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# 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 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

## 35 **Introduction**

36 Modern agriculture needs to develop transition pathways towards sustainable, resilient, agro-ecological  
37 cropping systems. Cropping system diversification using multispecies crops or intercropping, *i.e.* two  
38 or more crops with overlapping growing season, and notably cereal-grain legume mixtures is a key  
39 pathway to such agroecological intensification (Malézieux et al. 2009). Transitioning from classical sole  
40 cropping (*i.e.* pure stand on the same species variety) to intercropping can bring many benefits such as  
41 a reduction in fertilizer use, greater drought and disease resistance, higher productivity, pests - diseases  
42 -weeds suppression and increased carbon sequestration (Bedoussac et al. 2015; Yu et al. 2015;  
43 Raseduzzaman and Jensen 2017; Martin-Guay et al. 2018; Jensen et al. 2020; Tilman 2020; Yin et al.  
44 2020; Beillouin et al. 2021; Li et al. 2021). However, these benefits require plant complementarity and  
45 facilitation processes to outperform competitive interspecific interactions (Justes et al. 2021).  
46 Consequently, there is a need for soil-crop models that can examine large combinations of species,  
47 agricultural practices, climate and soil through virtual experiments to evaluate the potential of intercrop  
48 productivity, resilience and sustainability (Gaudio et al. 2022). Soil-crop models are particularly well  
49 suited for such objectives, as they usually simulate the most important processes such as phenology,  
50 light interception, plant growth, yield formation, carbon and nutrient cycles, and water balance (Stomph  
51 et al. 2020).

52 Very few soil-crop models are able to simulate interspecific interactions, even for the simplest case of  
53 bi-specific intercrops. This is mainly due to the difficulty of designing generic and simple new  
54 formalisms that consider the dynamic interactions between plants for all processes while maintaining a  
55 few, easily measurable parameters and a fast computation time. Some attempts have been made to adapt  
56 existing classical 1D sole crop models to bi-specific intercrops, for instance STICS (Brisson et al. 2004),  
57 APSIM (Keating et al. 2003) and CROPSYST (see Chimonyo, Modi, et Mabhaudhi (2015) and Gaudio  
58 et al. (2019) for more details). The first results were encouraging, but some discrepancies were identified  
59 between simulations and observations, mainly due to the lack of an integrative representation of the  
60 processes accounting for the interactions in the soil-crop system. Singh et al. (2013), for instance,  
61 identified high levels of simulated nitrogen (N) uptake for rice using CROPSYST in a wheat-rice  
62 intercropping system as the cause of underestimating crop performance. Berghuijs et al. (2021) found  
63 that APSIM overestimates faba bean performance compared to the associated wheat crop, probably due  
64 to a poor simulation of plant height that affected the simulation of faba bean-wheat competition for light.

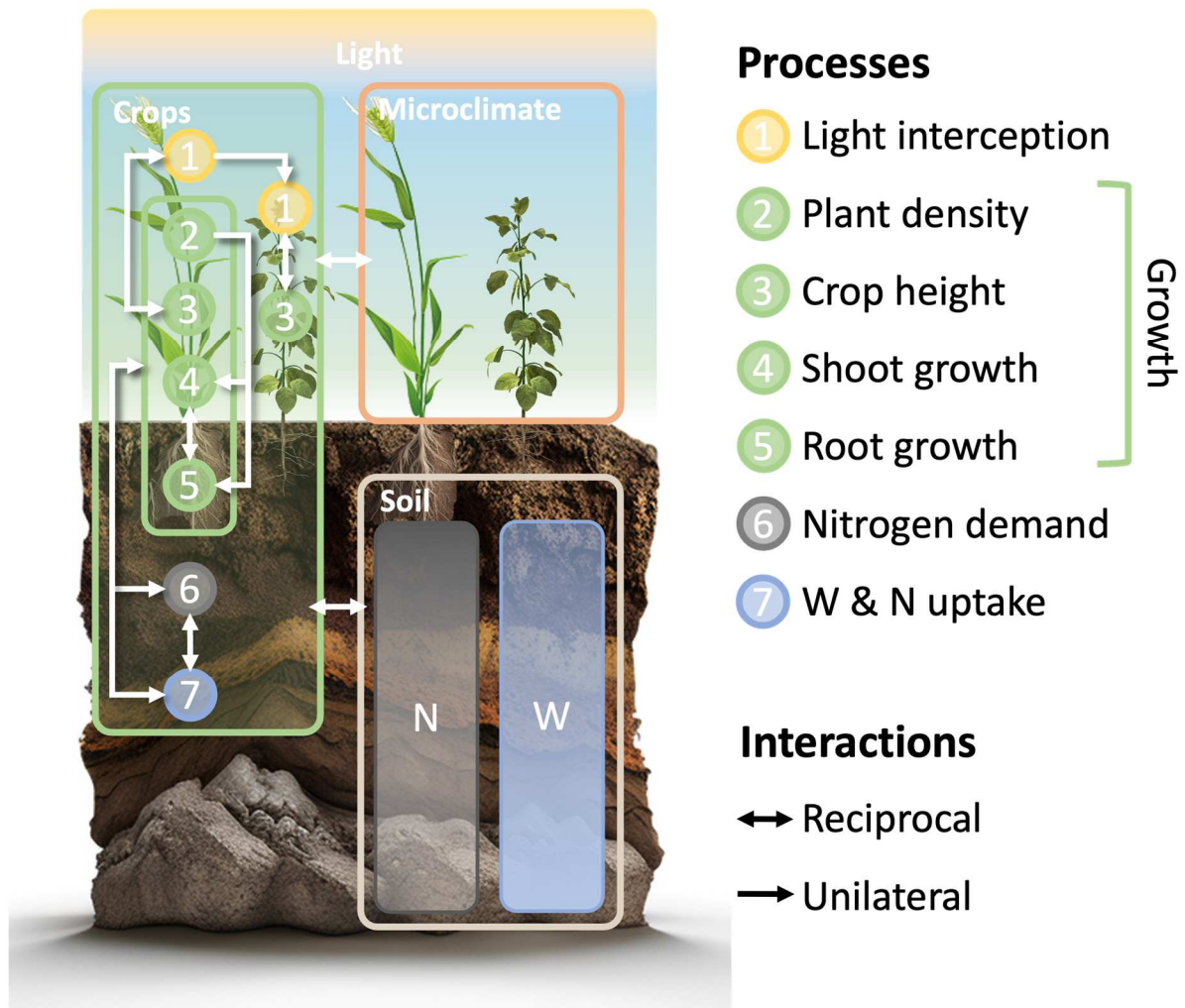
65 More extensive literature is available for the intercrop algorithms in STICS. This model generally  
66 performs correctly compared to observations, thus providing the first relevant basis for simulating bi-  
67 specific intercrops (Brisson et al. 2004; Launay et al. 2009; Kherif et al. 2022), but several  
68 inconsistencies were identified in some cases. Indeed, Shili-Touzi et al. (2010) applied the model on a  
69 winter wheat-red fescue intercrop and found a tendency to overestimate N uptake for the fescue. Corre-

