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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 for simulating key interactions in 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, Sunflower-Soybean, 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 yield).

This is the first time a complete set of formalisms has been developed and published for simulating 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

Introduction

Modern agriculture needs to develop transition pathways towards sustainable, resilient, agro-ecological cropping systems. Cropping system diversification using multispecies crops or 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 et al. 2018; Jensen et al. 2020; Tilman 2020; Yin et al. 2020; Beillouin et al. 2021; Li et al. 2021). However, these benefits require plant complementarity and facilitation processes to outperform competitive interspecific interactions (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 bi-specific intercrops. 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 and a fast computation time. Some attempts have been made to adapt existing classical 1D sole crop models to bi-specific intercrops, for instance STICS (Brisson et al. 2004), APSIM (Keating et al. 2003) and CROPSYST (see Chimonyo, Modi, et Mabhaudhi (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 interactions 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 crop performance. Berghuijs et al. (2021) found that APSIM overestimates faba bean performance compared to the associated wheat crop, probably due to a poor simulation of plant height 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, thus providing the first relevant basis for simulating bi-specific intercrops (Brisson et al. 2004; Launay et al. 2009; Kherif et al. 2022), 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. Corre-

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70   Hellou et al. (2007, 2009) had difficulties in computing light competition related to poor simulation of

71   plant height, an issue also found in APSIM (Berghuijs et al. (2021) that can be critical for obtaining a

72   correct simulation. We also identified some discrepancies between observations and simulations for

73   STICS using a database from works published by Bedoussac (2009) and Bedoussac and Justes (2010)

74   in a preliminary work, indicating that the model needs further improvements before being used with

75   confidence for simulating scenarii. Those discrepancies were found in the computation of Leaf Area

76   Index (LAI), aerial and belowground biomass, N acquisition and light interception using the radiative

77   transfer option; a formalisms published two decades ago (Brisson et al. 2004).

78   The challenge of properly simulating intercrops with formalisms that are easy to integrate into 1D soil-

79   crop models, with few parameters, correct accuracy and genericity involve designing or revisiting both

80   scientific concepts and software algorithms. In this study, we considered that the main processes in

81   interaction in the intercropping system were the light interception, microclimatic conditions, nitrogen

82   acquisition and water uptake (Figure 1). Consequently, the three-fold objectives of our work exposed in

83   this paper are to:

84   (1) Review the formalisms in the initial 1D soil-crop STICS model related to those processes and

85   evaluate the consistency of the algorithms;

86   (2) Propose new simple, yet powerful novel formalisms to improve the simulation of the main

87   processes in the initial version (1D model), which were considered unsatisfactory, and evaluate

88   their relevance;

89   (3) Evaluate the genericity and validity domain of these new formalisms implemented in STICS

90   using both a conceptual assessment and a comparison with observations for various types of

91   arable bi-specific intercrops of winter and spring legume-based intercrops associated with cereal

92   or sunflower with a wide range of measured agronomic plant traits.

93   These goals were investigated keeping in mind several constraints and choices. First, the formalisms

94   had to be generic, simple and robust. Second, the number of parameters had to be minimal with

95   parameters derived from sole-crop data without the need for any re-calibration to simulate intercrops.

96   Last, the formalisms implemented in STICS had to generate a similar or lower range of error for bi-

97   specific intercrops compared to sole crops to ensure they could be used for *in silico* comparisons of

98   species mixtures or management, for example by calculating their land equivalent ratio as shown by

99   Launay et al. (2009).

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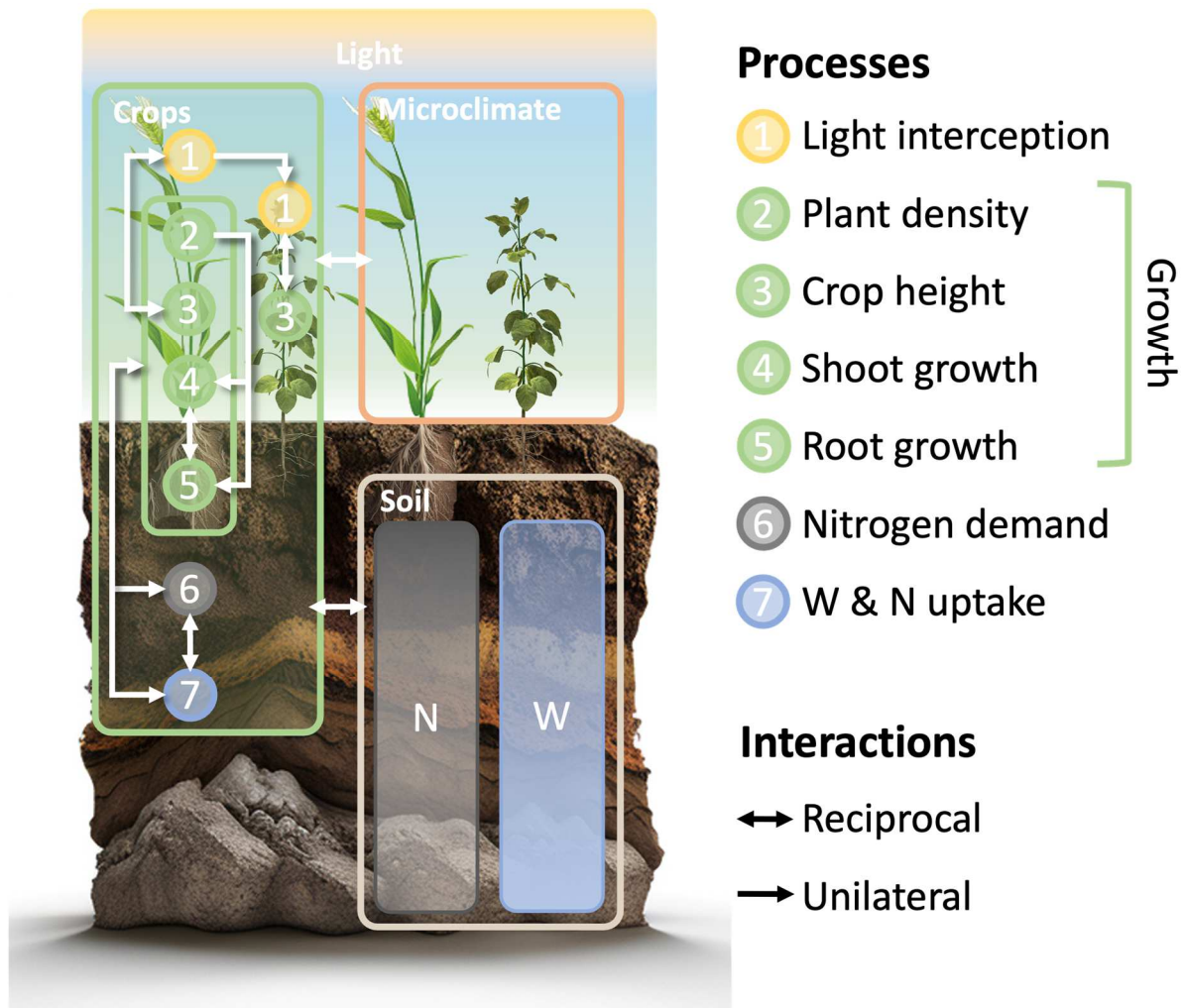
Figure 1. Conceptual diagram of the processes reviewed and modified in STICS (simulated in the voxel scale of the model) for the interactions in the intercropping system. The diagram does not represent all interactions in the model, only the ones that were investigated in this work, which include: light 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.

Material and methods

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, nitrogen, energy and water cycles of the soil-crop system (Brisson et al. 1998, 2003, 2008; Beaudoin et al. 2022). 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 nitrogen content of each soil layer. The crop is represented as a set of organs with a given development stage, biomass and nitrogen content. The biomass growth is mainly driven by light interception as a function of leaf area index with a big leaf approach, *i.e.* using the so-called Beer-Lambert law of light extinction coupled with a radiation use efficiency, while crop development is driven by thermal time corrected by vernalization and photoperiodic effects. Stress effects from frost,

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117   insufficient supply of nitrogen or water, and root anoxia can all potentially affect development, leaf area,

118   growth and yield.

119   The STICS model was adapted to simulate bi-specific crop mixtures in alternate rows by Brisson et al.

120   (2004) and further by Launay et al. (2009). Both crop species are simulated sequentially starting from

121   the *a priori* dominant one (*i.e.* the taller one) and the model simulates several interactions between the

122   two crops, allowing inversion of dominancy during the crop cycle. These interspecific interactions were

123   reviewed and are described below and this paper focus on new formalisms proposed for the

124   improvement of some processes that were found incorrect or not sufficient to simulate daily plant-plant

125   interactions.

