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► **To cite this version:**

Rémi Vezy, Sebastian Munz, Noémie Gaudio, Marie Launay, Patrice Lecharpentier, et al.. Modeling soil-plant functioning of intercrops using comprehensive and generic formalisms implemented in the STICS model. *Agronomy for Sustainable Development*, 2023, 43 (5), pp.61. 10.1007/s13593-023-00917-5 . hal-04189857

HAL Id: hal-04189857

<https://hal.inrae.fr/hal-04189857>

Submitted on 29 Aug 2023

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

Rémi Vezy^{a,b,*}, Sebastian Munz^c, Noémie Gaudio^d, Marie Launay^e, Patrice Lecharpentier^e, Dominique Ripoche^e, Eric Justes^f

^aCIRAD, UMR AMAP, F-34398 Montpellier, France.

^bAMAP, Univ Montpellier, CIRAD, CNRS, INRAE, IRD, Montpellier, France.

^cInstitute of Crop Science, Cropping Systems and Modeling, University of Hohenheim, 70599 Stuttgart, Germany

^dINRAE, AGIR, University of Toulouse, Castanet-Tolosan, France

^eINRAE, US1116 AgroClim, Avignon Cedex 9 France

^fCIRAD, Persyst Department, F-34398 Montpellier, France

*Corresponding author. Email address: remi.vezy@cirad.fr (Rémi Vezy, orcid: 0000-0002-0808-1461).

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.

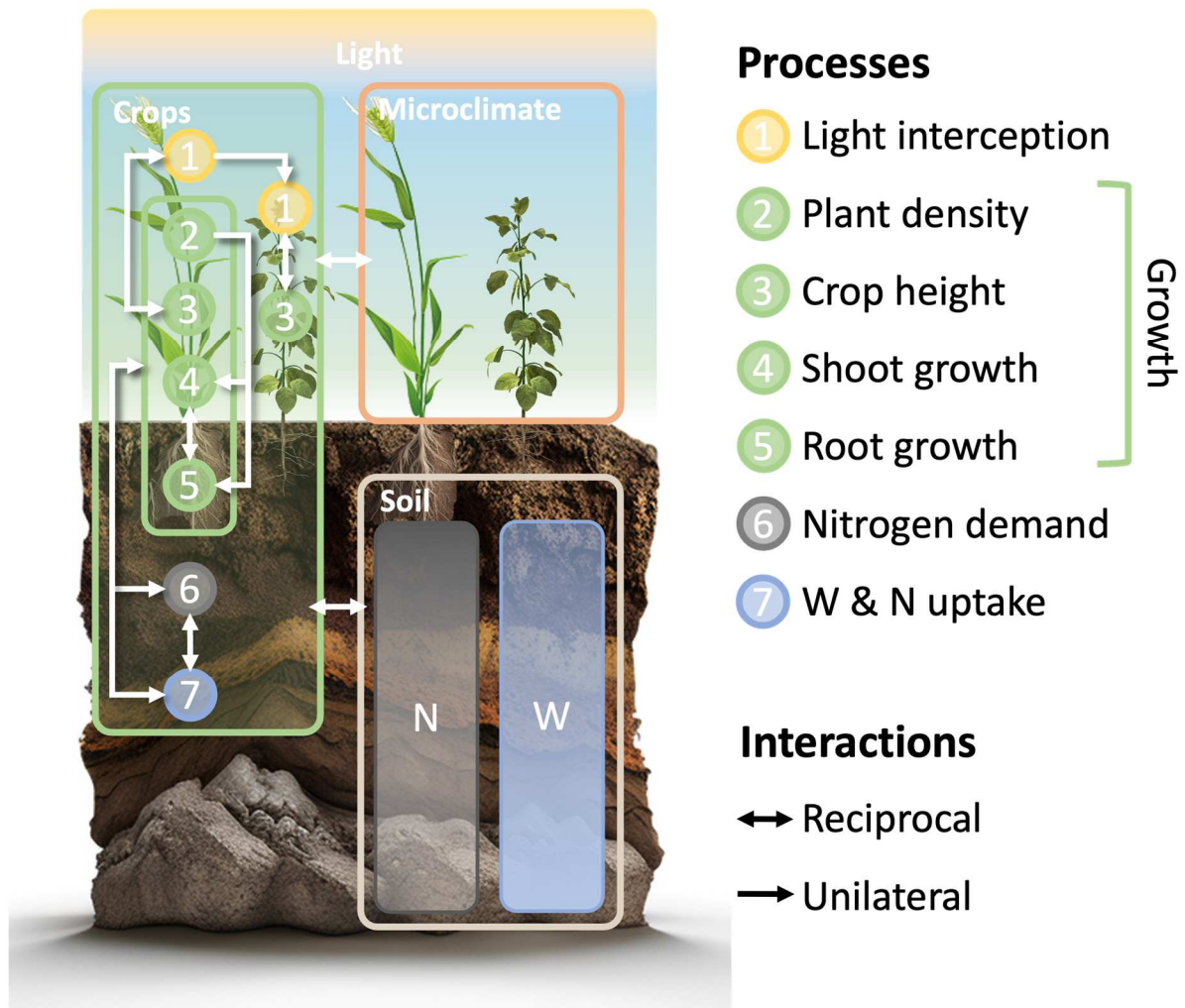
65 More extensive literature is available for the intercrop algorithms in STICS. This model generally
66 performs correctly compared to observations, thus providing the first relevant basis for simulating bi-
67 specific intercrops (Brisson et al. 2004; Launay et al. 2009; Kherif et al. 2022), but several
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 Analyses 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