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 scenarios. 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).



100

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

## 106 **Material and methods**

### 107 **General description of the STICS soil-crop model**

108 The STICS model is a dynamic 1D soil-crop model that combines crop development, growth and yield  
 109 formation with the carbon, nitrogen, energy and water cycles of the soil-crop system (Brisson et al. 1998,  
 110 2003, 2008; Beaudoin et al. 2022). The model runs at a daily time-step using input data related to  
 111 climate, crop species, soil, agricultural management, and the state of the system at initialization, such as  
 112 the water and nitrogen content of each soil layer. The crop is represented as a set of organs with a given  
 113 development stage, biomass and nitrogen content. The biomass growth is mainly driven by light  
 114 interception as a function of leaf area index with a big leaf approach, *i.e.* using the so-called Beer-  
 115 Lambert law of light extinction coupled with a radiation use efficiency, while crop development is driven  
 116 by thermal time corrected by vernalization and photoperiodic effects. Stress effects from frost,

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.

## 132 **Modifications of the model**

### 133 **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).

### 140 **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.

149 **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

183 depends on its biomass and is relatively independent from its plant density due to tillering in cereals or  
184 ramification in other species.

185 However, plants cannot always offset the effect of lower density in intercropping, because they are in  
186 competition with plants of other species. Therefore, the expected biomass per ground surface area for a  
187 crop grown in mixture at a given development stage is often lower than its counterpart in sole crop,  
188 hereby artificially increasing its N demand because the dilution curve uses parameters fitted on sole  
189 crops. For intercrops, we use the total biomass of the intercrop (*i.e.* both crops together, see  
190 supplementary materials) as a proxy for the equivalent biomass in sole crop, as proposed by Louarn et  
191 al. (2021), to use the same parameter values than in sole crops. This modification helps avoiding an  
192 underestimation of the N status of crops simulated in intercrops, as shown by Corre-Hellou et al. (2009).  
193 This assumption should be valid for a wide range of cases, unless both development and biomass of the  
194 two crops are largely different (Louarn et al. 2021).

### 195 **Water and nitrogen competition and complementarity**

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

198 Root systems of the intercrop do not directly interact, but affect each other via their influence on the  
199 status of water and N availability in the soil over the whole profile and for each 1 cm layer corresponding  
200 to the discretization of soil layer in the model. As for a sole crop, the root development and growth of  
201 each species in the intercrop depends on species-specific parameters, thermal time of soil temperature,  
202 several potential stresses, such as anoxia, drought, soil properties (high bulk density), frost, or low N  
203 content, and potentially a trophic linked production depending on the simulation option (Brisson et al.  
204 2004, 2008).

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

### 210 **Microclimate**

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



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**

251 **Parameter calibration**

252 The parameters and options of STICS were first calibrated manually using data from literature and  
253 expert knowledge. Then, an automatic calibration was performed based on the recommendations of  
254 Guillaume et al. (2011) and Buis et al. (2011) on the most influential parameters following the same  
255 procedure consisting of 15 steps of calibration for 25 parameters optimized over 13 variables; there were  
256 identified both by expertise and sensitive analysis. The parameters were first optimized using the Beer-  
257 Lambert law of extinction for the light interception, and then using the radiative transfer option, because  
258 the latter can fall back to the Beer-Lambert law whenever the plant height of the two species are close,  
259 and by doing so, the light extinction parameter of the Beer-Lambert law is used.

260 The parameters were optimized using the “CROptimizeR” R package (Buis et al. 2023) with the Nelder-  
261 Mead simplex algorithm (Nelder and Mead 1965) and seven repetitions with different initial parameter  
262 values to better sample the range of values while minimizing the risk of converging to a local minimum.  
263 Analyzes of the estimated values were performed to investigate whether the initial values had any impact  
264 on the optimized value.

265 **Parameters calibrated for intercrops**

266 The new formalisms of STICS were designed to be calibrated on sole crops and then applied to  
267 intercrops without any further parameterization. This method assumes that there is either no significant  
268 influence of the other crop on a given process, and the model explicitly simulates those interspecific  
269 interactions, including trait plasticity such as enhanced shoot elongation growth or root exploration in  
270 the soil. This is to say that interspecific interactions and the balance between dynamic competition and  
271 complementarity are emerging properties of the model functioning.

