



Modeling soil-plant functioning of intercrops using comprehensive and generic formalisms implemented in the STICS model

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Abstract

The growing demand for sustainable agriculture is raising interest in intercropping for its multiple potential benefits to avoid or limit the use of chemical inputs or increase the production per surface unit. Predicting the existence and magnitude of those benefits remains a challenge given the numerous interactions between interspecific plant-plant relationships, their environment, and the agricultural practices. Soil-crop models are critical in understanding these interactions in dynamics during the whole growing season, but few models are capable of accurately simulating intercropping systems. In this study, we propose a set of simple and generic formalisms (i.e. the structure and mathematical representation necessary for designing a model) for simulating key interactions in bi-specific intercropping systems that can be readily included into existing dynamic crop models. This requires simulating important processes such as development, light interception, plant growth, N and water balance, and yield formation in response to management practices, soil conditions, and climate. These formalisms were integrated into the STICS soil-crop model and evaluated using observed data of intercropping systems of cereal and legumes mixtures, including Faba bean-Wheat, Pea-Barley, Soybean-Sunflower, and Wheat-Pea mixtures. We demonstrate that the proposed formalisms provide a comprehensive simulation of soil-plant interactions in various types of bispecific intercrops. The model was found consistent and generic under a range of spring and winter intercrops (nRMSE = 25% for maximum leaf area index, 23% for shoot biomass at harvest, and 18% for grain yield). This is the first time a complete set of formalisms has been developed and published for simulating bi-specific intercropping systems and integrated into a soil-crop model. With its emphasis on being generic, sufficiently accurate, simple, and easy to parameterize, STICS is well-suited to help researchers designing *in silico* the agroecological transition by virtually pre-screening sustainable, manageable intercrop systems adapted to local conditions.

Keywords Species mixture · Spatial design · Wheat · Pea · Faba bean · Sunflower · Barley · Soybean

1 Introduction

Modern agriculture needs to develop transition pathways towards productive, sustainable, resilient, agro-ecological cropping systems. Cropping system diversification using intercropping, i.e. two or more crops with overlapping growing season, and notably cereal-grain legume mixtures is a key pathway to such agroecological intensification (Malézieux et al. 2009). Transitioning from classical sole cropping (i.e. pure stand on the same species variety) to intercropping can bring many benefits such as a reduction in fertilizer use, greater drought and disease resistance, higher productivity, pests–diseases–weeds suppression, and increased carbon sequestration (Bedoussac et al. 2015; Yu et al. 2015; Raseduzzaman and Jensen 2017; Martin-Guay

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et al. 2018; Jensen et al. 2020; Tilman 2020; Yin et al. 2020; Beillouin et al. 2021; Li et al. 2021). However, these potential benefits cannot be realized without a strong complementarity between plants for different facilitation processes to compensate for eventual competitive interspecific interactions, the ideal situation being a synergistic intercrop functioning (Justes et al. 2021).

Consequently, there is a need for soil-crop models that can examine large combinations of species, agricultural practices, climate, and soil through virtual experiments to evaluate the potential of intercrop productivity, resilience, and sustainability (Gaudio et al. 2022). Soil-crop models are particularly well suited for such objectives, as they usually simulate the most important processes such as phenology, light interception, plant growth, yield formation, carbon and nutrient cycles, and water balance (Stomph et al. 2020).

Very few soil-crop models are able to simulate interspecific interactions, even for the simplest case of intercropping systems. This is mainly due to the difficulty of designing generic and simple new formalisms that consider the dynamic interactions between plants for all processes while maintaining a few, easily measurable parameters (e.g. crop height is easy to measure, number of leaves and their angles are not) and a fast computation time. Some attempts have been made to adapt existing classical sole crop models to bi-specific intercrops, for instance STICS (Brisson et al. 2004), APSIM (Keating et al. 2003), and CROPSYST (see Chimonyo et al. (2015) and Gaudio et al. (2019) for more details). The first results were encouraging, but some discrepancies were identified between simulations and observations, mainly due to the lack of an integrative representation of the processes accounting for the dynamic interactions between species in the soil-crop system. Singh et al. (2013), for instance, identified high levels of simulated nitrogen (N) uptake for rice using CROPSYST in a wheat-rice intercropping system as the cause of underestimating rice crop performance. Berghuijs et al. (2021) found that APSIM overestimates faba bean performance compared to the associated wheat crop, due to a poor simulation of plant height for both plants that affected the simulation of faba bean-wheat competition for light.

More extensive literature is available for the intercrop algorithms in STICS. This model generally performs correctly compared to observations (e.g. grain yield nRMSE 13–21% in Kherif et al. 2022), thus providing the first relevant basis for simulating bi-specific intercrops (see also Brisson et al. 2004; Launay et al. 2009), but several inconsistencies were identified in some cases. Indeed, Shili-Touzi et al. (2010) applied the model on a winter wheat-red fescue intercrop and found a tendency to overestimate N uptake for the fescue (EF 0.46 – 0.49). Corre-Hellou et al. (2007, 2009) had difficulties in computing light competition related to poor simulation of plant height (EF –0.04 – 0.51), an issue also

found in APSIM (RMSE 49 – 55 cm, Berghuijs et al. 2021) that can be critical for obtaining a correct simulation. We also identified some discrepancies between observations and simulations for STICS using a database from works published by Bedoussac (2009) and Bedoussac and Justes (2010) in a preliminary work, indicating that the model needs further improvements before being used with confidence for simulating scenario. Those discrepancies were found in the computation of Leaf Area Index (LAI), aerial and belowground biomass, N acquisition, and light interception using the radiative transfer option, a formalism published two decades ago (Brisson et al. 2004).

The challenge of properly simulating intercrops with formalisms that are easy to integrate into 1D soil-crop models, with few parameters, correct accuracy, and genericity involve designing or revisiting both scientific concepts and software algorithms. In this study, we focused on the light interception, changes in microclimatic conditions, N acquisition, and water uptake processes (Fig. 1) because we identified them as the main processes in plant-plant interactions in the intercropping system. The objectives of this work are to:

- (1) Review the formalisms in the initial soil-crop STICS model related to those processes and evaluate the consistency of the algorithms from a conceptual point of view and identify the weak parts of the algorithms;

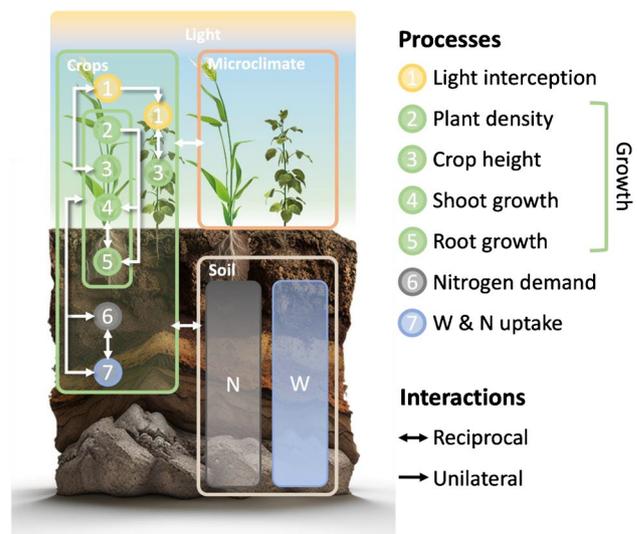


Fig. 1 Conceptual diagram of the processes reviewed and modified in STICS (simulated in the voxel scale of the model) for the interactions in the intercropping system. The diagram does not represent all interactions in the model, only the ones that were investigated in this work, which include: light interception, crop height in response to the environment (e.g. elongation), effect of plant density, shoot and root growth, microclimate, nitrogen (N) demand, and water (W) and N uptake.

- (2) Propose new simple formalisms to improve the simulation of the main processes in the initial version, which were considered unsatisfactory, and evaluate their relevance with a data-driven evaluation;
- (3) Evaluate the genericity and validity domain of the new version including the improved formalisms, i.e. the specific situations and types of intercrops under which the model's predictions or results are considered relevant, reliable, robust, and sufficiently accurate.

These goals were investigated keeping in mind several constraints and choices, in alignment with the requirements and the approach of crop models. First, the formalisms had to be generic, simple, and robust in order to be able to simulate widely diversified cropping systems. The robustness of the algorithms was tested by evaluating the ability of the model to simulate intercropping systems with different characteristics: soil type, climate, species associations, and spatial designs. Second, the number of parameters had to be minimal with parameters derived from sole-crop data without the need for any re-calibration to simulate intercrops. This method assumes that there is either no significant influence of the other crop on a given process, and the model explicitly simulates those interspecific interactions, including trait plasticity such as enhanced shoot elongation growth or root exploration in the soil. This is to say that plant-plant interspecific interactions and the balance between dynamic competition and complementarity are emerging properties of the STICS model functioning. Last, the formalisms implemented in STICS had to generate a similar or lower range of error for bi-specific intercrops compared to sole crops, as defined by the error assessment proposed by Coucheney et al. (2015). This step was defined to ensure the formalisms could be used for *in silico* comparisons of species mixtures or management, for example by calculating their land equivalent ratio (LER) as shown by Launay et al. (2009). The underlying assumption here being that the sole crop model is the reference model, so any improvement to the sole crop model will reflect positively on the intercrop simulation, without any reparameterization for intercrop.