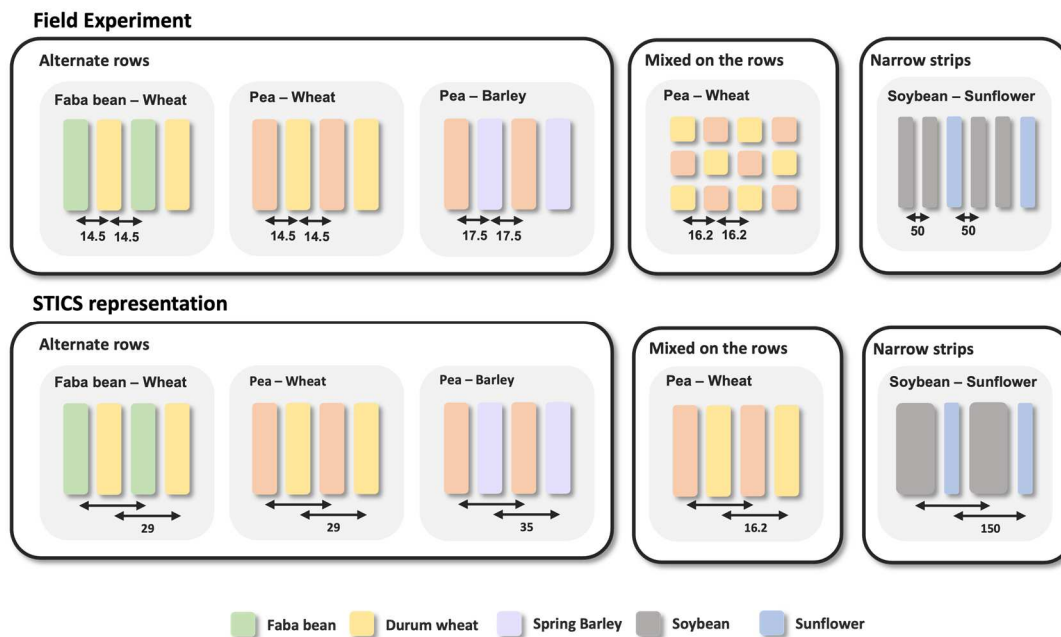
319 alternate rows, 2) durum wheat and winter pea mixed on the row, 3) durum wheat and faba bean in
320 alternate rows, and 4) sunflower and soybean in alternating narrow strips.

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⁻¹), 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, m² m⁻²), N acquisition (kg N ha⁻¹) and proportion of N fixed by legumes in the
 357 aboveground biomass (kg N ha⁻¹) estimated by ¹⁵N natural abundance method (Bedoussac and Justes
 358 2010); and iii) grain yield (Grain, t ha⁻¹) 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⁻¹), *QN* is the amount of N
 363 accumulated by the legume crop (kg N ha⁻¹) and *i* the index of the day.