126   In this paper, we only describe the formalisms that were modified in or added to STICS (see

127   supplementary materials for more details). The other equations are available from the first version

128   published by Brisson et al. (2004), in other previous papers (Brisson et al. 1998, 2003) and in the STICS

129   book detailing all equations and associated information (Brisson et al. 2008; Beaudoin et al. 2022).

130   In addition, various bugs were fixed in the algorithms, mainly in the computation of light capture, leaf

131   senescence, effect of frost and energy balance, that are not all detailed in this paper.

Modifications of the model

Radiative transfer

134   The radiative transfer option (Brisson et al. 2004) is a module corresponding to a simplified version of

135   a more complex 3D projection of the crop with homogeneous structure within the row. In the case of bi-

136   specific intercrops, the same computation for light interception is applied iteratively for each crop using

137   only the transmitted light as a medium, without any explicit knowledge of the shape of the other crop.

138   This formalism was found relevant and only computation bugs were corrected (see supplementary

139   material).

Beer-Lambert law of light extinction

141   The radiative transfer formalism is generic and allows simulating a wide range of intercropping designs

142   with heterogeneous canopies due to the relative independence between the shapes of both crops.

143   However, some intercrops present well mixed canopies, where the assumption of spatially divided crop

144   canopies or dominance in terms of height is not verified. Therefore, a simpler approach to account for

145   intercrops with well-mixed canopies of the two species was also implemented as a second option to

146   simulate light capture. This new formalism uses the Beer-Lambert law of light extinction in plant

147   canopies adapted for intercropping (Keating and Carberry 1993) by considering the leaf area index and

148   extinction coefficients of both crops.

5

Plant density effect

150 When simulating a classical sole crop, the intraspecific competition for light interception and growth is

151 computed using a density effect (S_D). This effect is used to downregulate the growth of the crop with

152 higher plant density (Brisson et al. 2003, 2008). The same algorithm is now used in bi-specific intercrops

153 to represent the intra-row competition, but using twice the intercrop plant density to use the same

154 parameters determined on sole crops, *i.e.* conceptually a sole crop can be viewed as an intercrop of a

155 crop with itself.

156 **Plant traits and dimensions**

157 The crop canopy height was computed using the LAI for sole crops, and is often ignored by users

158 because it has no impact on other output variables in STICS, except when using the radiative transfer

159 option, which was previously mandatory for intercrops (Brisson et al. 2003, 2008). The calculation of

160 crop height was previously found inconsistent over the course of the crop development, and in particular

161 after the flowering stage (Corre-Hellou et al. 2009). We developed a new formalism that computes plant

162 height using crop phasic development instead, with an implementation based on the same approach

163 proposed by Gou et al. (2017) and Berghuijs et al. (2020), but with some refinements, mainly concerning

164 the addition of the effect of stresses (see supplementary materials).

165 The height of a crop can also be up- or down-regulated in response to stresses, such as light competition

166 with another species, drought, root anoxia, low nitrogen availability and frost. The resulting integrated

167 effect arising from those individual stresses is computed as the minimum of all down-regulating effects,

168 and the up-regulating effect (*i.e.* the shoot elongation) separately, which are both applied to the daily

169 height increment.

170 The magnitude of the elongation of the crop height can theoretically change with the associated species

171 depending on light quantity and quality, *e.g.* a proxy of the photomorphogenetic effect. However, the

172 type of response, *i.e.* shade avoidant or shade tolerant, remains stable based on the plant species. Hence,

173 we implement a formalism that elongates the stem of the plant based on the relative surface of the plant

174 that is shaded and a parameter of maximum elongation effect when the species is fully shaded.

175 **Nitrogen demand**

176 The nitrogen (N) uptake of the crop depends on its N demand, N availability in the soil layers and root

177 exploration. The latter is computed using the rooting depth and the root length density along the soil

178 profile. The N requirements are computed using a dilution curve that relates the crop aboveground

179 biomass to its N concentration (Corre-Hellou et al. 2009). The underlying hypothesis is that leaves have

180 a higher N content compared to other organs, and as the plant/crop grows, the proportion of leaves

181 compared to structural organs (*e.g.* straw) decreases, thereby diluting the N content in the aboveground

182 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, plants cannot always offset the effect of lower density in intercropping, because they are in competition with plants of other species. Therefore, the expected biomass per ground surface area for a crop grown in mixture at a given development stage is often lower than its counterpart in sole crop, hereby artificially increasing its N demand because the dilution curve uses parameters fitted on sole crops. 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).

Water and nitrogen competition and complementarity

In addition to light interception, other competition and complementarity for water and N are mainly determined by the presence and density of roots in the soil layers over the entire soil profile.

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).

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 et Wallace (1985).

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217   This approach is relatively simple and coherent to simulate canopy temperature in intercropping, and

218   was kept in its original formalism.

219   **Spatial designs that theoretically define the validity domain of STICS**

220   Before simulating intercrops with the improved version of STICS, the user should address how the two

221   crops interact in the soil-intercrop system, and whether these interactions are correctly considered in the

222   model. Based on the main processes described above, STICS is able to simulate intercropping in

223   alternate rows (each species in a different row, inter-row set to distance between rows of the same

224   species) and mixed within-row (inter-row set to distance between each row). These two intercropping

225   spatial designs can be simulated for any plant density as long as their root distribution can be assumed

226   horizontally homogeneous. For the light interception, the geometrical approach should be used for

227   heterogeneous canopies, but only for crops with homogeneous canopies along the row, and as long as

228   there is a dominant plant. If not, the option of Beer-Lambert approach for intercrop canopies should be

229   used.

230   The type of spatial design to avoid using the proposed formalisms is a horizontally heterogeneous

231   canopy with no strong dominance between species, *e.g.* crops grown further apart with the same height,

232   or crops grown in wide strips with interaction only at the interface of both crops. However, strip designs

233   that present a clear dominant crop sown in one or few narrow rows should conceptually be in the domain

234   of validity of the model as each strip is represented as a single averaged row. Users should only simulate

235   narrow strips relative to crop dimensions, because the model has a pseudo 3D representation based on

236   the assumption of interactions for light, temperature, nitrogen and water between both crops.

237   Consequently, this assumption might fail for wider strips, where species interactions are mostly limited

238   to the border rows of the strips leading to a clear spatial and strong heterogeneity in the plant-plant

239   interactions at the whole canopy level.

240   In addition, theoretically and technically, STICS is also able to simulate relay intercropping in alternate

241   rows -or with the second crop sown in the inter-row of the first crop- where the two species are not

242   sown, neither harvested, at the same time; however, we have not tested this type of intercropping in this

243   paper by unavailable observed data.

244   Finally, and as a rule of thumb, the improved version of STICS can simulate a wide range of bi-specific

245   intercrop system that presents the following three characteristics:

246   - root systems that interact horizontally, for soil layers where both root systems are present;

247   - shoots forming a canopy that is at least homogeneously distributed in the row;

248   - shoots interacting for light capture, either mixed or with a significant or large dominance

249   between the two species, the dominance may change over time.

250   **Methodology for the calibration and evaluation of STICS**

Parameter calibration

The parameters and options of STICS were first calibrated manually using data from literature and expert knowledge. Then, an automatic calibration was performed based on the recommendations of Guillaume et al. (2011) and Buis et al. (2011) on the most influential parameters following the same procedure consisting of 15 steps of calibration for 25 parameters optimized over 13 variables; there were identified both by expertise and sensitive analysis. 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 "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 minimizing the risk of converging to a local minimum. Analyzes of the estimated values were performed to investigate whether the initial values had any impact on the optimized value.

Parameters calibrated for intercrops

The new formalisms of STICS were designed to be calibrated on sole crops and then applied to intercrops without any further parameterization. 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 interspecific interactions and the balance between dynamic competition and complementarity are emerging properties of the model functioning.

The formalisms implemented only need two parameters to be calibrated when necessary for the simulation of bi-specific intercrops: i) a threshold for the difference in crop height activating the dominance effect, and ii) elongation effect due to shading (*i.e. ep* from equation (11)). The former defines the threshold of difference in plant height under which both canopies are considered well-mixed and 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 of the validity domain of the 1D and 3D representations. 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.

9

Combination of strategies to evaluate the relevance and the genericity of 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 in detail using a purely conceptual approach with the hypothesis that it should provide the same results when simulating a sole crop as usual or simulating the same sole crop using the intercrop formalisms. 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 algorithm. We refer to these simulations as "self-intercrop", where sole crops are simulated by considering half a sole crop combined with another half same sole crop. 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. Our hypothesis is that the maximum delay of one-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.