2 Material and methods

2.1 General description of the STICS soil-crop model

The STICS model is a dynamic 1D soil-crop model that combines crop development, growth and yield formation with the carbon, N, energy, and water cycles of the soil-crop system (Brisson et al. 1998, 2003, 2008; Beaudoin et al. 2023). The model runs at a daily time-step using input data related to climate, crop species, soil, agricultural

management, and the state of the system at initialization, such as the water and N content of each soil layer. The crop is represented as a set of organs with a given development stage, biomass, and N content. The biomass growth is mainly driven by light interception as a function of leaf area index with a big leaf approach, while crop development is driven by thermal time corrected by vernalization and photoperiodic effects. The big leaf approach uses the so-called Beer-Lambert law of light extinction coupled with a radiation use efficiency. Stress effects from frost, insufficient supply of N or water, and root anoxia can all potentially affect development, leaf area, growth, and yield.

The STICS model was adapted to simulate bi-specific crop mixtures in alternate rows by Brisson et al. (2004) and further by Launay et al. (2009). Both crop species are simulated sequentially starting the first day from the *a priori* dominant one (i.e. the usually taller one in sole crop conditions) and then dynamically computing dominance during the crop cycle based on crop height. The model simulates several plant-plant interspecific interactions, which are reviewed and described in the next section. New formalisms are also proposed for the improvement of some processes that were found incorrect or not sufficiently relevant to simulate daily plant-plant interactions (Brisson et al. 2004; Corre-Hellou et al. 2007, 2009; Launay et al. 2009; Shili-Touzi et al. 2010; Kherif et al. 2022).

In this paper, we only describe the formalisms that were modified in or added to STICS (see supplementary materials for more details). The other equations are available from the first version published by Brisson et al. (2004), in other previous papers (Brisson et al. 1998, 2003), and in the STICS book detailing all equations and associated information (Brisson et al. 2008; Beaudoin et al. 2023).

In addition, various inconsistencies were fixed in the algorithm's implementation following code review, mainly in the computation of light capture, leaf senescence, effect of frost, and energy balance, that are not all detailed in this paper.

2.2 Modifications to the model

2.2.1 Radiative transfer

The radiative transfer option (Brisson et al. 2004) is a module corresponding to a 2.5D projection of the crop with homogeneous structure within the row. The crop leaf area density is represented using a geometric primitive (a rectangle or an up- or down-facing triangle) projected onto the 2D vertical plane, and the light interception computation is performed considering this shape re-projected in 3D along the crop row, e.g. the rectangle is used as a hexahedral volume to represent the whole row (see the corresponding section from the supplementary material for more details).

In the case of bi-specific intercrops, the same computation for light interception is applied iteratively for each crop using only the transmitted light as a medium, without any explicit knowledge of the shape of the other crop. This formalism was found relevant, and only computation errors were corrected.

2.2.2 Beer-Lambert law of light extinction

The radiative transfer formalism is generic and allows simulating a wide range of intercropping designs with heterogeneous canopies due to the relative independence between the shapes of both crops. However, some intercrops present well-mixed canopies, where the assumption of spatially divided crop canopies or dominance in terms of height is not verified. Therefore, a simpler approach to account for intercrops with well-mixed canopies of the two species was also implemented as a second option to simulate light capture. This new formalism uses the Beer-Lambert law of light extinction in plant canopies adapted for intercropping (Keating and Carberry 1993) by considering the leaf area index and extinction coefficients of both crops.

2.2.3 Plant density effect

When simulating a classical sole crop, the intraspecific competition for light interception and growth is computed using a density effect (S_D). This effect is used to downregulate the growth of the crop with higher plant density (Brisson et al. 2003, 2008). The same algorithm is now used in bi-specific intercrops to represent the intra-row competition, but using twice the intercrop plant density to use the same parameters determined on sole crops, i.e. conceptually a sole crop can be viewed as an intercrop of a crop with itself.

2.2.4 Plant traits and dimensions

The height of the crop canopy significantly influences the competition for light capture between the two species, and any inaccuracies in this aspect can potentially introduce errors in several downstream variables depending on light absorption (i.e. biomass growth, N acquisition, etc...). The crop canopy height was computed using the LAI for sole crops and is often ignored by users because it has no impact on other output variables in STICS, except when using the radiative transfer option, which was previously mandatory for intercrops (Brisson et al. 2003, 2008). The calculation of crop height was previously found inconsistent over the course of the crop development, and in particular after the flowering stage (Corre-Hellou et al. 2009). We developed a new formalism that computes plant height using crop phasic development instead, with an implementation based on the same approach proposed by Gou et al. (2017) and Berghuijs

et al. (2020), but with some refinements, mainly concerning the addition of the effect of stresses (see supplementary materials).

The height of a crop can also be up- or down-regulated in response to stresses, such as light competition with another species, drought, root anoxia, low N availability, and frost. The resulting integrated effect arising from those individual stresses is computed as the minimum of all down-regulating effects, and the up-regulating effect (i.e. the shoot elongation) separately, which are both applied to the daily height increment.

The magnitude of the elongation of the crop height can theoretically change with the associated species depending on light quantity and quality, e.g. a proxy of the photomorphogenetic effect. However, the type of response, i.e. shade avoidant or shade tolerant, remains stable based on the plant species. Hence, we implement a formalism that elongates the stem of the plant based on the relative surface of the plant that is shaded and a parameter of maximum elongation effect when the species is fully shaded.

2.2.5 Nitrogen demand

The N uptake of the crop depends on its N demand, N availability in the soil layers, and root exploration. The latter is computed using the rooting depth and the root length density along the soil profile. The N requirements are computed using a dilution curve that relates the crop aboveground biomass to its N concentration (Corre-Hellou et al. 2009). The underlying hypothesis is that leaves have a higher N content compared to other organs, and as the plant/crop grows, the proportion of leaves compared to structural organs (e.g. straw) decreases, thereby diluting the N content in the aboveground biomass (Justes et al. 1994). This computation is fine for sole crops because the N requirement of a crop depends on its biomass and is relatively independent from its plant density due to tillering in cereals or ramification in other species.

However, crops cannot always offset the effect of lower density in intercropping due to interspecific plant-plant competition. Consequently, at a specific stage of development, when a crop is grown in intercrop, the anticipated biomass per unit of ground surface area is typically lower than when grown in sole crop. This leads to an artificial increase in its N demand since the dilution curve relies on parameters derived from sole crop experiments. For intercrops, we use the total biomass of the intercrop (i.e. both crops together, see supplementary materials) as a proxy for the equivalent biomass in sole crop, as proposed by Louarn et al. (2021), to use the same parameter values than in sole crops. This modification helps avoiding an underestimation of the N status of crops simulated in intercrops, as shown by Corre-Hellou et al. (2009). This assumption should be valid for a wide

range of cases, unless both development and biomass of the two crops are largely different (Louarn et al. 2021).

2.2.6 Water and nitrogen competition and complementarity

The competition and/or complementarity processes for water and N dynamic budgets are mainly determined by the roots, their biomass, and density in the soil layers. Root systems of the intercrop do not directly interact, but affect each other via their influence on the status of water and N availability in the soil over the whole profile and for each 1-cm layer corresponding to the discretization of soil layer in the model. As for a sole crop, the root development and growth of each species in the intercrop depends on species-specific parameters, thermal time of soil temperature, several potential stresses, such as anoxia, drought, soil properties (high bulk density), frost, or low N content, and potentially a trophic linked production depending on the simulation option (Brisson et al. 2004, 2008).

The computation of the plant density effect is already considered in the shoot growth when using the trophic-linked root length expansion option. However, it is not the case when choosing the self-governing root length expansion option, which is the default option. Consequently, we introduced a down-regulating effect of intra-specific plant density on the root length growth rate (see supplementary materials for the details).

2.2.7 Microclimate

Microclimate can be impacted by crops, especially when the canopy is heterogeneous. In intercropping, the taller species can decrease the wind experienced by the smaller one by increasing the size of the boundary layer above its canopy. It can also increase air humidity and regulate the local temperature. All these effects can greatly influence the development of a crop by modifying the daily and cumulative thermal time. These effects are taken into account in STICS by using a resistive approach already implemented, first presented in Brisson et al. (2004) and adapted from Shuttleworth and Wallace (1985). This approach is relatively simple and coherent to simulate canopy temperature in intercropping, and was kept in its original formalism.

2.3 Spatial designs that theoretically define the validity domain of STICS

Before simulating intercrops with the new version of STICS, the user should address how the two crops interact in the soil-intercrop system, and whether these interactions are correctly considered in the model. Based on the main processes described above, STICS is conceptually able to simulate

intercropping in alternate rows (each species in a different row, inter-row set to distance between rows of the same species) and mixed within-row (inter-row set to distance between each row). These two intercropping spatial designs can be simulated for any plant density as long as their root distribution can be assumed horizontally homogeneous, or in other words, that the distribution of roots is uniform inside each horizontal soil layer of 1 cm. For the light interception, the radiative transfer option should be used for heterogeneous canopies, with the assumption that both crop canopies are homogeneous along the row, and that one of the two crops is dominant over the other in terms of height. If the assumptions are not verified, the new option for the Beer-Lambert algorithm adapted for intercrops should be used.