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

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

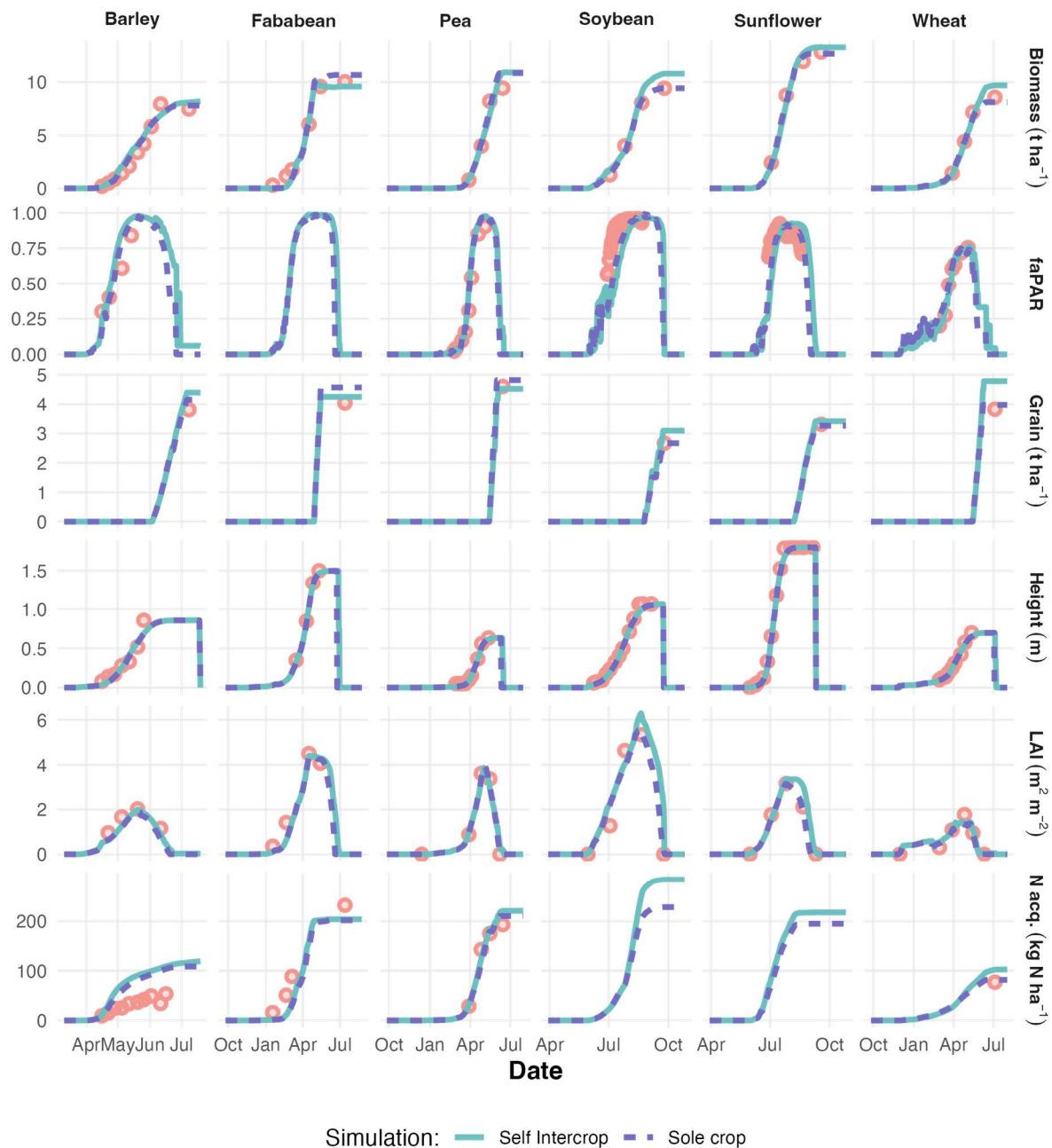
365 where $Yield_{ic}$ is the grain yield in intercrop and $Yield_{sc}$ is the grain yield in sole crop. A value of $pLER$
366 above 0.5 indicates a higher per-area performance in the intercrop than grown as a sole crop, which is
367 most often called over-yielding. The evaluation of the overall intercrop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