Dataset

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. The experiment included four cropping systems, plants either grown as sole crops or intercrops in a replacement design (half density of sole crops for each species): 1) durum wheat and winter pea in

alternate rows, 2) durum wheat and winter pea mixed on the row, 3) durum wheat and faba bean in
alternate rows, and 4) sunflower and soybean in alternating narrow strips.

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). 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). 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). The last experiment consisted in growing sunflower (cv.
Ethic) and soybean (*Glycine max* (L.) Merr., cv. Ecudor) either in sole crop or strip-intercrop composed
of 1 row of sunflower and 2 rows of soybean.

The second site corresponds to data published by Corre-Hellou, Fustec, and Crozat (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. We used one treatment of this published
paper with spring barley and pea intercrops in alternate rows and the two sole crops with no N fertilizer
application. 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).

Figure 2 represents the five types of intercrops simulated using STICS, and illustrate how the spatial
design tested in the field experiments are represented in the simulation.

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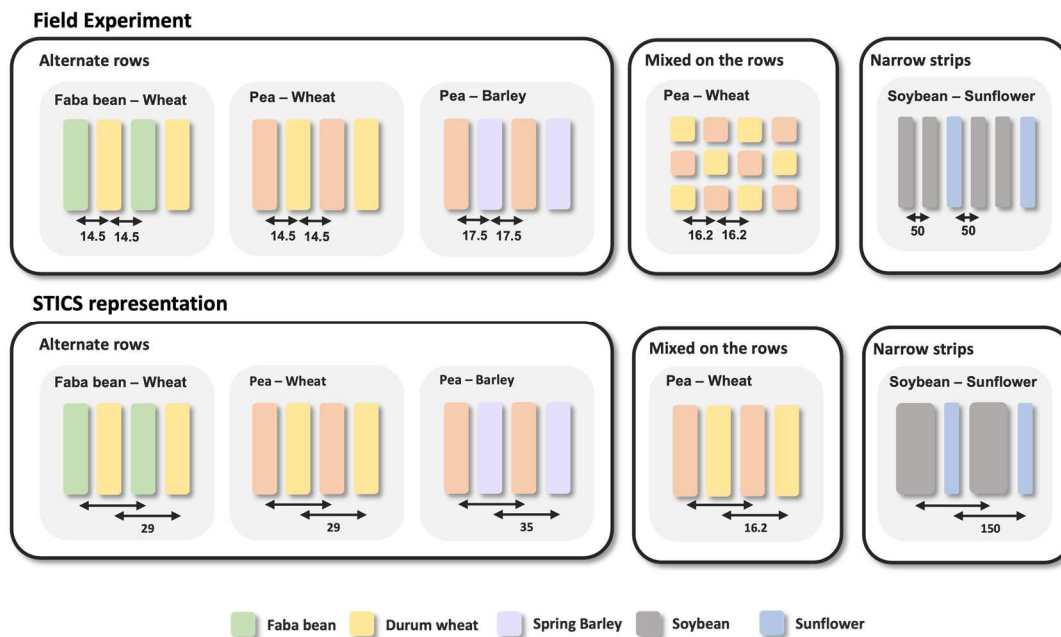
Figure 2. Representation of the five types of intercropping designs tested in the field experiments (up), and how they are represented in STICS (down). In the model, interrow is given for each species independently. Arrows represent the interrow distances (cm) between each row in the field experiment, 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.

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, m^2 m^{-2}), N acquisition (kg N ha^{-1}) and proportion of N fixed by legumes in the aboveground biomass (kg N ha^{-1}) estimated by ^{15}N natural abundance method (Bedoussac and Justes 2010); and iii) grain yield (Grain, t ha^{-1}) and harvest index. Each data point is the result of distinct samples along the crop growth cycle.

Two variables were calculated using either simulations or observations.

First, the ratio of N derived from the atmosphere (*NDFA*, %), computed as follows:

$$NDFA_i = \frac{Qfix_i}{QN_i} \qquad (1)$$

where $Qfix$ 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):

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$$\text{pLER} = \frac{\text{Yield}_{ic}}{\text{Yield}_{sc}} \qquad (2)$$

365 where $Yield_{ic}$ is the grain yield in intercrop and $Yield_{sc}$ is the grain yield in sole crop. A value of $pLER$

366 above 0.5 indicates a higher per-area performance in the intercrop than grown as a sole crop, which is

367 most often called over-yielding. The evaluation of the overall intercrop performance is then made using

368 the *LER* by summing up the $pLER$ of each crop composing the bispecific intercrop (*pLER-species1* +

369 *pLER-species2*) and comparison is made to the reference value of one (for replacement half density

370 design), *i.e.* no difference compared to sole crops.

371 Graphical evaluations and statistics were computed using the CroPlotR package (Vezy et al. 2023) in

372 order to evaluate the quality of calibration of sole crops and the quality of prediction for intercrops. The

373 full description and equations of the statistics are available from the package documentation.

Results and Discussion

Intraspecific interactions

376 The same sole crops were simulated using STICS as a regular sole crop, and as a "self-intercrop", *i.e.*

377 considering twice half of the same species. The purpose of this simulation was to test whether the

378 formalisms governing the simulation of the plant-plant and plant-environment interactions for both types

379 of canopies, the sole and intercrop, are consistent. The "self-intercrop" simulations are close to the

380 regular sole-crop simulations for all variables and all crops (Figure 3) at key stages for all important

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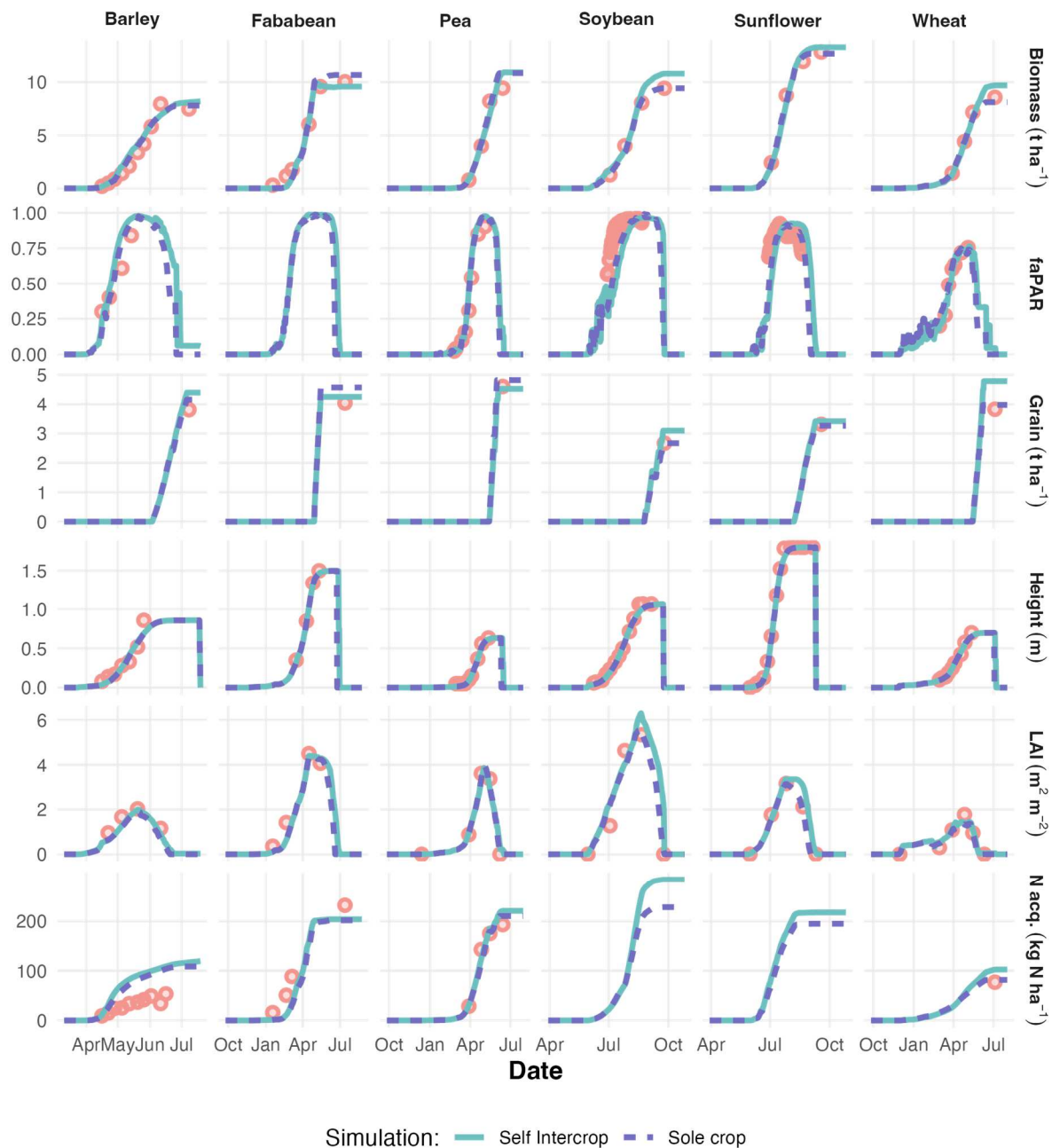
Figure 3. Sole crops either simulated as a regular sole crop or a self-intercrop (half-density intercropped with itself). Simulated variables include from top to bottom: 1. Aboveground biomass (Biomass), 2. Fraction of absorbed photosynthetically active radiation (faPAR), 3. Grain yield (Grain), 4. Plant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