In addition, theoretically and technically, STICS is also able to simulate relay intercropping in alternate rows—or with the second crop sown in the inter-row of the first crop—where the two species are not sown, neither harvested, at the same time; however, we have not tested this type of intercropping in this paper by unavailable observed data.

Finally, and as a rule of thumb, the improved version of STICS can simulate a wide range of bi-specific intercrop system that presents the following three characteristics:

- root systems that are homogeneously distributed along the horizontal soil layers;
- shoots forming a canopy that is at least homogeneously distributed in the row;
- shoots interacting for light capture, either mixed or with a significant or large dominance between the two species, the dominance may change over time.

2.4 Methodology for the calibration and evaluation of STICS

2.4.1 Parameter calibration

The parameters of STICS were first calibrated manually using data from literature and expert knowledge to find boundary values that are consistent with the species considered. Then, an automatic calibration was performed based on the recommendations of Guillaume et al. (2011), Buis et al. (2011), and Ruget et al. (2002) on the most influential parameters following the same procedure consisting of 15 steps of calibration for 25 parameters optimized over 13 variables. The parameters were first optimized using the Beer-Lambert law of extinction for the light interception, and then using the radiative transfer option, because the latter can fall back to the Beer-Lambert law whenever the plant height of the two species are close, and by doing so, the light extinction parameter of the Beer-Lambert law is used.

The parameters were optimized using the standard workflow proposed by the “CROptimizeR” R package (Buis et al.

2023) with the Nelder–Mead simplex algorithm (Nelder and Mead 1965) and seven repetitions with different initial parameter values to better sample the range of values while reducing the risk of converging to a local minimum. Analyses of the estimated against initial values were performed to investigate whether the initial values had any impact on the optimized value.

2.4.2 Parameters calibrated for intercrops

The formalisms implemented only need two parameters to be calibrated in the case of the radiative transfer option for the simulation of bi-specific intercrops: (i) a threshold for the difference in crop height defining a dominance effect from one crop over the other, i.e. the model falls back to the computation of Beer-Lambert below this value, and (ii) an elongation effect due to shading for the dominated crop (i.e. ep from equation (11) in supplementary materials). The first one defines the threshold of height difference between the two crops below which both canopies are considered well-mixed (i.e. leaves are randomly distributed in the canopy layer). In this case, no clear dominance is occurring between the two species, indicating that light is shared depending on the LAI of each species and their respective light extinction coefficient. It is associated to the intercrop system under consideration, but its value should be consistent between intercropping systems because it defines the limit between the validity domain of the 1D representation of the Beer-Lambert formalism and the 2.5D representation of the radiative transfer formalism. The parameter for the elongation effect in intercropping system cannot be parameterized on sole crops as it is the result of plant-plant interactions of the two species and should be measured in the field when the given crop is dominated by the other, or in growth chambers with light control. The value of this parameter can change depending on the type of species associated. However, and surprisingly, we did not observe a significant elongation effect in the data set used, so this parameter was set to 1.0 for all species in a first approximation, i.e. no elongation due to shading for the intercrops tested.

2.4.3 Combination of strategies to evaluate the new formalisms in STICS

Three complementary approaches were adopted to evaluate the new version of STICS for bi-specific intercrops presented in this paper.

First, the model formalisms were evaluated on sole crops, with the assumption that simulating an intercrop made of twice the same crop parameters should provide results close to a classical simulation of a sole crop. This means simulating a sole crop as an intercrop with itself, which also allows analyzing if intraspecific interactions are correctly taken into

consideration and implemented in the algorithms. We refer to these simulations as “self-intercrop,” where sole crops are simulated by considering half a sole crop combined with another half of the same sole crop. The reference sole crop simulation is made using the new version of STICS to compare with the same formalisms in both setups, including the corrections made in the code.

Another objective of this analysis was to investigate whether there is an effect of the order each plant is computed in the sequence, i.e. whether the dominant crop grows more because it has priority in resource acquisition each day as it is simulated first. If there was any influence in the order of simulation, one of the crops would deviate from the other in terms of light interception, N and water acquisition, leaf area development, biomass accumulation, and ultimately grain yield. Our hypothesis is that the maximum delay of 1 day between the crops has a very low impact on the simulation, i.e. the dominated species can also be considered having priority over the dominant species because it acquired resources last on day $i-1$. Nevertheless, this assumption needed to be validated.

Second, we used data from two crops either grown as sole crops or intercropped and simulated both cases to evaluate the ability of STICS to reproduce the interspecific interactions as well as the intraspecific interactions.

Third, we evaluated the model using experimental data of bispecific intercrops with contrasting species mixtures and spatial heterogeneity, at contrasting sites, to investigate its potential genericity and the domain of validity of STICS for intercropping systems.

Note that all simulations of intercrop treatments presented in the paper are independent evaluations of the model as it is only calibrated on sole crop situations.

2.5 Dataset

2.5.1 Sites and experiments

We used data from two experimental sites with different experiments analyzing bispecific grain legume–cereal (or sunflower) intercrops. The first experimental site is located on the INRAE research station in Auzeville (43°31'N, 1°30'E) in South of France (from published and unpublished data). The climate is temperate oceanic under Mediterranean influence and characterized by summer droughts and cool, wet winters (Cfa in Köpper-Geiger climate classification, Beck et al. 2018). The 25-year mean annual rainfall in Auzeville is 650 mm, and the mean annual air temperature is 13.7°C. The site has a deep loamy soil with little or no stoniness. Phosphorus and potassium are assumed non-limiting at this site.

In this study, we use four datasets from this site. The first one is a durum wheat (*Triticum turgidum* L., cv.

Nefer) and winter pea (*Pisum sativum* L., cv. Lucy) experiment carried out during the 2005–2006 growing season, and sown as sole crops or in an alternate row intercrop design (Bedoussac and Justes 2010) with an initial mineral N of 39 kg N ha⁻¹ over the whole soil profile (0–1.2-m depth). An incorporation of 7 t ha⁻¹ (C:N = 63) of sorghum (*Sorghum bicolor* (L.) Moench) residues, the previous crop, was performed on 26 September 2005 by tillage at 20–25-cm depth.

Similarly, for the second one, the same species and varieties were grown as sole or intercrops in Auzeville during the 2012–2013 growing season, but this time the intercrops were mixed on the row instead of sown in alternate rows (Kammoun 2014; Kammoun et al. 2021). Initial mineral N content was 41 kg N ha⁻¹ over the 0–1.2-m soil profile. Mineral fertilizers were applied on 25 March with 80 kg N ha⁻¹ and on 14 May with 60 kg N ha⁻¹.

The third experiment setup included durum wheat (cv. Nefer) and faba bean (*Vicia Faba* L., cv. Castel) grown in sole and intercrop during the 2006–2007 growing season. The intercrop consisted of alternate rows of each crop species (Bedoussac 2009; Falconnier et al. 2019). Initial mineral N content was 30 kg N ha⁻¹ on the whole soil profile down to 1.2-m depth. Management included ploughing prior to sowing, 20-mm irrigation after sowing for crop establishment and an incorporation of 5 t ha⁻¹ (C:N = 49) sunflower residues, the previous crop, on 25 September 2006 by tillage at 20–25-cm depth.

The last experiment consisted in growing sunflower (cv. Ethic) and soybean (*Glycine max* (L.) Merr., cv. Ecurdor) either in sole crop or strip-intercrop composed of 1 row of sunflower and 2 rows of soybean. Initial mineral N content was 181 kg N ha⁻¹ within the whole soil profile down to 1.2-m depth. The crop was rain-fed, and no N fertilizers were applied.

The second site corresponds to data published by Corre-Hellou et al. (2006) from an experiment located at the FNAMS near Angers, France (47°27' N, 0°24' W). The location benefits from a temperate climate with oceanic influence with no dry season and warm summer (Cfb in Köpper-Geiger climate classification). Angers has a mean temperature of 12.4 °C and mean annual rainfall of 703 mm averaged over 20 years (1999 and 2019). The soil is a clay-loam. The field experiment was carried out in Angers in 2003 with field pea (*Pisum sativum* L., cv. Baccara) and spring barley (*Hordeum vulgare* L., cv. Scarlett) grown as sole crops and alternate row intercrops (Corre-Hellou et al. 2006). The soil contained 71 kg ha⁻¹ inorganic N at sowing from 0 to 0.7-m depth, and no N fertilizer was applied.

The five types of intercrops simulated using STICS and how the spatial designs tested in the field experiments are represented in the simulations are illustrated in Fig. 2.