272 The formalisms implemented only need two parameters to be calibrated when necessary for the  
273 simulation of bi-specific intercrops: i) a threshold for the difference in crop height activating the  
274 dominance effect, and ii) elongation effect due to shading (*i.e.*  $ep$  from equation (11)). The former  
275 defines the threshold of difference in plant height under which both canopies are considered well-mixed  
276 and no clear dominance is occurring between the two species, indicating that light is shared depending  
277 on the LAI of each species and their respective light extinction coefficient. It is associated to the  
278 intercrop system under consideration, but its value should be consistent between intercropping systems  
279 because it defines the limit of the validity domain of the 1D and 3D representations. The parameter for  
280 the elongation effect in intercropping system cannot be parameterized on sole crops as it is the result of  
281 plant-plant interactions of the two species and should be measured in the field when the given crop is  
282 dominated by the other, or in growth chambers with light control. The value of this parameter can change  
283 depending on the type of species associated. However, and surprisingly, we did not observe a significant  
284 elongation effect in the data set used, so this parameter was set to 1.0 for all species in a first  
285 approximation, *i.e.* no elongation due to shading for the intercrops tested.

## 286 **Combination of strategies to evaluate the relevance and the genericity of STICS**

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

289 First, the model formalisms were evaluated in detail using a purely conceptual approach with the  
290 hypothesis that it should provide the same results when simulating a sole crop as usual or simulating the  
291 same sole crop using the intercrop formalisms. This means simulating a sole crop as an intercrop with  
292 itself, which also allows analyzing if intraspecific interactions are correctly taken into consideration and  
293 implemented in the algorithm. We refer to these simulations as “self-intercrop”, where sole crops are  
294 simulated by considering half a sole crop combined with another half same sole crop. Another objective  
295 of this analysis was to investigate whether there is an effect of the order each plant is computed in the  
296 sequence, *i.e.* whether the dominant crop grows more because it has priority in resource acquisition each  
297 day as it is simulated first. Our hypothesis is that the maximum delay of one-day between the crops has  
298 a very low impact on the simulation, *i.e.* the dominated species can also be considered having priority  
299 over the dominant species because it acquired resources last on day  $i-1$ . Nevertheless, this assumption  
300 needed to be validated.

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

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

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

## 309 **Dataset**

310 We used data from two experimental sites with different experiments analyzing bispecific grain legume–  
311 cereal (or sunflower) intercrops. The first experimental site is located on the INRAE research station in  
312 Auzeville (43°31'N, 1°30'E) in South of France (from published and unpublished data). The climate is  
313 temperate oceanic under Mediterranean influence and characterized by summer droughts and cool, wet  
314 winters (Cfa in Köpper-Geiger climate classification, Beck et al., 2018). The 25-year mean annual  
315 rainfall in Auzeville is 650 mm and the mean annual air temperature is 13.7°C. The site has a deep  
316 loamy soil with little or no stoniness. Phosphorus and potassium are assumed non-limiting at this site.  
317 The experiment included four cropping systems, plants either grown as sole crops or intercrops in a  
318 replacement design (half density of sole crops for each species): 1) durum wheat and winter pea in

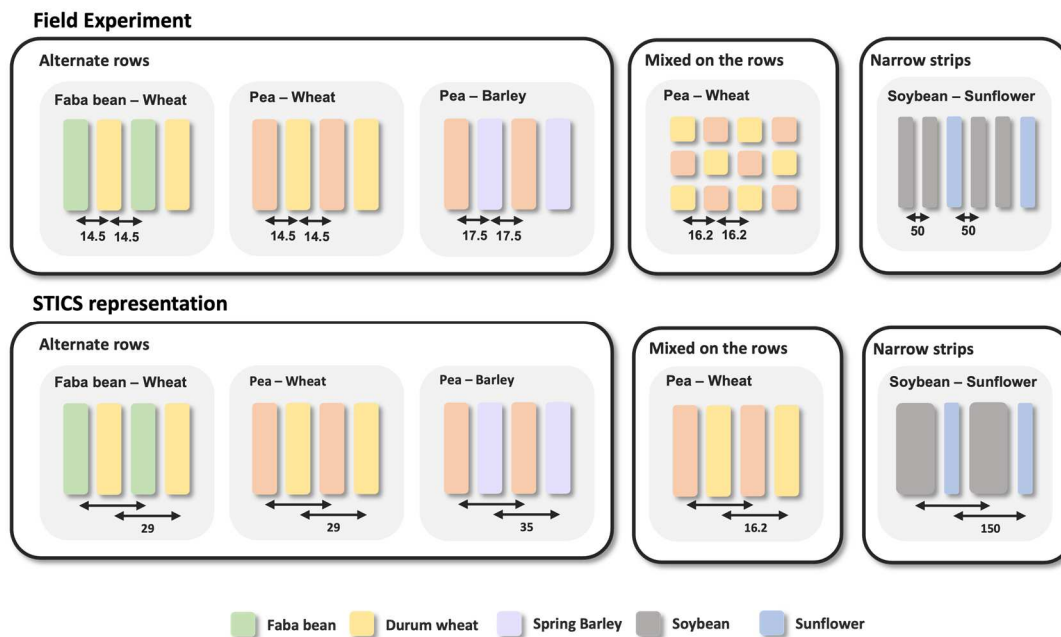
319 alternate rows, 2) durum wheat and winter pea mixed on the row, 3) durum wheat and faba bean in  
320 alternate rows, and 4) sunflower and soybean in alternating narrow strips.