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. There is only a narrow difference between the simulations of all the variables, *e.g.* the difference in plant height is very low (< 0.001 m). The fraction of absorbed photosynthetically active radiation (faPAR) in the "self-intercrop" is the same than in sole crop, with an

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394   average difference of only 0.1% at the maximum value, coupled to an increase of 20.6 kg N ha^{-1} in N

395   acquisition at harvest (+11.9%), leads to an increase in the aboveground biomass at harvest (+0.17 t ha^{-1}

396   , +5.2%) and grain yield (+0.8 t ha^{-1}, +4.4%).

397   The N acquisition is the variable that presents the highest modeling error for soil-crop models, a behavior

398   that was recognized in previous versions of the model (Coucheney et al. 2015), but the difference

399   between the sole crop and self-intercrop remains quite low in comparison to the complexity of the

400   processes to be represented and functioning in dynamic interactions, indicating that any improvement

401   in the sole-crop formalism may directly improve the intercrop simulation too.

402   Another important result is that there is little difference between the two simulation options in the soil-

403   water content and N acquisition, which indicates that the order each species is simulated in the sequence

404   has no substantial effect, *i.e.* the dominant crop may be simulated first and have priority in daily

405   resources acquisition.

406   In this study, we demonstrated that STICS had a consistent behavior in the simulation of both sole crops

407   simulated as usual and as "self-intercrops", which is crucial when analyzing system performances based

408   on sole crops vs. intercrop comparisons with high certainty. These results are a great improvement over

409   previous results using the initial version of STICS developed by Brisson et al. (2008, 2004), which

410   allows to go further in the *in silico* pre-optimization of more intercropping systems and for a wide range

411   of pedoclimatic conditions.

Interspecific interactions

413   The approach with STICS is to calibrate the model on sole-crop data only, and let the model simulate

414   the intercrop interactions without any re-calibration of the parameters, thus facilitating the evaluation of

415   the model's ability to simulate interspecific interactions and possible plant plasticity resulting from

416   calculations as an emerging property. Sole-crop and intercrop simulation results were compared to

417   observations for each individual species to investigate whether STICS simulates species behavior from

418   sole crop to intercrop. In sole crops, the simulations are close to the observations for all variables tested

419   (Figure 4). The plant height is particularly close between cropping systems in observations and

420   simulations. The model underestimates the N derived from the atmosphere (NDFA) from the beginning

421   of the crop growth and until the last measurement, at which point it becomes more accurate.

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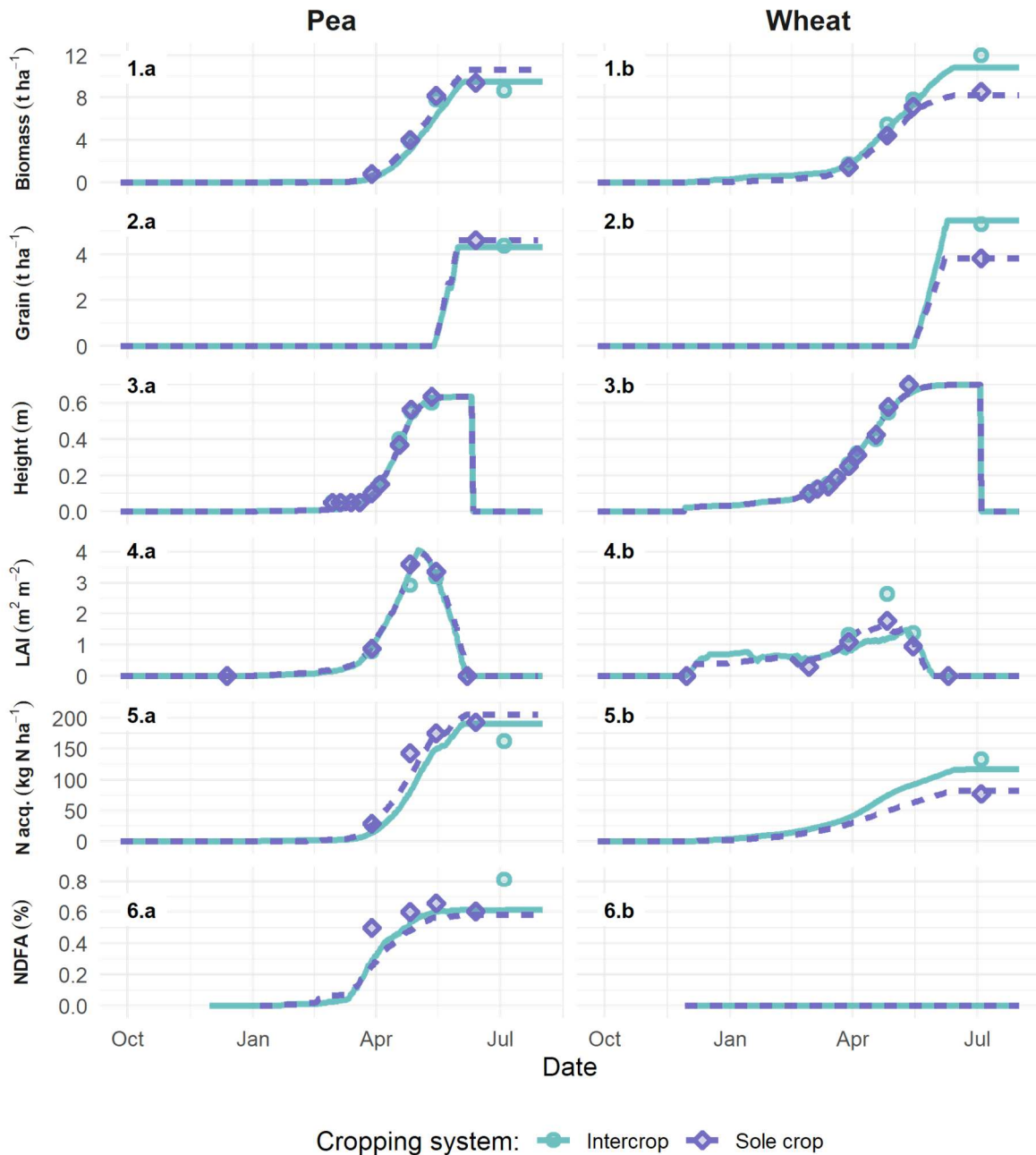
Figure 4. Observed (points) and simulated (lines) 1. Aboveground biomass (Biomass), 2. Grain yield (Grain), 3. Plant height (Height), 4. Leaf area index (LAI), 5. Nitrogen acquisition in the aboveground biomass (N acq.), and 6. Ratio of nitrogen derived from atmosphere (NDFA), for each plant species (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 (x2) 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.

As an example comparison, field observations show that at harvest, the aboveground biomass of the pea is 8% lower and the biomass of wheat is 40% higher when intercropped than when sole cropped. STICS effectively simulates the same behavior, with a decrease of 11% for the aboveground biomass of the pea crop and an increase of 32% for the wheat. The trend is similar for grain yield, LAI and acquired N, and

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434 the model is able to reproduce all these effects, even if the wheat LAI is slightly underestimated when

435 intercropped (Table 1). The results also show that STICS is able to simulate the niche complementarity

436 for N sources, which could also be considered as facilitation on a certain point. Indeed, even if unperfect,

437 the simulation clearly resulted in an increase in N derived from the atmosphere (NDFA, +6%, observed

438 +24%) for the intercropped pea and a considerably higher N uptake by intercropped wheat (+42%,

439 observed +73%) leading to a higher N acquisition by the intercrop compared to the sole crops (Figure

440 4, Table 1), which is a positive property provided by this new version.

441 Overall, the simulations are close to field observations, and more importantly, STICS reproduces all

442 trends observed when a crop is grown as an intercrop rather than a sole crop.