2.5.2 Measurements and calculations

The following data was available, measured for each species in intercrop: (i) phenology, date of flowering (Flowering, Julian days), date of physiological maturity (Maturity, Julian days); (ii) dynamics of plant height (Height, m), aboveground biomass (Biomass, t ha⁻¹), fraction of absorbed photosynthetically active radiation (faPAR) measured in continuous at INRAE Toulouse (complete set of PAR sensors allowing to calculate daily the PAR budget and then the PAR absorbed by the sole crop and intercrop), leaf area index (LAI, m² m⁻²), N acquisition (kg N ha⁻¹), and N fixed by legumes in the aboveground biomass (kg N ha⁻¹) estimated by ¹⁵N natural abundance method (Bedoussac and Justes 2010); and i(ii) grain yield (Grain, t ha⁻¹) and harvest index.

Two variables were calculated using either simulations or observations. First, the ratio of N derived from the atmosphere (N_{DFA}, %), computed as follows:

$$N_{DFA_i} = \frac{Q_{fix_i}}{QN_i} \quad (1)$$

where Q_{fix} is the cumulative amount of N fixed symbiotically (kg N ha⁻¹), QN is the amount of N accumulated by the legume crop (kg N ha⁻¹), and i the index of the day.

And second, the partial land equivalent ratio ($pLER$) computed after Willey and Osiru (1972):

$$pLER = \frac{Grain_{ic}}{Grain_{sc}} \quad (2)$$

where $Grain_{ic}$ is the grain yield in intercrop and $Grain_{sc}$ is the grain yield in sole crop. A value of $pLER$ above 0.5 indicates a higher per-area performance in the intercrop than grown as a sole crop, which is most often called over-yielding. The evaluation of the overall intercrop performance is then made using the LER by summing up the $pLER$ of each crop composing the bispecific intercrop ($pLER_{species1} + pLER_{species2}$), and comparison is made to the reference value of one (for replacement half density design), i.e. no difference compared to sole crops.

The most critical period to simulate for many key variables is the dynamics and maximum value, i.e. the value of the maximum LAI and when it occurs before senescence, and the maximum grain and aboveground biomass, which determine yield. These critical periods are referred to as “key stages” hereafter.

Graphical evaluations and statistics were computed using the CroPlotR package (Vezy et al. 2023a) in order to evaluate the quality of calibration of sole crops and the quality of prediction for intercrops. The full description and equations of the statistics are available from the package documentation; they included EF (modeling efficiency),

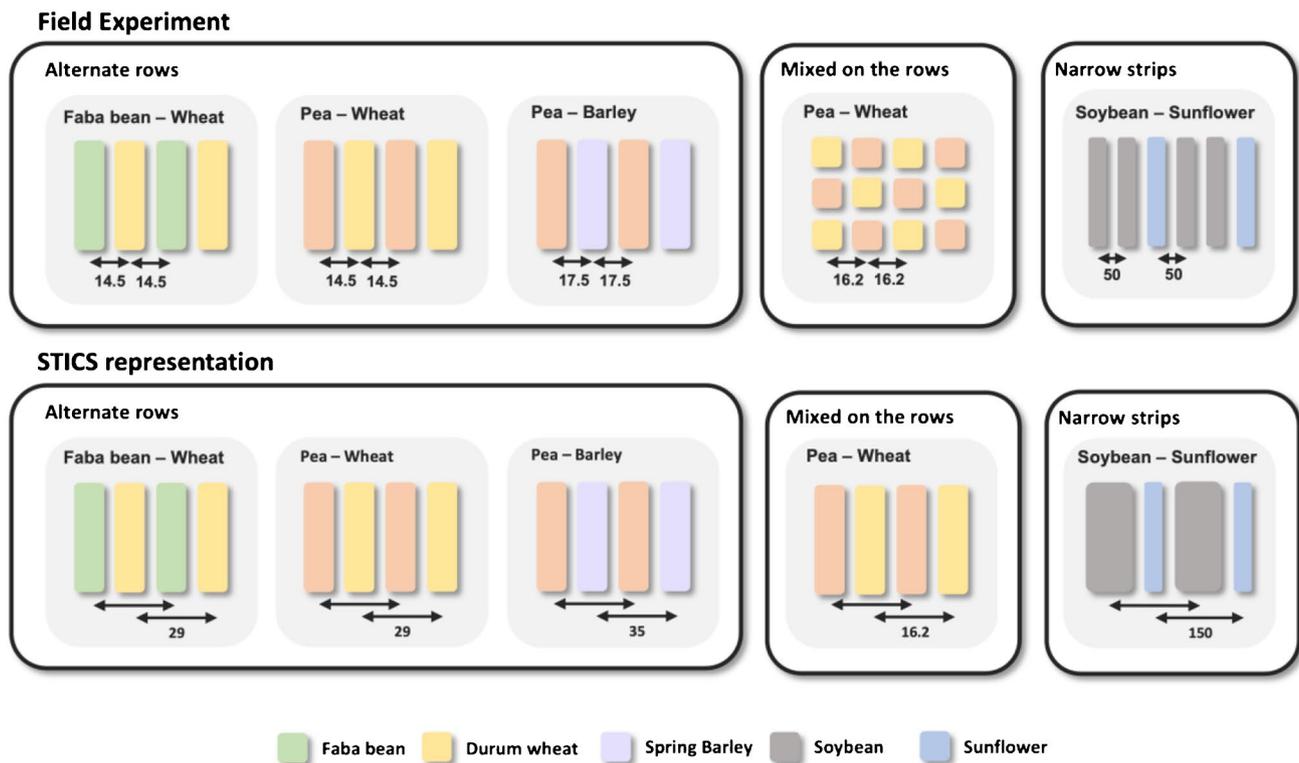


Fig. 2 Representation of the five types of intercropping designs tested in the field experiments (up), and how they are represented in STICS (down). In the model, interrow is given for each species independently. Arrows represent the interrow distances (cm) between each row in the field experiment, and the distance between the rows of the same crop (alternate rows and mixed on the row) or between strips (narrow strips) in the model.

RMSE (Root Mean Squared Error), nRMSE (normalized RMSE), and bias.

3 Results and discussion

3.1 Intraspecific interactions

The “self-intercrop” simulations were close to the regular sole-crop simulations for all variables and all crops (Fig. 3) at key stages for all important processes where the two simulation setups were compared.

There was only a narrow difference between the simulations of all the variables, e.g. the difference in plant height was very low (< 0.001 m). The fraction of absorbed photosynthetically active radiation (faPAR) in the “self-intercrop” was equal to that in the sole crop. The average difference for the maximum simulated value was only 0.1%. There was an increase of $20.6 \text{ kg N ha}^{-1}$ in N acquisition at harvest on average (+11.9%) in the self-intercrop. As a result of this increased N acquisition, there was a rise in aboveground biomass at harvest ($+0.17 \text{ t ha}^{-1}$, +5.2%) and grain yield ($+0.8 \text{ t ha}^{-1}$, +4.4%) in the self-intercrop.

Another important result was that there is little difference between the two simulation options in the soil-water content (3% difference maximum, not shown) and N acquisition (20% difference maximum, Fig. 3), which indicates that the order each species is simulated in the sequence has no substantial effect, i.e. the dominant crop may be simulated first and have priority in daily resources acquisition.

In this study, we demonstrated that STICS had a consistent behavior in the simulation of both sole crops simulated as usual and as “self-intercrops,” which is crucial when analyzing system performances based on sole crops vs intercrop comparisons with high certainty. These results are a great improvement over previous results using the initial version of STICS developed by Brisson et al. (2008, 2004), which allows to go further in the *in silico* pre-optimization of more intercropping systems and for a wide range of pedoclimatic conditions.

3.2 Interspecific interactions

The approach with STICS is to calibrate the model on sole-crop data only and let the model simulate the intercrop plant-plant interactions without any re-calibration of the parameters, thus facilitating the evaluation of the model’s