321 In this study, we use four datasets from this site. The first one is a durum wheat (*Triticum turgidum* L.,  
322 cv. Nefer) and winter pea (*Pisum sativum* L., cv. Lucy) experiment carried out during the 2005-2006  
323 growing season, and sown as sole crops or in an alternate row intercrop design (Bedoussac and Justes  
324 2010). Similarly, for the second one, the same species and varieties were grown as sole or intercrops in  
325 Auzeville during the 2012-2013 growing season, but this time the intercrops were mixed on the row  
326 instead of sown in alternate rows (Kammoun 2014; Kammoun et al. 2021). The third experiment setup  
327 included durum wheat (cv. Nefer) and faba bean (*Vicia Faba* L., cv. Castel) grown in sole and intercrop  
328 during the 2006-2007 growing season. The intercrop consisted of alternate rows of each crop species  
329 (Bedoussac 2009; Falconnier et al. 2019). The last experiment consisted in growing sunflower (cv.  
330 Ethic) and soybean (*Glycine max* (L.) Merr., cv. Ecuador) either in sole crop or strip-intercrop composed  
331 of 1 row of sunflower and 2 rows of soybean.

332 The second site corresponds to data published by Corre-Hellou, Fustec, and Crozat (2006) from an  
333 experiment located at the FNAMS near Angers, France (47°27' N, 0°24'W). The location benefits from  
334 a temperate climate with oceanic influence with no dry season and warm summer (Cfb in Köpper-Geiger  
335 climate classification). Angers has a mean temperature of 12.4 °C and mean annual rainfall of 703 mm  
336 averaged over 20 years (1999 and 2019). The soil is a clay-loam. We used one treatment of this published  
337 paper with spring barley and pea intercrops in alternate rows and the two sole crops with no N fertilizer  
338 application. The field experiment was carried out in Angers in 2003 with field pea (*Pisum sativum* L.,  
339 cv. Baccara) and spring barley (*Hordeum vulgare* L., cv. Scarlett) grown as sole crops and alternate row  
340 intercrops (Corre-Hellou et al. 2006).

341

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



344

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

### 350 Measurements and calculations

351 The following data was available, measured for each species in intercrop: i) phenology, date of flowering  
 352 (Flowering, Julian days), date of physiological maturity (Maturity, Julian days); ii) dynamics of plant  
 353 height (Height, m), aboveground biomass (Biomass, t ha<sup>-1</sup>), fraction of absorbed photosynthetically  
 354 active radiation (faPAR) measured in continuous at INRAE Toulouse (complete set of PAR sensors  
 355 allowing to calculate daily the PAR budget and then the PAR absorbed by the sole crop and intercrop),  
 356 leaf area index (LAI, m<sup>2</sup> m<sup>-2</sup>), N acquisition (kg N ha<sup>-1</sup>) and proportion of N fixed by legumes in the  
 357 aboveground biomass (kg N ha<sup>-1</sup>) estimated by <sup>15</sup>N natural abundance method (Bedoussac and Justes  
 358 2010); and iii) grain yield (Grain, t ha<sup>-1</sup>) and harvest index. Each data point is the result of distinct  
 359 samples along the crop growth cycle.

360 Two variables were calculated using either simulations or observations.

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

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

362 where *Qfix* is the cumulative amount of N fixed symbiotically (kg N ha<sup>-1</sup>), *QN* is the amount of N  
 363 accumulated by the legume crop (kg N ha<sup>-1</sup>) and *i* the index of the day.

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

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

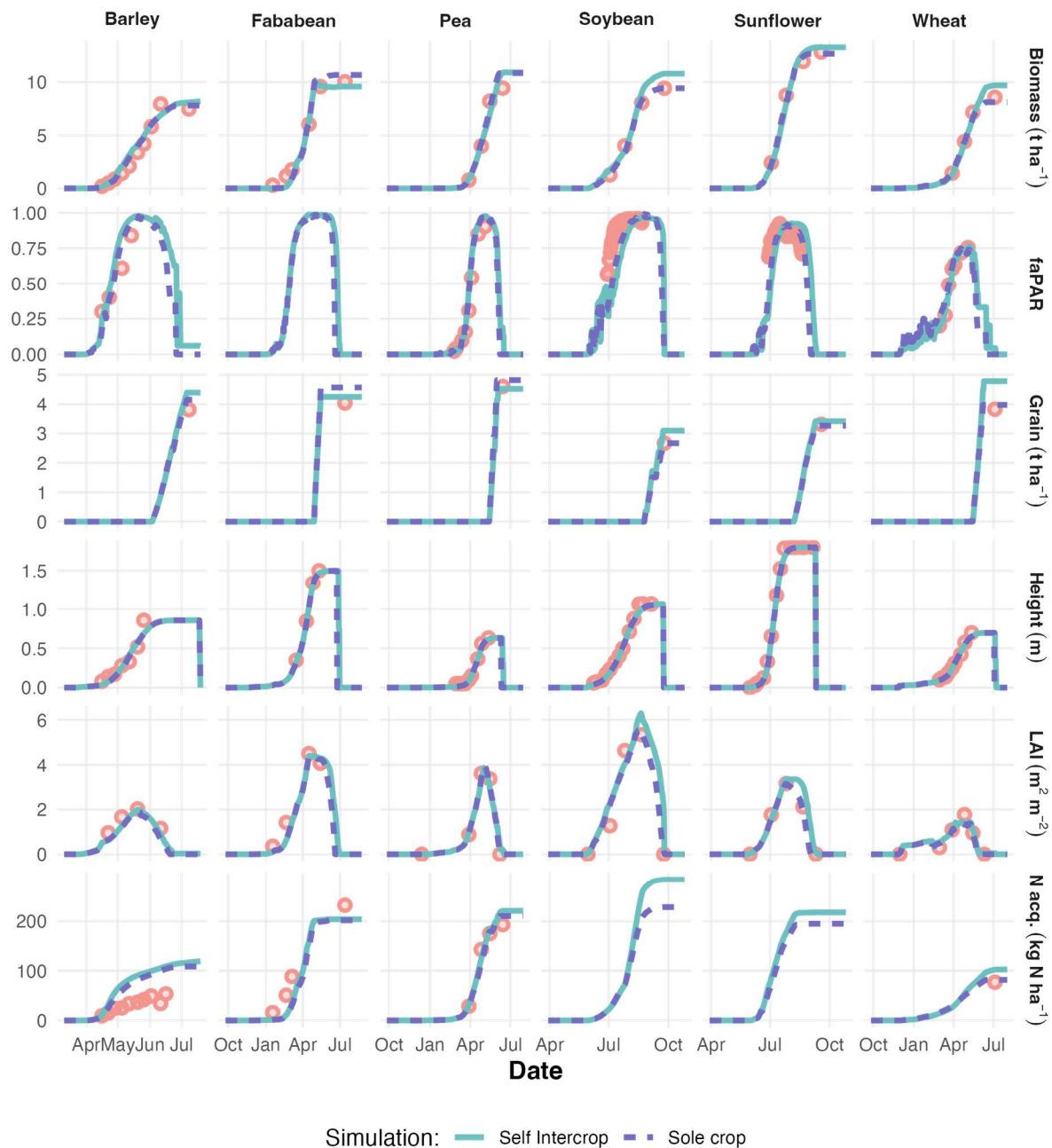
365 where  $Yield_{ic}$  is the grain yield in intercrop and  $Yield_{sc}$  is the grain yield in sole crop. A value of  $pLER$   
366 above 0.5 indicates a higher per-area performance in the intercrop than grown as a sole crop, which is  
367 most often called over-yielding. The evaluation of the overall 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.