443 **Table 1. Variable change from a sole crop to an intercrop (%),** *i.e.* **difference between a species grown in**
444 **intercrop compared to a sole crop. Values for the intercrop are adjusted (***i.e.* **multiplied by 2) for comparison**
445 **relative to the equivalent total surface area of the two sole crops. Biomass: aboveground biomass at harvest**
446 **(t ha^{-1}), Yield: grain yield (t ha^{-1}), Maximum LAI: maximum leaf area index (m^2 m^{-2}), N acquired: Nitrogen**
447 **acquisition in the aboveground biomass (kg N ha^{-1}), and NDFA: Ratio of nitrogen derived from atmosphere**
448 **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

449 Legume species usually have relatively low competitiveness for soil mineral N uptake compared to

450 cereal crops, thus allowing the latter to develop a better N nutrition status per plant, which initiates a

451 positive feedback loop with increased crop biomass leading to more N uptake thanks to greater root

452 exploration in the soil. During their first development phases, legume crops may experience an increase

453 in the number of nodules due to the soil nitrate concentration that drops off as a result of the greater

454 competition for N uptake by the cereal crop, which also stimulates N_2 fixation rate (Bedoussac and

455 Justes 2010). This niche complementarity for N sources between cereal and legume crops is an important

456 property of this type of intercropping and is precisely what we seek when designing intercrops, *i.e.* a

457 system that is less dependent to N fertilization (Malézieux et al. 2009; Stomph et al. 2020; Tilman 2020).

458 The simulations showed that the improved version of STICS could simulate niche complementarity for
459 N (Figure 4) with a significant increase in N acquisition per plant in wheat crops and in the N_2 fixation
460 rate (NDFA) in pea crops. This increase leads to a higher overall N content in the intercrop canopy
461 compared to cereal sole crop, and to an over-yielding illustrated by a land equivalent ratio (LER)
462 significantly above one (Stomph et al. 2020). These results reflect a particularly interesting emergent
463 property of STICS that is able to simulate niche complementarity without any explicit formalism
464 representing facilitation processes *stricto sensu*, and with equations that require no recalibration or new
465 specific implementation procedure. This is precisely what we seek in soil-crop models, *i.e.*
466 implementing simple and generic formalisms that once coupled make the model able to simulate the
467 functioning of more complex systems by simulating dynamic interactions of processes and emerging
468 properties of the systems. This approach has also proven useful in studies on nutrient stress (Bouain et
469 al. 2019), periodic patterns in plant development (Mathieu et al. 2008; Vezy et al. 2020), environmental
470 impact on plant architecture (Eschenbach 2005) and even population and community dynamics
471 predicted from individual-based algorithms (Hammond and Niklas 2009).

472 Numerous studies have found that plant architecture is influenced by the type of species mixture (Liu et
473 al. 2017). In STICS, we do not implement such behavior explicitly except for the shoot elongation,
474 which was not found significant in the field observations of our data base. Accordingly, simulations for
475 durum wheat were consistent for situations where the crop was dominant (associated with pea) and
476 dominated (associated with faba bean). Such results may indicate another possible emergent property of
477 STICS, showing that plant plasticity in the field may also act as a buffer to behavioral changes when
478 considering plants at the community scale, which could alleviate the need for changes in parameter
479 values (Louarn et al. 2020).

480 Another interesting result is that most of the errors found in the simulation of intercrops were also found
481 with the same level in the sole crops (Figure 3 and Figure 4), indicating that the errors either came from
482 the calibration of the model or from the formalisms shared with the sole crops, an issue not within the
483 scope of this paper. In STICS, new formalisms for intercrops were developed to share the sole crop
484 code-base, thus enabling free transfer of future improvements of the model to intercrop simulations.

Genericity of the formalisms: simulation of contrasted intercrops

486 The genericity of STICS is evaluated in a first approach using intercrops composed of various species
487 mixtures and spatial designs. The model consistently simulates all variables for the various types of
488 intercrops even for the sunflower-soybean intercrop that presents the most spatially heterogeneous
489 system as a narrow strip design with the larger inter-row space. Globally, as shown in Figure , the
490 evaluation indicates a modeling efficiency (EF) equal to or higher than 0.71 for all variables considered
491 dynamically throughout the growing season; this indicates correct performances per se and also in
492 comparison to what is widely published for crop models for classical sole crops.

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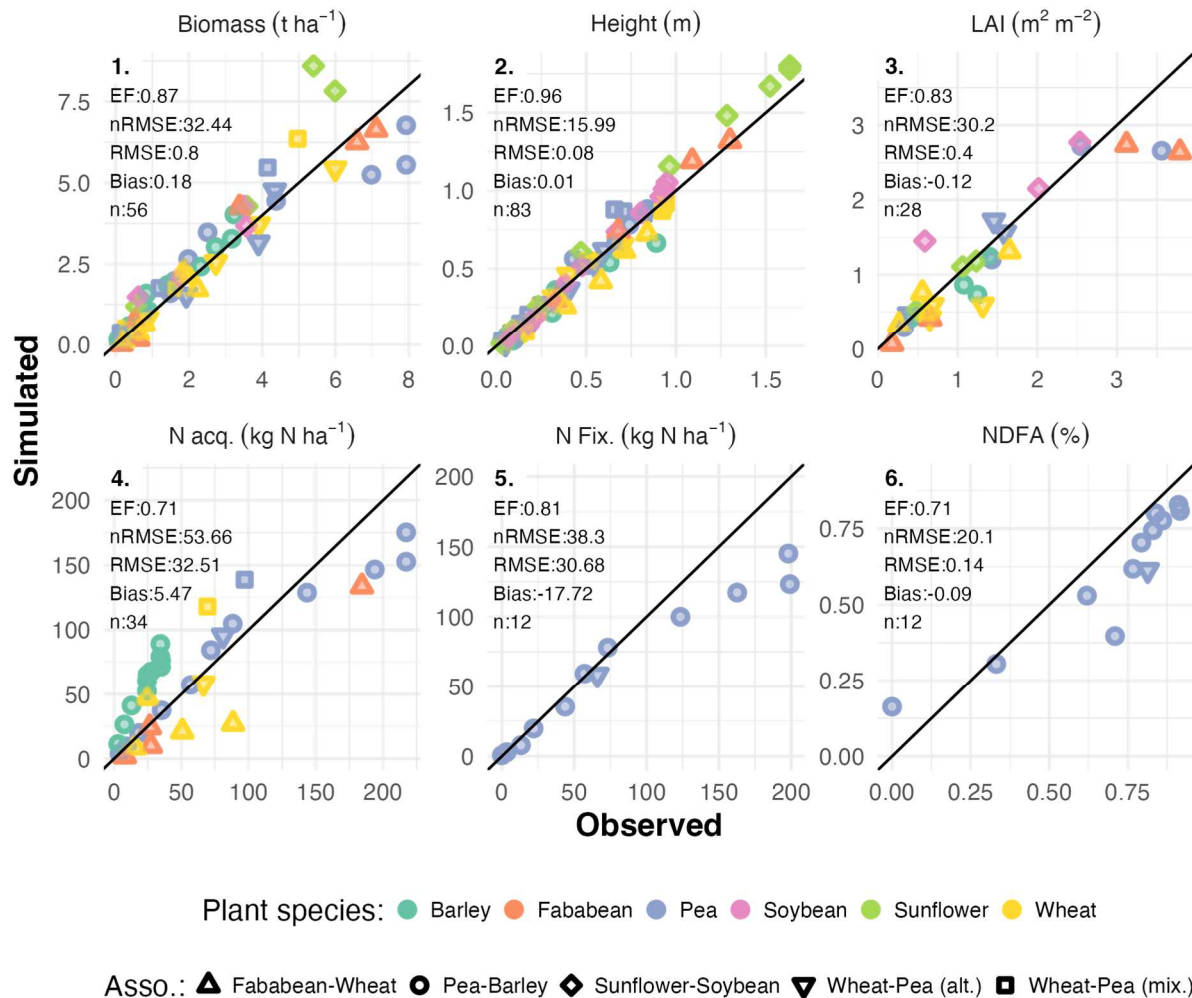
Figure 5. Observed (x) and simulated (y) values of contrasting intercrops for 1. Aboveground biomass (Biomass), 2. Plant height (Height), 3. Leaf area index (LAI), 4. N acquisition in the aboveground biomass (N acq.), 5. Accumulated nitrogen from symbiotic fixation (N Fix.), and 6. Ratio of nitrogen 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.

STICS is also evaluated at critical stages, which requires a more demanding value assessment for the model, but produces a better evaluation of its capability to reproduce the system behavior and dynamic processes at crucial stages and over time. STICS can 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, Figure 6). 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 presents a low bias of 0.13%, which is still encouraging.