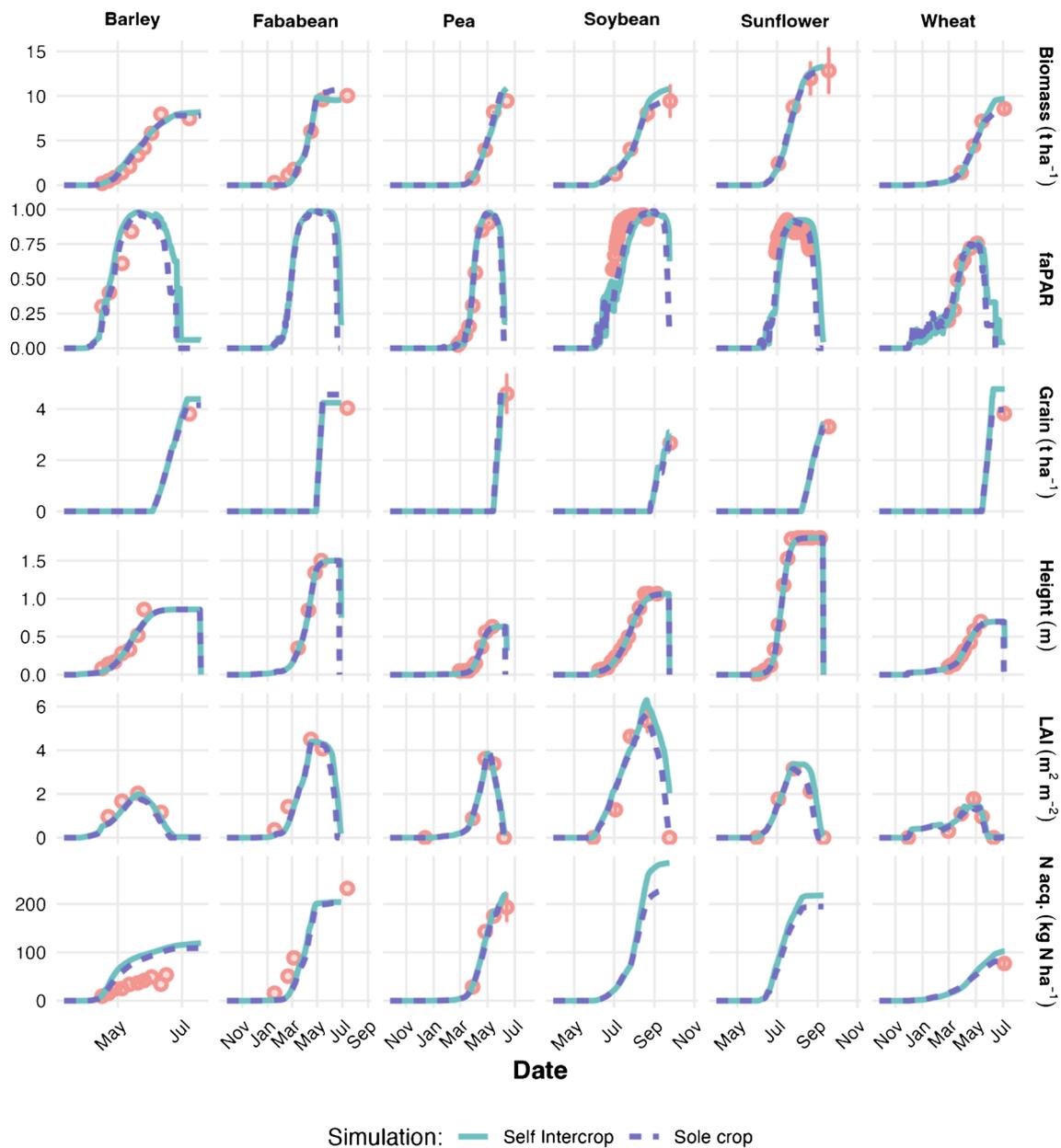


Fig. 3 Sole crops either simulated as a regular sole crop or a self-intercrop (half-density intercropped with itself). Simulated variables include from top to bottom: 1. Aboveground biomass (Biomass), 2. Fraction of absorbed photosynthetically active radiation (faPAR), 3. Grain yield (Grain), 4. Plant height (Height), 5. Leaf area index (LAI), and 6. Nitrogen acquisition in the aboveground biomass (N acq.). Points represent field measurements with standard error when available. Simulations stop at simulated harvest. The parameters of the model were optimized on sole crop systems and then used without any recalibration to simulate the self-intercrop.

ability to simulate interspecific interactions and possible plant plasticity resulting from calculations as an emerging property. Sole-crop and intercrop simulation results were compared to observations for each individual species to investigate whether STICS simulates species behavior from sole crop to intercrop. In sole crops, the simulations were close to the observations for all variables tested (Fig. 4). The plant height was particularly close between cropping systems in observations and simulations. For the sole crop,

the model underestimated Ndfa from the beginning of the crop growth and until the last measurement, at which point it became more accurate.

As an example comparison, field observations showed that at harvest, the aboveground biomass of the pea was 8% lower and the biomass of wheat was 40% higher when intercropped than when sole cropped. STICS effectively simulated the same behavior, with a decrease of 11% for the aboveground biomass of the pea crop and an increase of 32%

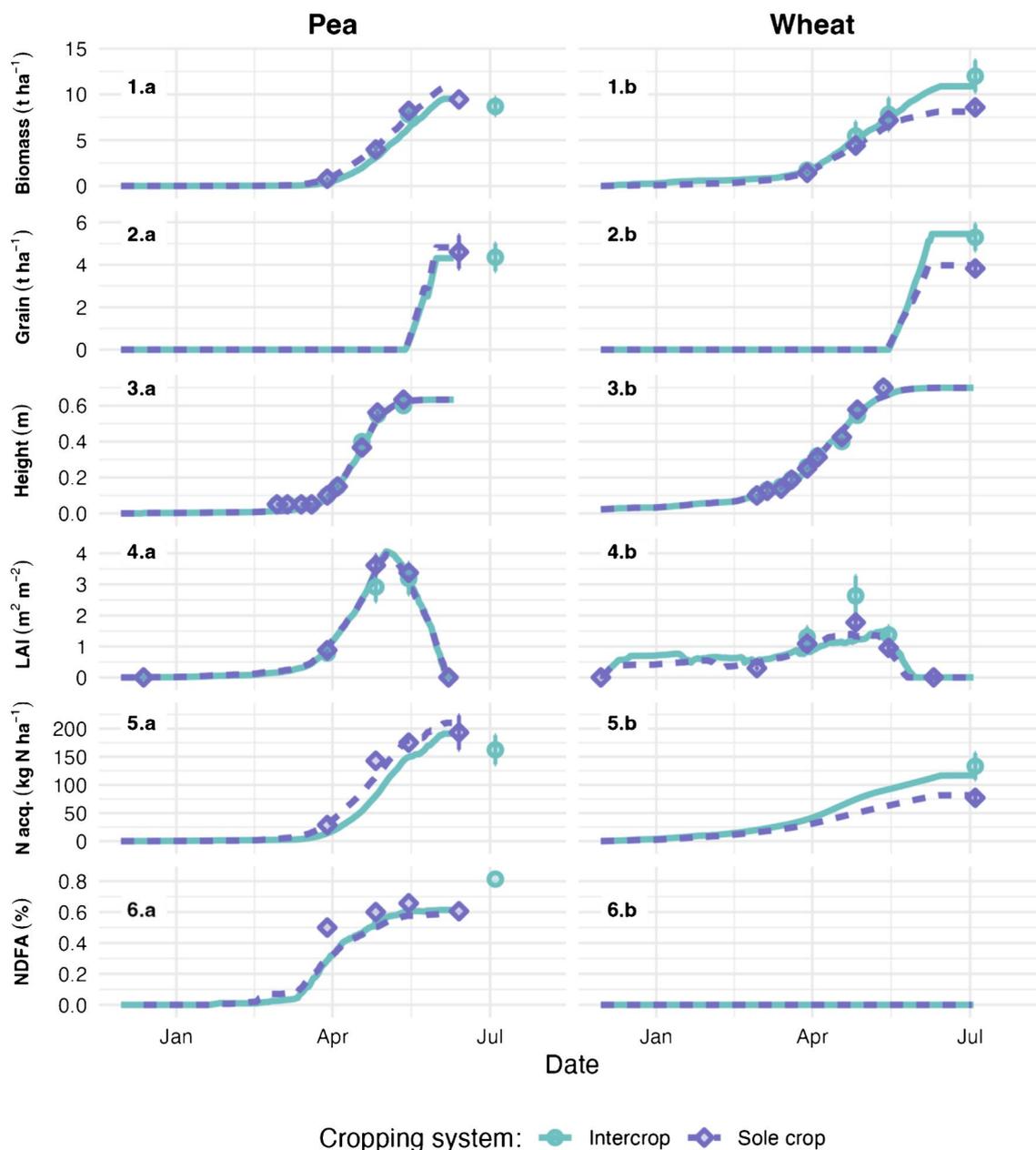


Fig. 4 Observed (points) and simulated (lines) 1. Aboveground biomass (Biomass), 2. Grain yield (Grain), 3. Plant height (Height), 4. Leaf area index (LAI), 5. Nitrogen acquisition in the aboveground biomass (N acq.), and 6. Ratio of nitrogen derived from atmosphere (NDFA), for each plant species (**a**: Pea, **b**: Wheat) both grown and simulated either in sole crop or intercrop at Auzeville during the 2005–2006 growing season. Values for the intercrop are adjusted ($\times 2$) for comparison relative to the equivalent total surface area of the two sole crops. The parameters of the model were optimized on sole crop systems and then used without any recalibration to simulate the intercrop systems.

for the wheat. The trend was similar for grain yield, LAI, and acquired N, and the model was able to reproduce all these effects, even if the wheat maximum LAI was underestimated when intercropped (-54% , Table 1). The results also show that STICS was able to simulate the niche complementarity for N sources. Indeed, the simulation resulted in an increased NDFA ($+6\%$, observed $+24\%$) for the intercropped pea

and a considerably higher N uptake by intercropped wheat ($+42\%$, observed $+73\%$) leading to a higher N acquisition by the intercrop compared to the sole crops (Fig. 4 and Table 1), which highlight the ability of the model to simulate facilitation for N between the two species.