## 374 **Results and Discussion**

### 375 **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.



382

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

389 The most critical period to simulate for many key variables is the dynamics and maximum value, *i.e.*  
 390 the value of the maximum LAI and when it occurs before senescence, and the maximum grain and  
 391 aboveground biomass, which determine yield. There is only a narrow difference between the simulations  
 392 of all the variables, *e.g.* the difference in plant height is very low (< 0.001 m). The fraction of absorbed  
 393 photosynthetically active radiation (faPAR) in the “self-intercrop” is the same than in sole crop, with an

394 average difference of only 0.1% at the maximum value, coupled to an increase of 20.6 kg N ha<sup>-1</sup> in N  
395 acquisition at harvest (+11.9%), leads to an increase in the aboveground biomass at harvest (+0.17 t ha<sup>-1</sup>,  
396 +5.2%) and grain yield (+0.8 t ha<sup>-1</sup>, +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.

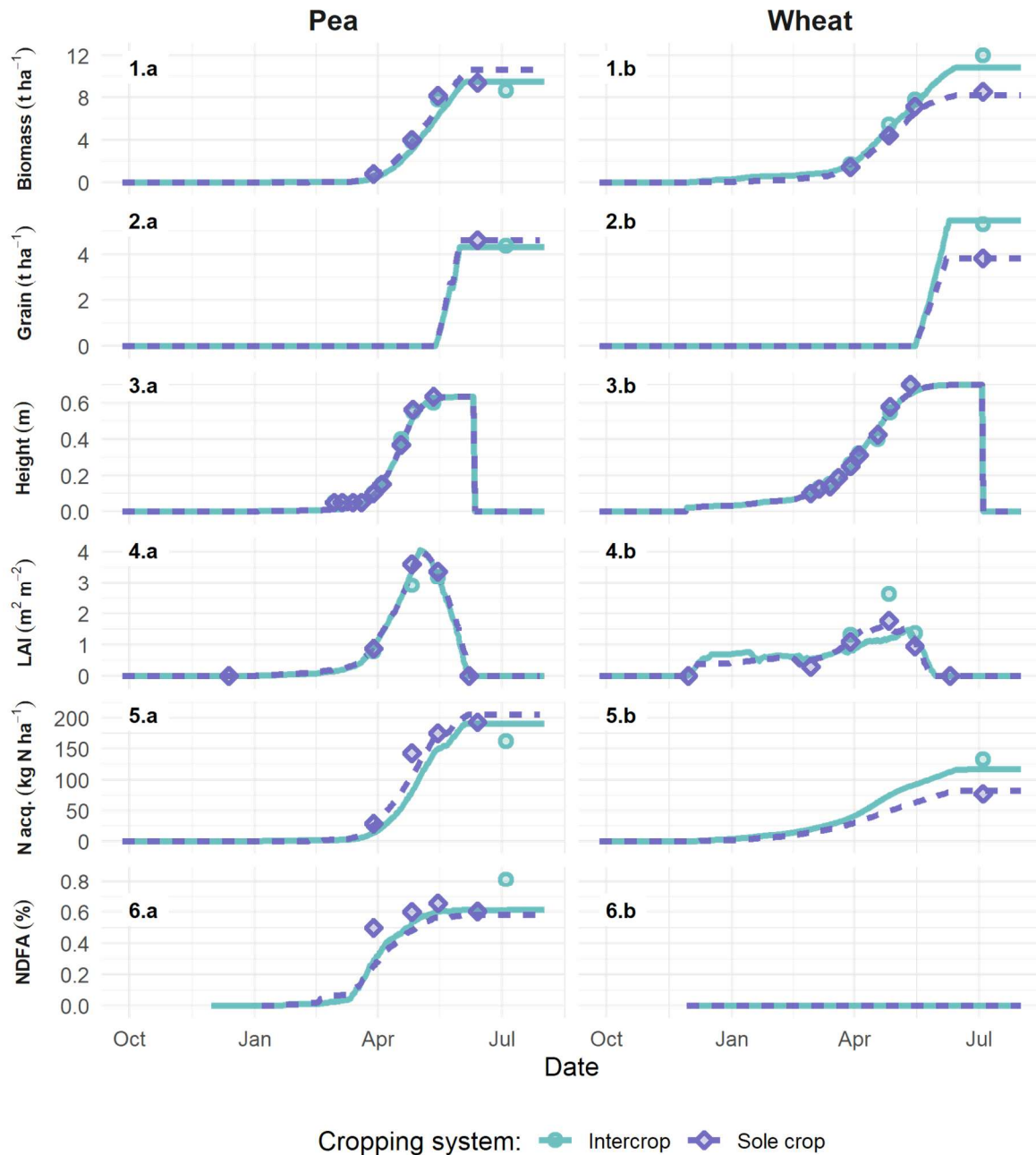
402 Another important result is that there is little difference between the two simulation options in the soil-  
403 water content and N acquisition, which indicates that the order each species is simulated in the sequence  
404 has no substantial effect, *i.e.* the dominant crop may be simulated first 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.