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 is that STICS is able to correctly simulate the performance of intercrop in terms of the partial LER calculated from the output variables simulated,

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510   with an EF of 0.78, an nRMSE of 21% and a bias close to zero. Furthermore, the total LER of intercrops

511   presents a relatively low error of 14% in average over all systems, with a minimum at 0.8% for wheat–

512   pea (alternate rows) intercrops, and a maximum error of 30% for sunflower-soybean (Table 1), which

513   is a correct performance relative to the challenge to be met, as LER is the final result of all the dynamic

514   processes occurring during the whole crop season (Justes et al. 2021).

515   **Table 2. Observed (obs.) and simulated (sim.) land equivalent ratio (LER) and the normalized error (%)**
516   **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

517   Plant height simulations are very close to observations, with little bias (0.04 m) and a high EF, which is

518   crucial for the simulation of light capture and interspecific competition for the two species. However,

519   STICS slightly underestimates the LAI at the end of the growing season for the pea intercropped with

520   barley (Figure .3), which in turn reduces its aboveground biomass and N acquisition (Figure .1, Figure

521   .4). However, these errors do not affect the prediction of yield, which is very close to levels observed

522   (Figure 6.6).

523   Moreover, for sunflower-soybean intercrop, sunflower biomass is slightly overestimated which in turn

524   leads to a higher yield and partial LER compared to the observations (Figure .1, Figure 6.6 and 6.9).

525   STICS is able to reproduce the low yield for the wheat intercropped with faba bean, but still

526   overestimates its value (Figure 6.6). This observation was particularly low for 2007 intercrops (0.23 t

527   ha^{-1}) compared to subsequent years (1.51 t ha^{-1} in 2010; 2.11 t ha^{-1} in 2011) which suggests that the

528   model's overestimation may have resulted from factors and processes that are not considered by the

529   model for now. As expected, the error is then reflected in the simulated partial LER (Figure 6.9), but

530   has relatively little effect on the overall predicted LER of the intercrop, with a normalized error of 18%

531   (Table 2).
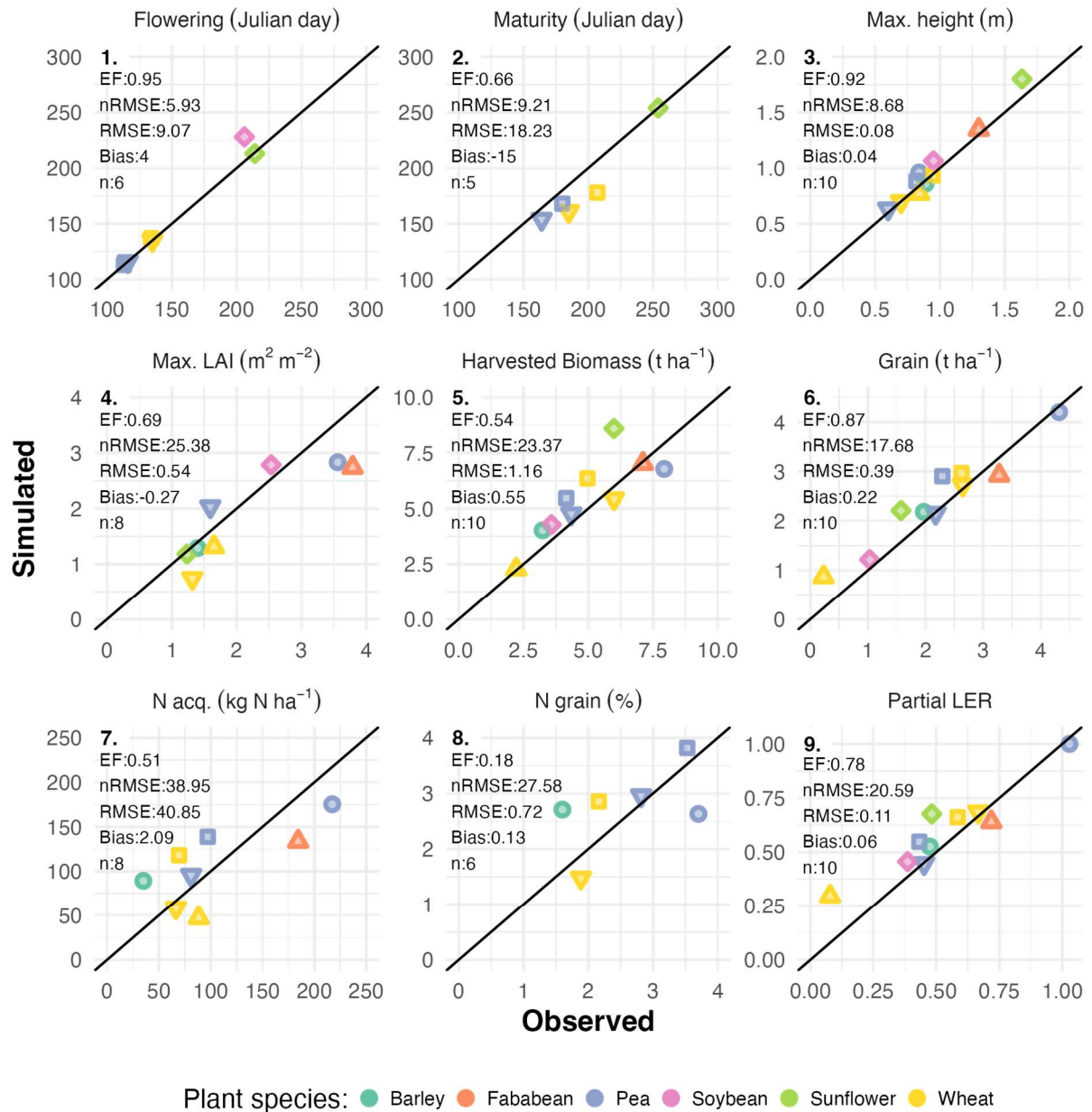
Figure 6. Observed (x) and simulated (y) values of contrasting intercrops at critical stages. 1. Julian date of flowering (Flowering), and 2. Physiological maturity (Maturity), 3. Maximum plant height (Max. height), 4. Maximum leaf area index (Max. LAI), 5. Aboveground biomass at harvest (Harvested biomass), 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.

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}, Figure 6.6).

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544   The improved version of STICS is promising with correct performances in comparison to other available

545   models, and globally in the same range than the measurements in experiments. For example, the APSIM

546   model was recently used to simulate maize and soybean with different row arrangements of strip or

547   mixed intercropping (Wu et al. 2021). This model was applied using parameters derived from

548   intercropping experiments, and found to predict key variables with an nRMSE of 7.6-11.6% for biomass

549   and 4.8-11.4% for grain yield. It was also applied on a pearl millet-cowpea intercrop with a resulting

550   RMSE of 1.1 m2 m-2 for LAI, 1.02 t ha^{-1} for biomass and 0.4 t ha^{-1} for grain yield (Nelson et al. 2021).

551   The M3 crop model was applied on a wheat-faba bean intercrop and presented an average RMSE over

552   the two crops of 0.78 m2 m^{-2} for LAI, 0.64 t ha^{-1} for aboveground biomass and 0.43 t ha^{-1} for yield

553   (Berghuijs et al. 2020). The previous standard version of STICS was also recently calibrated for

554   chickpea and wheat, and reached modeling efficiency of 0.23 for the chickpea yield and 0.48 for the

555   wheat (Kherif et al. 2022). Considering the high modeling efficiency value (0.9) obtained with STICS

556   with an independent evaluation using the improved formalisms, we can expect significantly more

557   accurate predictions for given situations, by either directly using STICS, or by implementing the new

558   formalisms in other models. More importantly, STICS was able to reproduce the partial LER and total

559   LER -calculated from simulated variables- with high accuracy, which is a crucial requirement when

560   using the model as a tool to investigate new systems *in silico* such as intercropping systems versus

561   classical sole crops, and to use the model for estimating output variables not measured in field

562   experiments, in particular all environmental outputs (drainage, NO_3 leaching, CO_2 and N_2O emissions,

563   organic C content in soil, etc.).

564   It should be noted that the formalisms proposed and implemented in this study, and more generally

565   STICS, were only calibrated on sole crops and applied with sole crop parameter values on intercrop

566   simulations, the hypothesis being that STICS should simulate all interactions directly rather than adding

567   or tuning parameters. STICS successfully simulated different intercropping systems regardless of soil,

568   weather conditions, fertilization, irrigation regimes and spatial complexity as a first evaluation: from the

569   well mixed wheat-pea and barley-pea canopy to the wheat-faba bean and sunflower-soybean system

570   known for its vertical and horizontal heterogeneity, indicating its potential genericity for simulating

571   arable bi-specific intercrops. Our results show that the combination of the new simple formalisms

572   implemented proved sufficient to reproduce the main processes at play in arable intercrops such as

573   competition and complementarity in the processes governing light interception, N balance and water

574   fluxes of the intercropping systems.