Legume species typically exhibit lower competitiveness for soil mineral N uptake when compared to cereal crops

Table 1 Variable change from a sole crop to an intercrop (%), i.e. difference between a species grown in intercrop compared to a sole crop. Values for the intercrop are adjusted (i.e. multiplied by 2) for comparison relative to the equivalent total surface area of the two sole crops. Biomass: aboveground biomass at harvest (t ha^{-1}), Yield: grain yield (t ha^{-1}), Maximum LAI: maximum leaf area index ($\text{m}^2 \text{m}^{-2}$), N acquired: Nitrogen acquisition in the aboveground biomass (kg N ha^{-1}), and NDFA: Ratio of nitrogen derived from atmosphere for leguminous crops (%).

Variable	Species	Observation	Simulation
Biomass	Pea	-8	-11
Biomass	Wheat	+40	+32
Yield	Pea	-5	-6
Yield	Wheat	+38	+42
Height	Pea	-5	0
Height	Wheat	0	0
Maximum LAI	Pea	-12	+1
Maximum LAI	Wheat	+48	-8
N acquired	Pea	-16	-7
N acquired	Wheat	+73	+42
NDFA	Pea	+24	+6

(Bedoussac and Justes 2010; Bedoussac et al. 2015). This characteristic enables cereal crops to achieve a superior N nutrition status per plant, initiating a positive feedback loop. As crop biomass increases, there is enhanced root exploration in the soil, resulting in greater N uptake (Bedoussac and Justes 2010). During their first development phases, legume crops may experience an increase in the number of nodules due to the soil nitrate concentration that drops off as a result of the greater competition for N uptake by the cereal crop, which also stimulates N_2 fixation rate (Bedoussac and Justes 2010). This niche complementarity for N sources between cereal and legume crops is an important property of this type of intercropping and is precisely what we seek when designing intercrops, i.e. a system that is less dependent to N fertilization (Malézieux et al. 2009; Stomph et al. 2020; Tilman 2020). The simulations showed that the improved version of STICS could simulate niche complementarity for N (Fig. 4) with an increase in N acquisition in wheat crops thanks to a higher competitiveness that forced the pea to increase its NDFA. This effect comes from a higher competition from the wheat to soil mineral-N, but is described as a facilitation process for the intercrop because it leads to a higher overall N content in the intercrop canopy compared to the cereal sole crop, and to an over-yielding illustrated by an LER significantly above one (Justes et al. 2021). This increase is in line with the results from Stomph et al. (2020) that shows that intercrops increase resource acquisition compared to sole crop rather than improving conversion efficiency. Our simulation results reflect a particularly interesting emergent property of STICS that is able to simulate this niche complementarity for N without any explicit formalism sensu

stricto, and with equations that require no recalibration or new specific implementation procedure. This is precisely what we seek in soil-crop models, i.e. implementing simple and generic formalisms that once coupled make the model able to dynamically simulate the functioning of more complex systems thanks to emerging properties arising from the process's interaction. This approach has also proven useful in studies on nutrient stress (Bouain et al. 2019), periodic patterns in plant development (Mathieu et al. 2008; Vezy et al. 2020), environmental impact on plant architecture (Eschenbach 2005), and even population and community dynamics predicted from individual-based algorithms (Hammond and Niklas 2009).

Numerous studies have found that plant architecture is influenced by the type of species mixture (Liu et al. 2017). In STICS, we do not implement such behavior explicitly except for the shoot elongation, which was not found significant in the field observations of our data base, so this new formalism was consequently not evaluated in this study. Accordingly, simulations for durum wheat were consistent for situations where the crop was dominant (associated with pea) and dominated (associated with faba bean, see Fig. 5). Such results may indicate another possible emergent property of STICS, showing that plant plasticity in the field may also act as a buffer to such behavioral changes when considering plants at the community scale instead of the plant scale. In other words, the heterogeneity in architectural traits of the dominant crop could help reduce the elongation effect of the dominated crop, and the intensity of the elongation effect of the dominated crop could also be uneven between individuals. These plasticity effects of both crops could then reduce the overall effect of plant elongation at the intercrop scale, which could be the reason why no significant effect was measured at this scale in our database, and in the end alleviate the need for changes in parameter values in the model (Louarn et al. 2020).

3.3 Genericity of the formalisms: simulation of contrasted intercrops

The genericity of STICS was evaluated in a first approach using intercrops composed of various species mixtures and spatial designs. The model consistently simulated all variables for the various types of intercrops even for the sunflower-soybean intercrop that presented the most spatially heterogeneous system as a narrow strip design with the larger inter-row space (Fig. 5). The simulation results indicated that the model failed to replicate the highest values for LAI, N acquired, and N fixation. This discrepancy can be attributed to the calibration of the model using a sole crop dataset where such values were not observed, resulting in inadequate calibration of the related parameters. This issue could be rectified in future studies by using a larger training

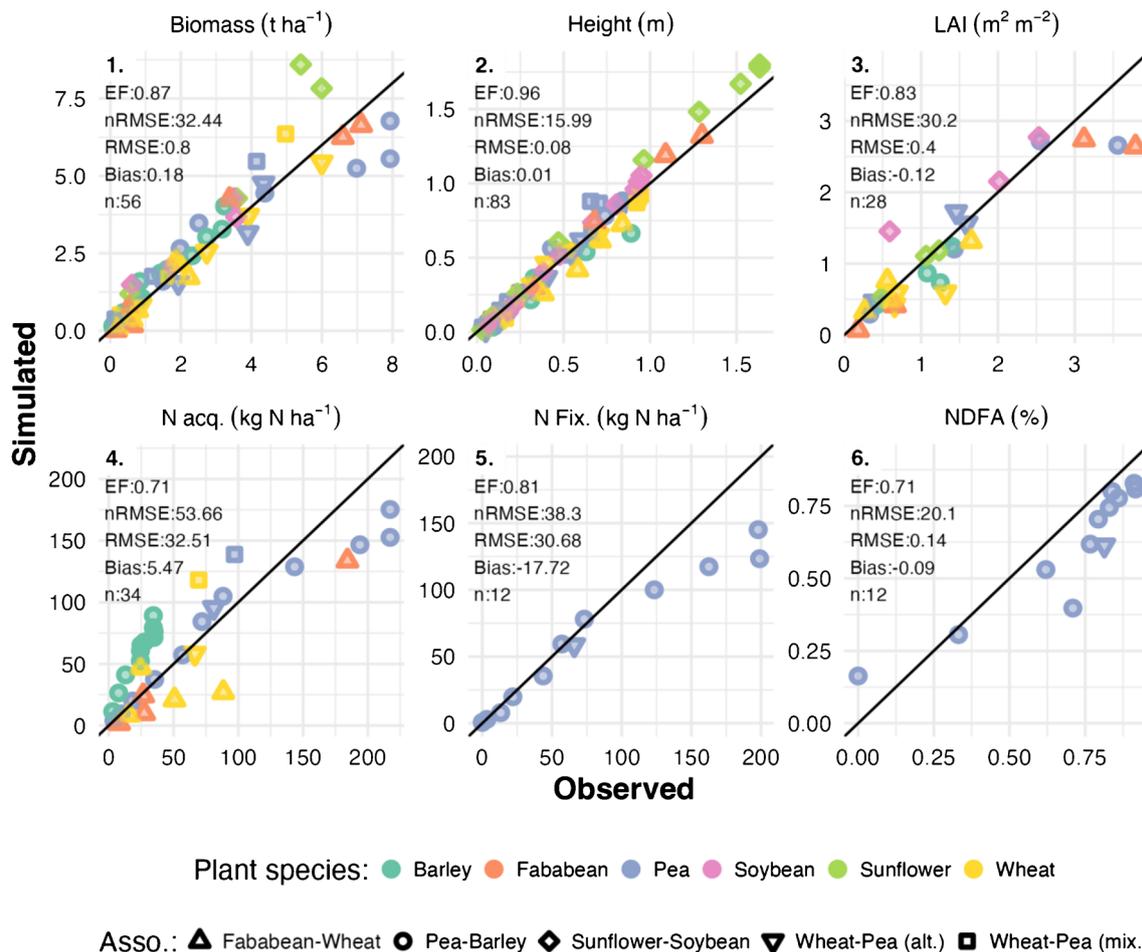


Fig. 5 Observed (x) and simulated (y) values of contrasting intercrops for 1. Aboveground biomass (Biomass), 2. Plant height (Height), 3. Leaf area index (LAI), 4. N acquisition in the aboveground biomass (N acq.), 5. Accumulated nitrogen from symbiotic fixation (N Fix.), and 6. Ratio of nitrogen derived from the atmosphere (NDFA) for legumes. Symbols are colored by plant species and shaped by cropping system. The parameters of the model were optimized on sole crop systems and then used without any recalibration to simulate the intercrop systems.

dataset encompassing a wider range of observed values. Additionally, a more robust evaluation could be conducted with the inclusion of additional data, considering that only 12 observations were available.

Globally, as shown in Fig. 5, the evaluation indicated a modeling efficiency (EF) equal to or higher than 0.71 for all variables considered dynamically throughout the growing season; this indicates correct performances per se and also in comparison to what is widely published for crop models for classical sole crops. The simulated variables were all assessed as “very good” using the method of Coucheney et al. (2015), except for NDFA and N acquired that were classified as “good” (see Figure A2).