## 412 **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.





422

423 **Figure 4. Observed (points) and simulated (lines) 1. Aboveground biomass (Biomass), 2. Grain yield (Grain),**  
 424 **3. Plant height (Height), 4. Leaf area index (LAI), 5. Nitrogen acquisition in the aboveground biomass (N**  
 425 **acq.), and 6. Ratio of nitrogen derived from atmosphere (NDFA), for each plant species (a: Pea, b: Wheat)**  
 426 **both grown and simulated either in sole crop or intercrop at Auzeville during the 2005-2006 growing season.**  
 427 **Values for the intercrop are adjusted (x2) for comparison relative to the equivalent total surface area of the**  
 428 **two sole crops. The parameters of the model were optimized on sole crop systems, and then used without**  
 429 **any recalibration to simulate the intercrop systems.**

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

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 imperfect,  
 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<sup>-1</sup>), Yield: grain yield (t ha<sup>-1</sup>), Maximum LAI: maximum leaf area index (m<sup>2</sup> m<sup>-2</sup>), N acquired: Nitrogen**  
 447 **acquisition in the aboveground biomass (kg N ha<sup>-1</sup>), 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<sub>2</sub> 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).

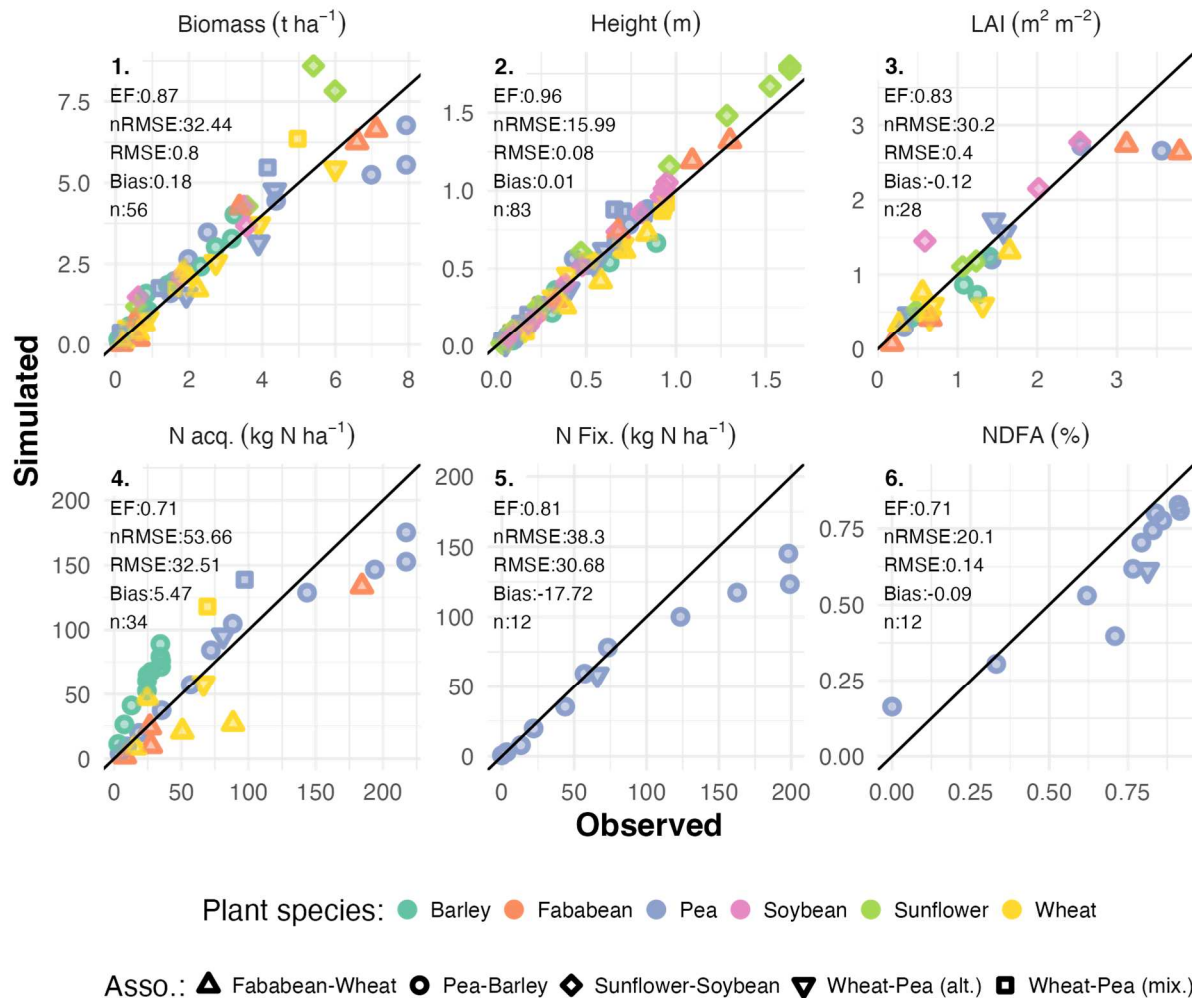
458 The simulations showed that the improved version of STICS could simulate niche complementarity for  
459 N (Figure 4) with a significant increase in N acquisition per plant in wheat crops and in the N<sub>2</sub> fixation  
460 rate (NDFA) in pea crops. This increase leads to a higher overall N content 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.