575   Of all the new formalisms implemented in STICS, one stands out particularly for its relevance and

576   accuracy, yet of a relative simplicity: the computation of plant height using the phasic development of

577   the crop based on the thermal time corrected by i) vernalization and photoperiodic effects, ii) abiotic

578   stresses on stem elongation rate, and iii) shading on etiolation of plants in intercropping. To the contrary

579   of the initial formalisms that used the crop LAI, the new algorithm was generic enough to provide

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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.

More generally, STICS can be applied to a wide range of bi-specific intercrops where the planting design allows direct interspecific interactions for resources between the two 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 interspecific 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. STICS-IC, and any other model that integrates the new formalisms, will be particularly well suited to address current challenges such as generalizing results of intercropping from one site to another, or virtually pre-screening innovative intercropping systems that are more sustainable, easier to manage, and well adapted to local conditions, as a tool for developing research supporting and agro-ecological transition, and to assess the impact of climate change scenarios on sole versus intercrop production and GHG emissions, and also assess if intercrop would be more resilient than the classical sole crops.

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, nitrogen 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

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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, and 18% for yield. This indicates that the model is capable of accurately capturing the behavior 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 nitrogen 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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Declarations

Funding

Competing Interests

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

Availability of data and material

The data used in this study is available in a Zenodo archive (Vezy et al. 2022). 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. 2022). The simulations, parameter value optimizations, analyzes, and graphical visualizations were performed using the "SticsRPacks" suite of R packages (Vezy et al. 2021).

The new version of STICS included 177 commits with a total of 220978 additions and 108471 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.

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 & Editing, RV, EJ, SM, ML and NG; Visualization, RV; Supervision, EJ; Project administration, EJ; Funding Acquisition, EJ.

References

Beaudoin N, Lecharpentier P, Ripoche D, et al (2022) Conceptual framework, equations and uses of the STICS soil-crop model. Quae, Versailles

Beck HE, Zimmermann NE, McVicar TR, et al (2018) Present and future Köppen-Geiger climate classification maps at 1-km resolution. Scientific data 5:1–12

Bedoussac L (2009) Analyse du fonctionnement des performances des associations blé dur-pois d'hiver et blé dur-féverole d'hiver pour la conception d'itinéraires techniques adaptés à différents objectifs de production en systèmes bas-intrants. Theses, Institut National Polytechnique (Toulouse)

Bedoussac L, Journet E-P, Hauggaard-Nielsen H, et al (2015) Ecological principles underlying the increase of productivity achieved by cereal-grain legume intercrops in organic farming. A review. Agron Sustain Dev 35:911–935. https://doi.org/10.1007/s13593-014-0277-7

Bedoussac L, Justes E (2010) Dynamic analysis of competition and complementarity for light and N use to understand the yield and the protein content of a durum wheat–winter pea intercrop. Plant Soil 330:37–54. https://doi.org/10.1007/s11104-010-0303-8

Beillouin D, Ben-Ari T, Malézieux E, et al (2021) Positive but variable effects of crop diversification on biodiversity and ecosystem services. Global Change Biology. https://doi.org/10.1111/gcb.15747

25

680 Berghuijs HNC, Wang Z, Stomph TJ, et al (2020) Identification of species traits enhancing yield in
681 wheat-faba bean intercropping: development and sensitivity analysis of a minimalist mixture model.
682 Plant Soil 455:203–226. https://doi.org/10.1007/s11104-020-04668-0

683 Berghuijs HNC, Weih M, van der Werf W, et al (2021) Calibrating and testing APSIM for wheat-faba
684 bean pure cultures and intercrops across Europe. Field Crops Research 264:108088.
685 https://doi.org/10.1016/j.fcr.2021.108088

686 Bouain N, Krouk G, Lacombe B, Rouached H (2019) Getting to the Root of Plant Mineral Nutrition:
687 Combinatorial Nutrient Stresses Reveal Emergent Properties. Trends in Plant Science 24:542–552.
688 https://doi.org/10.1016/j.tplants.2019.03.008

689 Brisson N, Bussière F, Ozier-Lafontaine H, et al (2004) Adaptation of the crop model STICS to
690 intercropping. Theoretical basis and parameterisation. Agronomie 24:409–421.
691 https://doi.org/10.1051/agro:2004031

692 Brisson N, Gary C, Justes E, et al (2003) An overview of the crop model stics. European Journal of
693 Agronomy 18:309–332. https://doi.org/10.1016/S1161-0301(02)00110-7

694 Brisson N, Launay M, Mary B, Beaudoin N (2008) Conceptual Basis, Formalisations and
695 Parameterization of the Stics Crop Model. Editions Quae, Paris

696 Brisson N, Mary B, Ripoche D, et al (1998) STICS: a generic model for the simulation of crops and
697 their water and nitrogen balances. I. Theory and parameterization applied to wheat and corn. Agronomie
698 18:311–346. https://doi.org/10.1051/agro:19980501

699 Buis S, Lecharpentier P, Vezy R, Giner M (2023) CroptimizR: A Package to Estimate Parameters of
700 Crop Models

701 Buis S, Wallach D, Guillaume S, et al (2011) The STICS crop model and associated software for
702 analysis, parameterization, and evaluation. Methods of introducing system models into agricultural
703 research 2:395–426. https://doi.org/10.2134/advagricsystmodel2.c14

704 Chimonyo VGP, Modi AT, Mabhaudhi T (2015) Perspective on crop modelling in the management of
705 intercropping systems. Archives of Agronomy and Soil Science 61:1511–1529.
706 https://doi.org/10.1080/03650340.2015.1017816

707 Corre-Hellou G, Brisson N, Launay M, et al (2007) Effect of root depth penetration on soil nitrogen
708 competitive interactions and dry matter production in pea–barley intercrops given different soil nitrogen
709 supplies. Field Crops Research 103:76–85. https://doi.org/10.1016/j.fcr.2007.04.008

710 Corre-Hellou G, Faure M, Launay M, et al (2009) Adaptation of the STICS intercrop model to simulate
711 crop growth and N accumulation in pea–barley intercrops. Field Crops Research 113:72–81.
712 https://doi.org/10.1016/j.fcr.2009.04.007

26

713   Corre-Hellou G, Fustec J, Crozat Y (2006) Interspecific Competition for Soil N and its Interaction with

714   N2 Fixation, Leaf Expansion and Crop Growth in Pea–Barley Intercrops. Plant Soil 282:195–208.

715   https://doi.org/10.1007/s11104-005-5777-4

716   Coucheney E, Buis S, Launay M, et al (2015) Accuracy, robustness and behavior of the STICS soil–

717   crop model for plant, water and nitrogen outputs: Evaluation over a wide range of agro-environmental

718   conditions   in   France.   Environmental   Modelling   &   Software   64:177–190.

719   https://doi.org/10.1016/j.envsoft.2014.11.024

720   Eschenbach C (2005) Emergent properties modelled with the functional structural tree growth model

721   ALMIS: Computer experiments on resource gain and use. Ecological Modelling 186:470–488.

722   https://doi.org/10.1016/j.ecolmodel.2005.02.013

723   Falconnier GN, Journet E-P, Bedoussac L, et al (2019) Calibration and evaluation of the STICS soil-

724   crop model for faba bean to explain variability in yield and N2 fixation. European Journal of Agronomy

725   104:63–77. https://doi.org/10.1016/j.eja.2019.01.001

726   Gaudio N, Escobar-Gutiérrez AJ, Casadebaig P, et al (2019) Current knowledge and future research

727   opportunities for modeling annual crop mixtures. A review. Agron Sustain Dev 39:20.

728   https://doi.org/10.1007/s13593-019-0562-6

729   Gaudio N, Louarn G, Barillot R, et al (2022) Exploring complementarities between modelling

730   approaches that enable upscaling from plant community functioning to ecosystem services as a way to

731   support   agroecological   transition.   in   silico   Plants   4:diab037.

732   https://doi.org/10.1093/insilicoplants/diab037

733   Gou F, van Ittersum MK, van der Werf W (2017) Simulating potential growth in a relay-strip

734   intercropping system: Model description, calibration and testing. Field Crops Research 200:122–142.