STICS was also evaluated at critical crop growth stages, which produces a better evaluation of its capability to reproduce the system behavior and dynamic processes at crucial stages and over time. STICS could also satisfactorily

reproduce crop functioning for all variables, with an EF above 0.5, except for the N content in the grains at harvest that showed lower efficiency (0.2, Fig. 6). The N acquisition is the variable that usually presents the highest modeling error for soil-crop models, a behavior that was recognized in previous versions of the model (Coucheney et al. 2015). This variable is one of the most complex to simulate because it depends on many processes that interact throughout the crop development cycle in intercrop systems (Bedoussac and Justes 2010). It is also worth noting that it presented a low bias of 0.13%, which is still encouraging.

Moreover, for sunflower-soybean intercrop, sunflower biomass was overestimated by 3.2 t ha⁻¹ (+44%) which in turn lead to a higher yield (+40%) and partial LER (+30%) compared to the observations (Fig. 5.1, Fig. 6.6, and Fig. 6.9). Nevertheless, STICS was able to reproduce the low yield for the wheat intercropped with faba bean, but

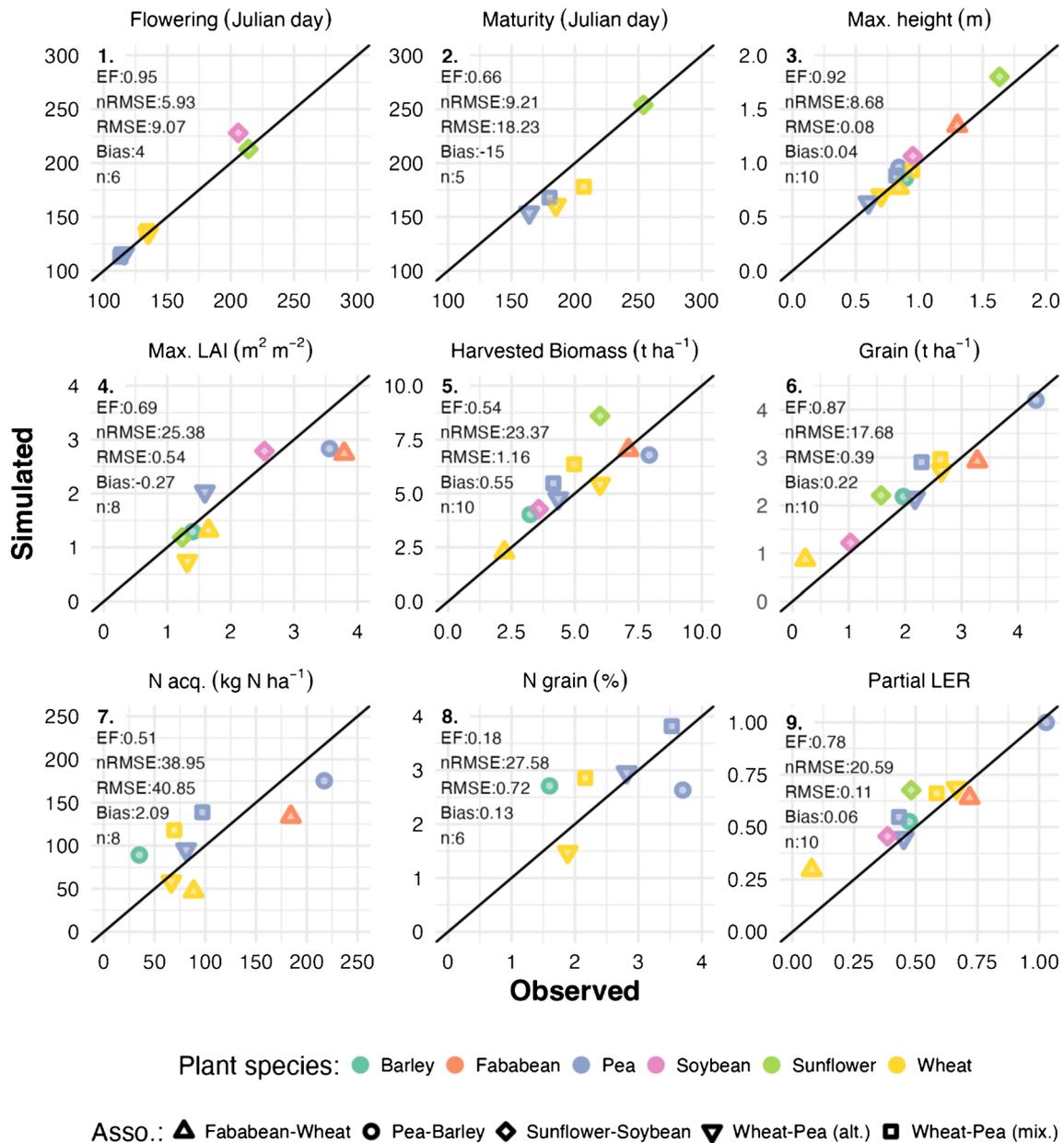


Fig. 6 Observed (x) and simulated (y) values of contrasting intercroops at critical stages. 1. Julian date of flowering (Flowering), and 2. Physiological maturity (Maturity), 3. Maximum plant height (Max. height), 4. Maximum leaf area index (Max. LAI), 5. Aboveground biomass at harvest (Harvested biomass), 6. Grain yield (Grain), 7. N acquisition in the aboveground biomass at harvest (N acq.), 8. N content in the grains at harvest (N grain), and 9. Partial land equivalent ratio (Partial LER, crops with values above 0.5 are over-yielding). Symbols are colored by plant species and shaped by cropping system. The parameters of the model were optimized on sole crop systems and then used without any recalibration to simulate the intercrop systems.

still overestimated its value (Fig. 6.6). This observation was particularly low for 2007 intercroops (0.23 t ha^{-1}) compared to subsequent years (1.51 t ha^{-1} in 2010; 2.11 t ha^{-1} in 2011) which suggests that the model’s overestimation may have resulted from factors and processes that are not considered by the model for now. As expected, the error was then reflected in the simulated partial LER (Fig. 6.9), but had relatively little effect on the overall predicted LER

of the intercrop, with a normalized error of 18% (Table 2). Partial and total LER are particularly difficult to simulate because they both require accurate simulations of the sole crop and the intercrop. A good surprise was that STICS was able to correctly simulate the performance of intercrop in terms of the partial LER calculated from the output variables simulated, with an EF of 0.78, an nRMSE of 21%, and a bias close to zero. Furthermore, the total LER

Table 2 Observed (obs.) and simulated (sim.) land equivalent ratio (LER) and the normalized error (%) computed as (sim.-obs.) / obs. for different species mixtures and intercropping designs.

Association	Intercropping design	Obs. LER	Sim. LER	Norm. error (%)
Faba bean-Wheat	Alternate rows	0.8	0.94	18
Pea-Barley	Alternate rows	1.5	1.53	2
Sunflower-Soybean	Alternate narrow strips	0.87	1.13	30
Wheat-Pea	Alternate rows	1.12	1.13	1
Wheat-Pea	Mixed	1.02	1.21	19

of intercrops presented a relatively low normalized error of 14% in average over all systems, with a minimum at 0.8% for wheat-pea (alternate rows) intercrops, and a maximum error of 30% for sunflower-soybean (Table 2), which is a correct performance considering the challenge of predicting LER, as it is resulting from numerous dynamic processes occurring during the whole crop season (Justes et al. 2021). Using STICS for applied expertise may need an even higher level of accuracy from the model. However, the model's ability to effectively simulate the trends between various species associations and spatial designs of intercropping systems, coupled with its low bias when compared to observations, indicates that it is already suitable for conducting reliable intercomparisons of different agricultural systems and scenario analyses.

Plant height simulations were very close to observations, with little bias (0.04 m) and a high EF, which is crucial for the simulation of light capture and interspecific competition for the two species. However, STICS slightly underestimated the LAI at the end of the growing season (−20%) for the pea intercropped with barley (Fig. 5.3), which in turn reduced its aboveground biomass (−14%, Fig. 5.1) and N acquisition (−19%, Fig. 5.4). However, these errors did not affect the prediction of grain yield, which was very close (−3%) to levels observed (Fig. 6.6).

Overall, STICS was able to simulate all key measured variables as evidenced by the consistency between simulations and observations in all intercrops tested, where the prediction of grain yield, for instance, had an nRMSE of 18%, an EF of 0.9 and a low bias towards overestimation (0.2 t ha^{−1}, Fig. 6.6). The accuracy of the model was “very good” for this variable according to the classification proposed by Coucheney et al. (2015), as for the flowering, maximum plant height, and partial LER. The simulation of maturity and maximum leaf area demonstrated a “good” performance, while the harvested biomass and N acquisition showed “satisfactory” performance. However, the N concentration in the grains was determined as “unsatisfactory” (see Figure A2 for further details). These findings suggest that our current formalism for simulating N concentration in grain needs to be improved for simulating the process of N assimilates transfer to grains in intercropping.