### 485 **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.



493

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

500 STICS is also evaluated at critical stages, which requires a more demanding value assessment for the  
 501 model, but produces a better evaluation of its capability to reproduce the system behavior and dynamic  
 502 processes at crucial stages and over time. STICS can also satisfactorily reproduce crop functioning for  
 503 all variables, with an EF above 0.5, except for the N content in the grains at harvest that showed lower  
 504 efficiency (0.2, Figure 6). This variable is one of the most complex to simulate because it depends on  
 505 many processes that interact throughout the crop development cycle in intercrop systems (Bedoussac  
 506 and Justes 2010). It is also worth noting that it presents a low bias of 0.13%, which is still encouraging.  
 507 Partial and total LER are particularly difficult to simulate because they both require accurate simulations  
 508 of the sole crop and the intercrop. A good surprise is that STICS is able to correctly simulate the  
 509 performance of intercrop in terms of the partial LER calculated from the output variables simulated,

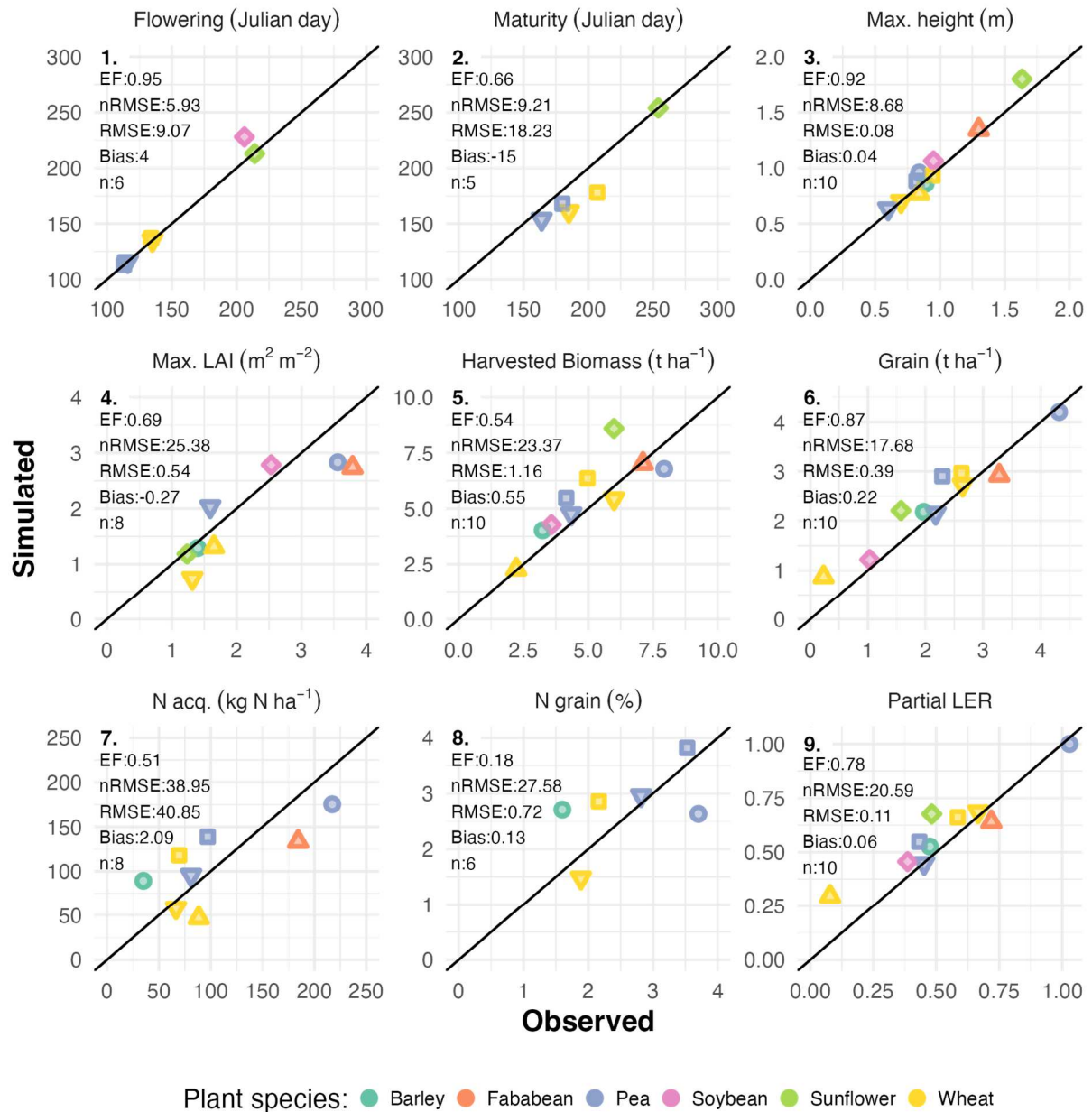
510 with an EF of 0.78, an nRMSE of 21% and a bias close to zero. Furthermore, the total LER of intercrops  
 511 presents a relatively low error of 14% in average over all systems, with a minimum at 0.8% for wheat–  
 512 pea (alternate rows) intercrops, and a maximum error of 30% for sunflower-soybean (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<sup>-1</sup>) compared to subsequent years (1.51 t ha<sup>-1</sup> in 2010; 2.11 t ha<sup>-1</sup> 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).