735   https://doi.org/10.1016/j.fcr.2016.09.015

736   Guillaume S, Bergez JE, Wallach D, Justes E (2011) Methodological comparison of calibration

737   procedures for durum wheat parameters in the STICS model. European Journal of Agronomy 35:115–

738   126. https://doi.org/10.1016/J.EJA.2011.05.003

739   Hammond ST, Niklas KJ (2009) Emergent properties of plants competing in silico for space and light:

740   Seeing   the   tree   from   the   forest.   American   Journal   of   Botany   96:1430–1444.

741   https://doi.org/10.3732/ajb.0900063

742   Jensen ES, Carlsson G, Hauggaard-Nielsen H (2020) Intercropping of grain legumes and cereals

743   improves the use of soil N resources and reduces the requirement for synthetic fertilizer N: A global-

744   scale analysis. Agron Sustain Dev 40:5. https://doi.org/10.1007/s13593-020-0607-x

745   Justes E, Bedoussac L, Dordas C, et al (2021) The 4C approach as a way to understand species
746   interactions determining intercropping productivity. Frontiers of Agricultural Science and Engineering.
747   https://doi.org/10.15302/J-FASE-2021414

748   Justes E, Mary B, Meynard J-M, et al (1994) Determination of a critical nitrogen dilution curve for
749   winter wheat crops. Annals of botany 74:397–407. https://doi.org/10.1006/anbo.1994.1133

750   Kammoun B (2014) Analyse des interactions génotype x environnement x conduite culturale de
751   peuplement bi-spécifique de cultures associées de blé dur et de légumineuses à graines, à des fins de
752   choix variétal et d'optimisation de leurs itinéraires techniques

753   Kammoun B, Journet E-P, Justes E, Bedoussac L (2021) Cultivar Grain Yield in Durum Wheat-Grain
754   Legume Intercrops Could Be Estimated From Sole Crop Yields and Interspecific Interaction Index.
755   Front Plant Sci 12:733705. https://doi.org/10.3389/fpls.2021.733705

756   Keating BA, Carberry PS (1993) Resource capture and use in intercropping: solar radiation. Field Crops
757   Research 34:273–301. https://doi.org/10.1016/0378-4290(93)90118-7

758   Keating BA, Carberry PS, Hammer GL, et al (2003) An overview of APSIM, a model designed for
759   farming systems simulation. European Journal of Agronomy 18:267–288.
760   https://doi.org/10.1016/S1161-0301(02)00108-9

761   Kherif O, Seghouani M, Justes E, et al (2022) The first calibration and evaluation of the STICS soil-
762   crop model on chickpea-based intercropping system under Mediterranean conditions. European Journal
763   of Agronomy 133:126449. https://doi.org/10.1016/j.eja.2021.126449

764   Launay M, Brisson N, Satger S, et al (2009) Exploring options for managing strategies for pea–barley
765   intercropping using a modeling approach. European Journal of Agronomy 31:85–98.
766   https://doi.org/10.1016/j.eja.2009.04.002

767   Li X-F, Wang Z-G, Bao X-G, et al (2021) Long-term increased grain yield and soil fertility from
768   intercropping. Nat Sustain 4:943–950. https://doi.org/10.1038/s41893-021-00767-7

769   Liu X, Rahman T, Song C, et al (2017) Changes in light environment, morphology, growth and yield of
770   soybean in maize-soybean intercropping systems. Field Crops Research 200:38–46.
771   https://doi.org/10.1016/j.fcr.2016.10.003

772   Louarn G, Barillot R, Combes D, Escobar-Gutiérrez A (2020) Towards intercrop ideotypes: non-random
773   trait assembly can promote overyielding and stability of species proportion in simulated legume-based
774   mixtures. Annals of Botany 126:671–685. https://doi.org/10.1093/aob/mcaa014

775   Louarn G, Bedoussac L, Gaudio N, et al (2021) Plant nitrogen nutrition status in intercrops– a review
776   of concepts and methods. European Journal of Agronomy 124:126229.
777   https://doi.org/10.1016/j.eja.2021.126229

28

778 Malézieux E, Crozat Y, Dupraz C, et al (2009) Mixing plant species in cropping systems: concepts, tools
779 and models. A review. Agron Sustain Dev 29:43–62. https://doi.org/10.1051/agro:2007057

780 Martin-Guay M-O, Paquette A, Dupras J, Rivest D (2018) The new Green Revolution: Sustainable
781 intensification of agriculture by intercropping. Science of The Total Environment 615:767–772.
782 https://doi.org/10.1016/j.scitotenv.2017.10.024

783 Mathieu A, Cournède P-H, Barthélémy D, de Reffye P (2008) Rhythms and Alternating Patterns in
784 Plants as Emergent Properties of a Model of Interaction between Development and Functioning. Annals
785 of Botany 101:1233–1242. https://doi.org/10.1093/aob/mcm171

786 Nelder JA, Mead R (1965) A simplex method for function minimization. The Computer Journal 7:308–
787 313. https://doi.org/10.1093/comjnl/7.4.308

788 Nelson WCD, Hoffmann MP, Vadez V, et al (2021) Can intercropping be an adaptation to drought? A
789 model-based analysis for pearl millet–cowpea. Journal of Agronomy and Crop Science n/a:
790 https://doi.org/10.1111/jac.12552

791 Raseduzzaman Md, Jensen ES (2017) Does intercropping enhance yield stability in arable crop
792 production? A meta-analysis. European Journal of Agronomy 91:25–33.
793 https://doi.org/10.1016/j.eja.2017.09.009

794 Shili-Touzi I, De Tourdonnet S, Launay M, Dore T (2010) Does intercropping winter wheat (Triticum
795 aestivum) with red fescue (Festuca rubra) as a cover crop improve agronomic and environmental
796 performance? A modeling approach. Field Crops Research 116:218–229.
797 https://doi.org/10.1016/j.fcr.2009.11.007

798 Shuttleworth WJ, Wallace JS (1985) Evaporation from sparse crops-an energy combination theory.
799 Quarterly Journal of the Royal Meteorological Society 111:839–855.
800 https://doi.org/10.1002/qj.49711146910

801 Singh AK, Goyal V, Mishra AK, Parihar SS (2013) Validation of CropSyst simulation model for direct
802 seeded rice–wheat cropping system. Current Science 104:1324–1331

803 Stomph T, Dordas C, Baranger A, et al (2020) Chapter One - Designing intercrops for high yield, yield
804 stability and efficient use of resources: Are there principles? In: Sparks DL (ed) Advances in Agronomy.
805 Academic Press, pp 1–50

806 Tilman D (2020) Benefits of intensive agricultural intercropping. Nat Plants 6:604–605.
807 https://doi.org/10.1038/s41477-020-0677-4

808 van Oort PAJ, Gou F, Stomph TJ, van der Werf W (2020) Effects of strip width on yields in relay-strip
809 intercropping: A simulation study. European Journal of Agronomy 112:125936.
810 https://doi.org/10.1016/j.eja.2019.125936

29

811   Vezy R, Buis S, Lecharpentier P, Giner M (2023) CroPlotR: A Package to Analyze Crop Model
812   Simulations Outputs with Plots and Statistics

813   Vezy R, Buis S, Lecharpentier P, Giner M (2021) SticsRPacks: Easily install and load `SticsRPacks`
814   packages

815   Vezy R, le Maire G, Christina M, et al (2020) DynACof: A process-based model to study growth, yield
816   and ecosystem services of coffee agroforestry systems. Environmental Modelling & Software
817   124:104609. https://doi.org/10.1016/j.envsoft.2019.104609

818   Vezy R, Munz S, Gaudio N, et al (2022) Data, code and software to reproduce the article entitled
819   "Modelling intercrops functioning to advance the design of innovative agroecological systems"

820   Willey RW, Osiru DSO (1972) Studies on mixtures of maize and beans (Phaseolus vulgaris) with
821   particular reference to plant population. The Journal of Agricultural Science 79:517–529.
822   https://doi.org/10.1017/S0021859600025909

823   Wu Y, He D, Wang E, et al (2021) Modelling soybean and maize growth and grain yield in strip
824   intercropping systems with different row configurations. Field Crops Research 265:108122.
825   https://doi.org/10.1016/j.fcr.2021.108122

826   Yin W, Chai Q, Zhao C, et al (2020) Water utilization in intercropping: A review. Agricultural Water
827   Management 241:106335. https://doi.org/10.1016/j.agwat.2020.106335

828   Yu Y, Stomph T-J, Makowski D, van der Werf W (2015) Temporal niche differentiation increases the
829   land equivalent ratio of annual intercrops: A meta-analysis. Field Crops Research 184:133–144.
830   https://doi.org/10.1016/j.fcr.2015.09.010

831