The improved version of STICS is promising and performed relatively well in comparison to other available models, and globally in the same range than the measurements in experiments. For example, the APSIM model was recently used to simulate maize and soybean with different row arrangements of strip or mixed intercropping (Wu et al. 2021). This model was applied using parameters derived from intercropping experiments and found to predict key variables with an nRMSE of 7.6–11.6% for final biomass and 4.8–11.4% for grain yield. It was also applied on a pearl millet-cowpea intercrop with a resulting nRMSE of 64% for LAI dynamic, 55% for biomass dynamic, and 44% for grain yield (Nelson et al. 2022). The M3 crop model was applied on a wheat-faba bean intercrop and presented an average RMSE over the two crops of 0.78 m² m^{−2} for LAI dynamic, 0.64 t ha^{−1} for aboveground biomass dynamic and 0.43 t ha^{−1} for yield (Berghuijs et al. 2020). The previous standard version of STICS was also recently calibrated for chickpea and wheat, and reached modeling efficiency of 0.23 for the chickpea yield and 0.48 for the wheat (Kherif et al. 2022). Considering the high modeling efficiency value (0.9) obtained with the new version of STICS with an independent evaluation using the improved formalisms, we can expect significantly more accurate predictions for given situations, by either directly using STICS, or by implementing the new formalisms in other models. More importantly, STICS was able to reproduce with high accuracy the grain yield and the partial LER and total LER, which were calculated using simulated variables. This accuracy is crucial when employing the model as a tool to study new systems computationally, such as intercropping systems versus traditional sole crops. Additionally, the model proves valuable in estimating output variables that are not directly measured in field experiments, particularly environmental outputs like drainage (Tournebize et al. 2004), NO₃ leaching (Schnebelen et al. 2004; Constantin et al. 2012; Jégo et al. 2012), emissions of CO₂ (Wattenbach et al. 2010) and N₂O (Plaza-Bonilla et al. 2018), and organic C content in the soil (Justes et al. 2009; Levvasseur et al. 2021).

It should be noted that the formalisms proposed and implemented in this study, and more generally STICS, were only calibrated on sole crops and applied with sole crop

parameter values on intercrop simulations, the hypothesis being that STICS should simulate all interactions directly rather than adding or tuning parameters. STICS successfully simulated different intercropping systems regardless of soil, weather conditions, fertilization, irrigation regimes, and spatial complexity as a first evaluation: from the well-mixed wheat-pea and barley-pea canopy to the wheat-faba bean and sunflower-soybean system known for its vertical and horizontal heterogeneity, indicating its potential genericity for simulating arable bi-specific intercrops. Our results showed that the combination of the new simple formalisms implemented proved sufficient to reproduce the main processes at play in arable intercrops such as competition and complementarity in the processes governing light interception, N balance, and water fluxes of the intercropping systems.

Of all the new formalisms implemented in STICS, one stands out particularly for its relevance and accuracy, yet of a relative simplicity: the computation of plant height using the phasic development of the crop based on the thermal time corrected by (i) vernalization and photoperiodic effects, (ii) abiotic stresses on stem elongation rate, and (iii) shading on etiolation of plants in intercropping. To the contrary of the initial formalisms that used the crop LAI (Corre-Hellou et al. 2009), the new algorithm was generic enough to provide accurate simulations for both sole crops and intercrops using the parameter values optimized on sole crops. This is particularly interesting because plant height was repeatedly identified as one of the most important factors for intercrop simulation because of its role in determining competition for light (Corre-Hellou et al. 2009; Launay et al. 2009; Berghuijs et al. 2021). The new formalism can be introduced into other crop models, the only crucial requirement being the correct simulation of the species developmental stages.

3.4 Model limitations and improvements

STICS can be applied to a wide range of bi-specific intercrops where the planting design allows direct interspecific plant-plant interactions for resources between the two crops. The type of spatial design to avoid using the proposed formalisms is a horizontally heterogeneous canopy with no strong dominance between species, e.g. crops grown further apart with the same height, or crops grown in wide strips with interaction only at the interface of both crops. Although the threshold value for the acceptable width of the strip has not yet been determined, we recommend not simulating large strip intercrops with a strip width superior to the plant height or to the horizontal root distribution, in agreement with the concepts used in the model. Our results showed that STICS can simulate strip intercrops with narrow width and few rows (i.e. 2 to 3 close rows per strip), which were found to exhibit the most benefits from intercropping (van Oort et al. 2020). Intercropping systems that are more spatially complex are excluded

from the validity domain unless proven otherwise and probably need to be simulated using a 3D approach. They may include low-density agroforestry systems or intercrops that do not present a periodic row-manner of mixing (e.g. one row of one crop, then two of the other, and two of the first one). Although not considered in this study, on a conceptual basis, STICS can also simulate bi-varietal or population mixtures, relay intercropping and all intercrop mixtures using two set of plant parameters, for spatial designs of mixtures within the row and in alternate rows. Overall, we show for the first time an implementation of a complete set of formalisms that are generic enough to simulate properly different types of inter-specific plant-plant interactions regardless of the two species intercropped. These formalisms are simple enough to parameterize and fast to compute, which is required for long-term simulations and mathematical optimization of parameters that need repeated execution of the model until convergence of the statistical criteria. The new formalisms implemented for intercrops were developed to share the sole crop code-base, thus enabling free transfer of future improvements of the model to intercrop simulations. For example, there is an opportunity for future studies to refine the formalism concerning the N demand calculation, which can lead to improved simulations of N acquisition in aboveground biomass and N content in grains.

While the evaluation of the model based on a limited number of data points in this study may raise concerns (5 to 83 observations depending on the variable), it is crucial to consider that the model in question is a process-based model, rather than a statistical model. Notably, the model was not specifically calibrated (or trained) to simulate intercrop systems but instead calibrated on the sole crop system. Consequently, the accuracy of the model when applied to intercrops demonstrates its ability to replicate such systems successfully without prior knowledge of species interactions.

However, it is worth noting that further investigation is necessary to comprehensively assess the new formalisms across a wider range of conditions, including climates, soils, species, and associations. If the model proves to generalize effectively under these varied conditions, it could serve as a valuable tool for addressing present and future challenges. For instance, it could aid in generalizing intercropping results from one site to another or facilitate virtual screening of innovative intercropping systems that are sustainable, easily manageable, and well-suited to local conditions, both currently and in the future.

4 Conclusion

In this study, we present a new version of the STICS model that includes important processes for both sole crop and intercropping systems, such as development,

light interception, plant growth, N and water balance, and yield formation. The formalisms included in the model are designed to be generic and sufficiently simple to understand and parameterize, making the model well-suited to address current challenges in agriculture such as promoting sustainability while maintaining production. The results of this study show that the STICS model has a relatively high consistency, with an nRMSE of 25% for maximum leaf area index, 23% for shoot biomass at harvest, 18% for yield, 28% for the N content in the grains (28%), and a higher error of 39% for the N acquired in the aboveground biomass at harvest. This indicates that the model is relevant and capable of accurately capturing the functional dynamic behavior and yield of bispecific intercropping systems.

The new version of STICS aims to capture the interactions in intercropping bispecific systems by incorporating a comprehensive set of formalisms. This is the first time that such a comprehensive approach has been taken to describe the complex relationships between crops and their environment in intercropping systems. The model was evaluated using a data-driven approach to determine its consistency, genericity, and accuracy. The results of this evaluation showed good agreement with observed results for a variety of species mixtures. The model was able to reproduce the trends in crop response to changes from a sole crop to a bispecific intercrop design and even showed evidence of niche complementarity for N sources in legume-based mixtures.

The implementation of our new formalisms into STICS provides a promising step forward in this direction by providing a comprehensive and robust description of the interactions in intercropping systems as a proof of concept and a first practical demonstration. By including the most important processes for intercropping systems, the model has the potential to help researchers to support the development of more sustainable and locally adapted intercropping systems. The genericity of the model also makes it well-suited to generalizing results from one site to another, which is an important step in promoting the wider adoption of sustainable agroecological practices.

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Authors' contributions Conceptualization, RV, EJ, SM, ML, and NG; methodology, RV, EJ, SM, ML, and NG; software, RV, PL, DR; validation, RV; formal analyses, RV; investigation, RV; resources, EJ, NG, SM; data curation, NG, SM, RV; writing—original draft, RV, EJ.; writing—review and editing, RV, EJ, SM, ML, and NG; visualization, RV; supervision, EJ; project administration, EJ; funding acquisition, EJ.

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Data availability The data used in this study is available in a Zenodo archive (Vezy et al. 2023c). The parameter values are all available from the specific input files for each species, soil, site, meteorology, and crop management.

Code availability The source code of STICS and the code needed to replicate the simulations, statistics, and figures of this study are available in open access from a Github repository (<https://github.com/VEZY/STICS-IC-paper>) and replicated on the Zenodo archive (Vezy et al. 2023c). The simulations, parameter value optimizations, analyses, and graphical visualizations were performed using the “SticsRPacks” suite of R packages (Vezy et al. 2023b).

The new version of STICS included 177 commits with a total of 220,978 additions and 108,471 deletions. The changes were applied to the source-code of the STICS version 8.5, and the formalisms are planned to be included in the upcoming version of STICS in the coming months, in order to provide a version 11 of the standard STICS model.

Declarations

Ethics approval Not applicable

Consent to participate Not applicable

Consent for publication Not applicable

Competing interests The authors declare no competing interests.

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