532

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

541 Overall, STICS was able to simulate all key measured variables as evidenced by the consistency between  
 542 simulations and observations in all intercrops tested, where the prediction of grain yield, for instance,  
 543 had an nRMSE of 18%, an EF of 0.9 and a low bias towards overestimation (0.2 t ha<sup>-1</sup>, Figure 6.6).

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 m<sup>2</sup> m<sup>-2</sup> for LAI, 1.02 t ha<sup>-1</sup> for biomass and 0.4 t ha<sup>-1</sup> 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 m<sup>2</sup> m<sup>-2</sup> for LAI, 0.64 t ha<sup>-1</sup> for aboveground biomass and 0.43 t ha<sup>-1</sup> 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<sub>3</sub> leaching, CO<sub>2</sub> and N<sub>2</sub>O 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

580 accurate simulations for both sole crops and intercrops using the parameter values optimized on sole  
581 crops. This is particularly interesting because plant height was repeatedly identified as one of the most  
582 important factors for intercrop simulation because of its role in determining competition for light (Corre-  
583 Hellou et al. 2009; Launay et al. 2009; Berghuijs et al. 2021). The new formalism can be introduced into  
584 other crop models, the only crucial requirement being the correct simulation of the species  
585 developmental stages.

586 More generally, STICS can be applied to a wide range of bi-specific intercrops where the planting design  
587 allows direct interspecific interactions for resources between the two crops. Although the threshold value  
588 for the acceptable width of the strip has not yet been determined, we recommend not simulating large  
589 strip intercrops with a strip width superior to the plant height or to the horizontal root distribution, in  
590 agreement with the concepts used in the model. Our results showed that STICS can simulate strip  
591 intercrops with narrow width and few rows (*i.e.* 2 to 3 close rows per strip), which were found to exhibit  
592 the most benefits from intercropping (van Oort et al. 2020). Intercropping systems that are more spatially  
593 complex are excluded from the validity domain unless proven otherwise, and probably need to be  
594 simulated using a 3D approach. They may include low-density agroforestry systems or intercrops that  
595 do not present a periodic row-manner of mixing (*e.g.* one row of one crop, then two of the other, and  
596 two of the first one). Although not considered in this study, on a conceptual basis, STICS can also  
597 simulate bi-varietal or population mixtures, relay intercropping and all intercrop mixtures using two set  
598 of plant parameters, for spatial designs of mixtures within the row and in alternate rows.

599 Overall, we show for the first time an implementation of a complete set of formalisms that are generic  
600 enough to simulate properly different types of interspecific plant-plant interactions regardless of the two  
601 species intercropped. These formalisms are simple enough to parameterize and fast to compute, which  
602 is required for long-term simulations and mathematical optimization of parameters that need repeated  
603 execution of the model until convergence of the statistical criteria. STICS-IC, and any other model that  
604 integrates the new formalisms, will be particularly well suited to address current challenges such as  
605 generalizing results of intercropping from one site to another, or virtually pre-screening innovative  
606 intercropping systems that are more sustainable, easier to manage, and well adapted to local conditions,  
607 as a tool for developing research supporting and agro-ecological transition, and to assess the impact of  
608 climate change scenarios on sole versus intercrop production and GHG emissions, and also assess if  
609 intercrop would be more resilient than the classical sole crops.

## 610 **Conclusion**

611 In this study, we present a new version of the STICS model that includes important processes for both  
612 sole crop and intercropping systems, such as development, light interception, plant growth, nitrogen and  
613 water balance, and yield formation. The formalisms included in the model are designed to be generic  
614 and sufficiently simple to understand and parameterize, making the model well-suited to address current



615 challenges in agriculture such as promoting sustainability while maintaining production. The results of  
616 this study show that the STICS model has a relatively high consistency, with an nRMSE of 25% for  
617 maximum leaf area index, 23% for shoot biomass at harvest, and 18% for yield. This indicates that the  
618 model is capable of accurately capturing the behavior of bispecific intercropping systems.

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

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

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## 636 **Declarations**

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640 systems based on species mixtures, <https://www.remix-intercrops.eu/>) project from 2017 to 2021 [grant  
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642 Ecosystem Services delivery in Europe and Southern countries) project starting from 2022 [grant  
643 number 101081973].

### 644 **Competing Interests**

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

### 646 **Availability of data and material**

647 The data used in this study is available in a Zenodo archive (Vezy et al. 2022). The parameter values are  
648 all available from the specific input files for each species, soil, site, meteorology and crop management.

### 649 **Code availability**

650 The source code of STICS and the code needed to replicate the simulations, statistics and figures of this  
651 study are available in open access from a Github repository (<https://github.com/VEZY/STICS-IC-paper>)  
652 and replicated on the Zenodo archive (Vezy et al. 2022). The simulations, parameter value optimizations,  
653 analyzes, and graphical visualizations were performed using the “SticsRPacks” suite of R packages  
654 (Vezy et al. 2021).

655 The new version of STICS included 177 commits with a total of 220978 additions and 108471 deletions.  
656 The changes were applied to the source-code of the STICS version 8.5 and the formalisms are planned  
657 to be included in the upcoming version of STICS in the coming months, in order to provide a version  
658 11 of the standard STICS model.

### 659 **Authors' contributions**

660 Conceptualization, RV, EJ, SM, ML and NG; Methodology, RV, EJ, SM, ML and NG; Software, RV,  
661 PL, DR; Validation, RV; Formal Analyses, RV; Investigation, RV; Resources, EJ, NG, SM; Data  
662 Curation, NG, SM, RV; Writing – Original Draft, RV, EJ.; Writing – Review & Editing, RV, EJ, SM,  
663 ML and NG; Visualization, RV; Supervision, EJ; Project administration, EJ; Funding Acquisition, EJ.

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