observed pLER superior to 1 was not simulated the second year of the experiment, probably due to much wetter conditions (see Section 4.3).

4.2. Ability of the model to simulate interspecific interactions in cereal-legume intercropping

To the best of our knowledge, this study is among the first to systematically compare simulated and observed interspecific interactions in intercropping using a framework focused on the effect of water and N limitations. Our approach is in line with the 4 C approach proposed by Justes et al. (2021) to distinguish between competition-dominated or complementarity and facilitation-dominated intercropping systems, adapted to non-substitutive spatial patterns. When analysing results as averages per irrigation and fertilisation treatments per site (across all other factors, see Fig. 6), the STICS model successfully captured key interspecific interactions in intercropping systems. However, model performance differed between cereal species, with poorer results for millet–cowpea intercrops than for sorghum–cowpea systems. In the case of millet, the model underestimated intercropped millet aboveground biomass, which led to an overestimation of cowpea yields, likely due to an insufficient simulated reduction in cowpea light interception. The very low cowpea number of plants per m^2 in intercropping compared with sole cropping (relative density = 0.12) further amplified simulation errors in Senegal. This highlights the strong sensitivity of the $\text{pLER}_{\text{cor.dens}}$ approach to relative density. By contrast, when each situation was analysed individually, model performance differed between crops, and interspecific interactions were better simulated for cowpea than for cereals. This discrepancy may be related to differences in the dynamic dominant competitive processes affecting legumes and cereals in intercropping systems. Cowpea is generally the dominated species, and its growth is primarily constrained by competition for light, whereas cereals may be more strongly affected by belowground competition for water and nitrogen.

Another way of assessing interactions between intercrops was developed by Demie et al. (2025) for spring wheat-fababean intercropping. They computed the Absolute Mixture Effect (AME), i.e., the difference between the yield in intercropping and the yield in sole cropping multiplied by the relative density in intercropping to sole cropping, for each crop. They simulated this indicator using SIMPLACE model with an R^2 of 0.59 and 0.42 for aboveground biomass and grain yield. We obtained similar R^2 of 0.43 and 0.56 for the same variables (results not shown). Both indicators are sensitive to the relative density of each crop in the intercropping, which amplifies yield simulation errors when the density of a crop in intercropping is very low compared with its density in sole cropping. However, we hypothesize that it is conceptually more robust to use $\text{pLER}_{\text{cor.dens}}$ to understand interspecific interactions since it distinguishes four situations adapted from the 4 C approach (Fig. 1).

We found that light distribution in the bispecific canopy influenced a large proportion of the interactions between intercrops. Indeed, after deactivation of water and N stresses, the simulations of bispecific interactions were still correct in 41% of the situations for aboveground biomass and 56% for grain yield observed in field conditions. Activating N stress in the simulation reduced deviations between simulated and observed interspecific interactions for cereals across all sites. While N stress was expected to restrict the growth of intercropped cereal and consequently diminish the negative effect by shading on cowpea, our results of simulations showed that cowpea yield was not significantly influenced by the N stress imposed on cereals. Finally, water stress had the least impact on the simulation of interspecific interactions, not because STICS did not simulate water stress, but because it simulated a similar response to water stress in intercropping and sole cropping (Fig. S5). Such response suggests that no competition or complementarity processes regarding water were simulated between intercrops, except for sorghum-cowpea intercropping in the driest year of the experiment in Burkina Faso (Fig. 7). Indeed, water stress activation shifted cowpea from a situation where the competition with the cereal was higher than the complementarity effects towards a situation where there was almost as much competition effects as complementarity and compensation effects (Fig. 7 and S4). This effect was probably caused by lower light competition from the cereal simulated in drier conditions, favouring cowpea's growth, which could be seen as a form of compensation for the decrease in sorghum biomass.

While these results are encouraging and highlight the model's capacity to capture key interspecific interactions, some limitations should be acknowledged. Activation of water and N stresses was not sufficient to eliminate the discrepancies between simulated and observed interspecific interactions in some cases. This suggests that either the contrasting impacts of water and N stresses on sole cropping versus intercropping were not fully captured, or that other non-simulated limiting factors may play a role. A bias could partly be caused by biotic limiting factors such as pest and diseases as well as macro and micronutrient limitations (e.g., S, Ca, Mg) that are difficult to fully suppress even in field experiments and could have contrasting effects on the two cropping systems, as suggested by field experiments in the Sudano-Sahelian region (Farsia Djidjonri et al., 2021; Chimonyo et al., 2023; Mbengue et al., 2024). Another important issue lies in how the model calculates crop N demand with intercropping, highlighted by large deviations between simulated and observed effects of N stress on interspecific interactions affecting cowpea in Senegal. In the latest version of the STICS model, the calculation of N demand of each crop in intercropping was improved compared to the previous version to avoid overestimating N stresses. But this calculation is not suited for crops with very contrasting aboveground biomasses (Vezy et al., 2023). N demand of each species is calculated using each species-specific N dilution curve, not based on individual aboveground biomass but on the total intercropping aboveground biomass. This approach underestimates crop N requirements and therefore N stresses, especially if intercrops have very contrasting aboveground biomasses.

Overall, the STICS intercrop model offers a robust and accurate tool to expand the insights gained from place-based, single-season experiments on intercropping, even if there is room for improvement for specific situations, such as a very high discrepancies between cereal and cowpea number of plants per m^2.

4.3. Robustness of intercropping simulations

The STICS model demonstrated robust performance across a wide range of soil, climate, and management conditions to simulate various plant variables like cycle duration, LAI, aboveground biomass at maturity, plant N uptake at maturity, number of grains, and grain yield. High model efficiencies were obtained for most variables across variations in agro-pedoclimatic variables and management practices. In addition, our dataset included a wide range of intercropping spatial arrangements, encompassing variations in sowing patterns (cereal and cowpea in

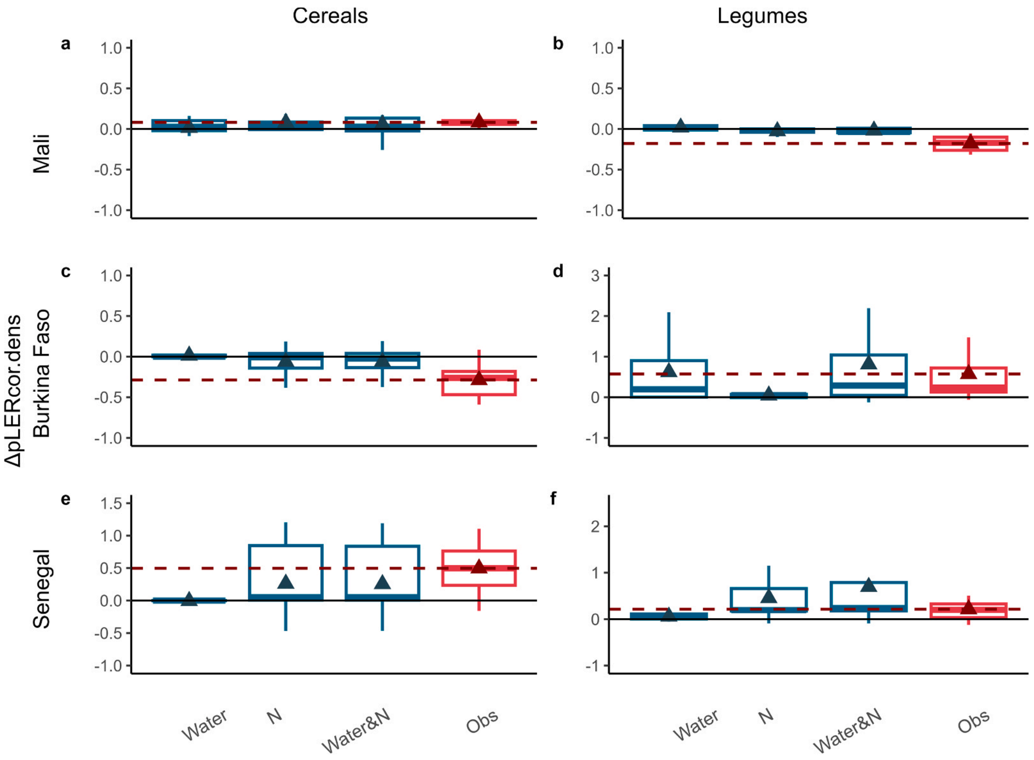

Fig. 7. Impact of model activation of water stress, N stress or combined water and N stresses (Water&N) on the simulation of cereal-legume interspecific interactions (pLER$_{cor.dens}$) in three West African sites (in blue) compared to the difference between observed interspecific interactions and interspecific interactions simulated in non-limiting conditions (red). The graphs show the ΔpLER$_{cor.dens}$ of cereal (a, c, e) and legume (b, d, f) grain yield, i.e., the difference between pLER$_{cor.dens}$ simulated with activation of stresses simulation and pLER$_{cor.dens}$ simulated without activation of stresses simulation (in non-limiting conditions). Triangle dots represent averages. The solid line ΔpLER$_{cor.dens}$ = 0 shows the value of ΔpLER$_{cor.dens}$ when stresses have no impact on simulation (pLER$_{cor.dens}$ with stresses = pLER$_{cor.dens}$ in non-limiting conditions). The red dashed line shows the average observed ΔpLER$_{cor.dens}$ (pLER$_{cor.dens}$ observed - pLER$_{cor.dens}$ simulated in non-limiting conditions) that quantifies the deviation between observed yields and simulated potential yields.

alternate rows or mixed within the row), row spacing and number of plants per m^2 (Table 2 and Fig. S1). The model accurately simulated crop performance across these contrasting spatial arrangements, including the hill planting, where one out of three planting holes contained one sorghum seed and one cowpea seed, while the remaining holes contained two sorghum seeds, used in Burkina Faso. This spatial arrangement is not explicitly supported by the model structure. This result highlights the flexibility of the light interception formalisms of STICS intercrop (see Section 2.2.2) for bispecific canopy representation (Brisson et al., 2004; Vezy et al., 2023), which is suitable for a variety of intercrop architectures, from alternate rows to within-row mixtures and for cereal and legume intercrops with contrasting heights. However, a more thorough evaluation of the model's accuracy would benefit from observations in more contrasting years, since the current calibration and evaluation dataset lacked situations with strong water stress contrasts, especially for cereals (Fig. S5), which may limit its assessment regarding model performance under extreme conditions.

Some limitations were also identified, notably plant N content at maturity was simulated by STICS with lower model efficiency (Ef) compared to other plant variables (cycle duration, number of grains, and grain yield) across several conditions (Fig. 4 and S2). It was also the case for aboveground biomass at maturity, which appeared sensitive to climatic and management conditions (Fig. S2). These deficiencies are likely due to soil data quality constraints, as soil characterisation was based on a single year of measurement and residual mineral N (which is a mandatory input to the model describing the initial status of the soil) was not measured at the start of the season. In our low-input systems, simulations are highly sensitive to small differences in soil mineral N. In addition, phenological dates, which can be difficult to measure for indeterminate crops such as cowpea, and a lack of N_2 fixation data, could have caused deviation in the model accuracy. However, there may also be potential shortcomings of the model itself. As shown in Fig. 4, STICS tended to overestimate plant N in low mineral N input conditions. This can be explained by the fact that the soil organic matter mineralisation function in STICS (Clivot et al., 2019; Beaudoin et al., 2023), developed for temperate conditions, has not yet been properly validated under tropical environments. One key parameter (the initial fraction of organic soil N inactive for mineralisation) had to be calibrated site-by-site to improve model reliability in accounting for available soil mineral N derived from mineralization of soil organic matter, but the need for local calibration calls for improvements in order to use the model across broader spatial scales. Equations for soil organic matter mineralisation (as a function of temperature, mineralogy, pH, soil water content for example) remain largely unevaluated in tropical conditions, and research is needed to develop models aligned with measurable pools (Campbell and Paustian, 2015; Couëdel et al., 2024). This limitation is illustrated by simulation outputs in Senegal: the model successfully simulated increases in soil organic matter mineralisation in plots with greater soil organic nitrogen during dry years (results not shown). In wetter years, the model underestimated soil organic matter mineralisation. Greater engagement from the modelling community is required to overcome these limitations, which are common to many models and not specific to intercropping simulations.

5. Conclusion

Cereal-legume intercropping is a promising sustainable intensification strategy in West Africa, in particular for situations where it increases land productivity thanks to crop complementarities and compensation of crop failure by one of the two crops in case of drastic climatic conditions. The evaluation of the STICS model on sorghum, millet, and cowpea in sole cropping, as well as cereal-cowpea intercropping showed that the model accurately simulated aboveground biomass and grain yield in semi-arid tropical climates of West Africa. Its performance was comparable to that of other intercropping models, while covering a wider range of conditions and spatial arrangements. The partial Land Equivalent Ratio of each crop (pLER) was simulated with good efficiency ($Ef > 0.6$) and accuracy (low bias). Despite a lack of precision in the simulation of pLER ($rRMSE > 40\%$), the STICS model was able to accurately simulate the interspecific interactions (i.e., competition and complementarity effects): when averaged by irrigation and fertilisation treatment per site, they were simulated with a success rate over 70%. The correct simulation of competition for light, mainly allowed by accurate simulation of development, potential growth, and N stresses, was decisive in accurately simulating sole cropping and intercropping performance.

This study demonstrates the ability of the STICS intercrop model to accurately and robustly simulate cereal-legume intercropping with a wide range of sowing patterns in low-input systems. These results offer prospects for the evaluation of intercropping as a promising sustainable intensification strategy in West Africa. These findings support the use of the STICS model to assess the impact of climate scenarios on intercropping performance and to optimize intercrop management in tropical agroecosystems through virtual experimentation.

CRediT authorship contribution statement

Traore Amadou: Writing – review & editing, Data curation. **Christina Mathias:** Writing – review & editing, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Falconnier Gatien N:** Writing – review & editing, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Affholder François:** Writing – review & editing, Data curation. **Balde Alpha Bocar:** Writing – review & editing, Data curation. **Sow Sidy:** Writing – review & editing, Data curation. **Senghor Yolande:** Writing – review & editing, Data curation. **Couëdel Antoine:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Justes Eric:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Mathilde De Freitas:** Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Adam Myriam:** Writing – review & editing, Data curation. **Ganeme Aminata:** Writing – review & editing, Data curation.

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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.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fcr.2026.110468.

Data availability

Data are available in the CIRAD dataverse at https://doi.org/10.18167/DVN1/MMJPKW

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