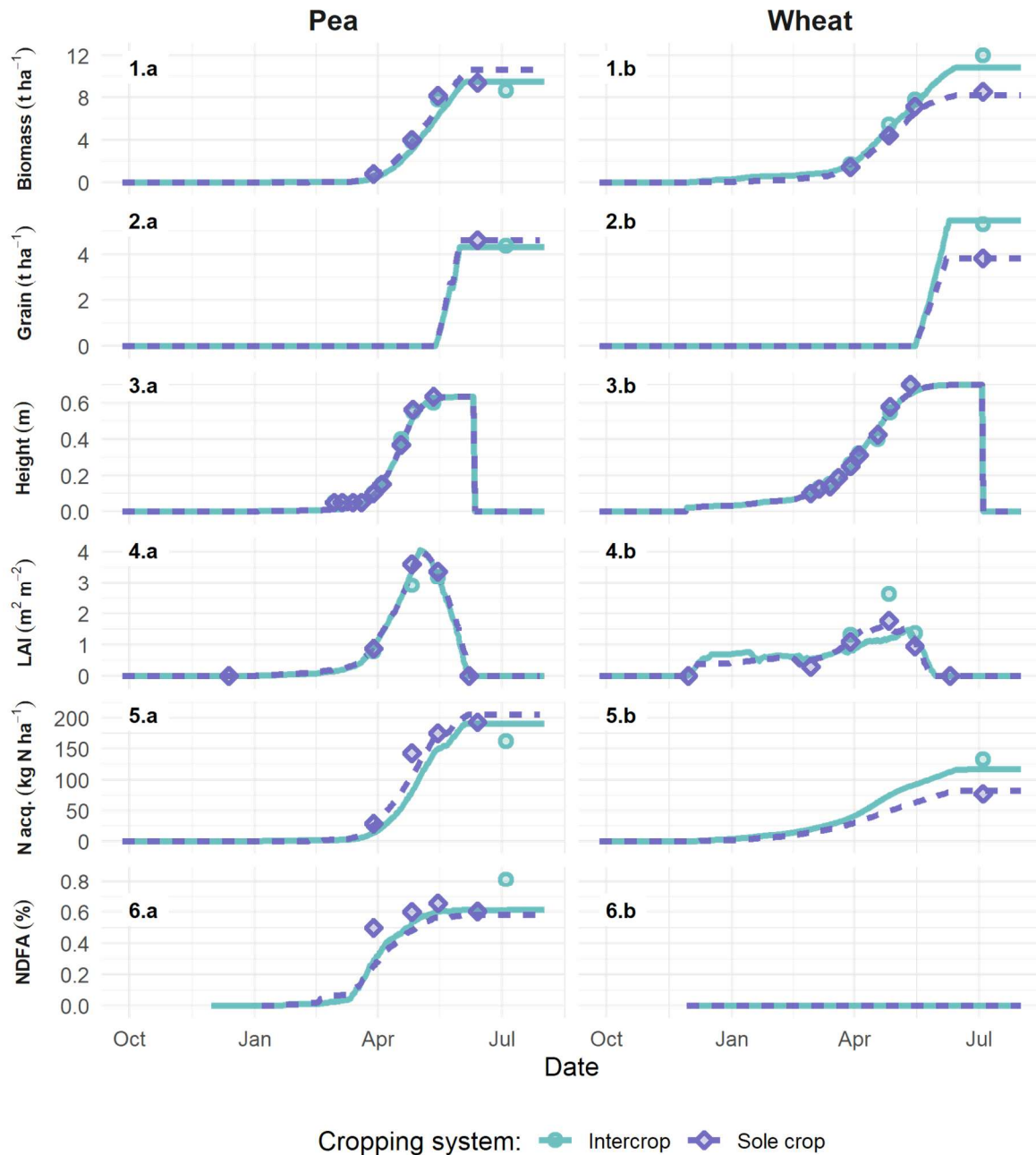
397 The N acquisition is the variable that presents the highest modeling error for soil-crop models, a behavior
398 that was recognized in previous versions of the model (Coucheney et al. 2015), but the difference
399 between the sole crop and self-intercrop remains quite low in comparison to the complexity 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.

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⁻¹), Yield: grain yield (t ha⁻¹), Maximum LAI: maximum leaf area index (m² 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 N₂ 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).

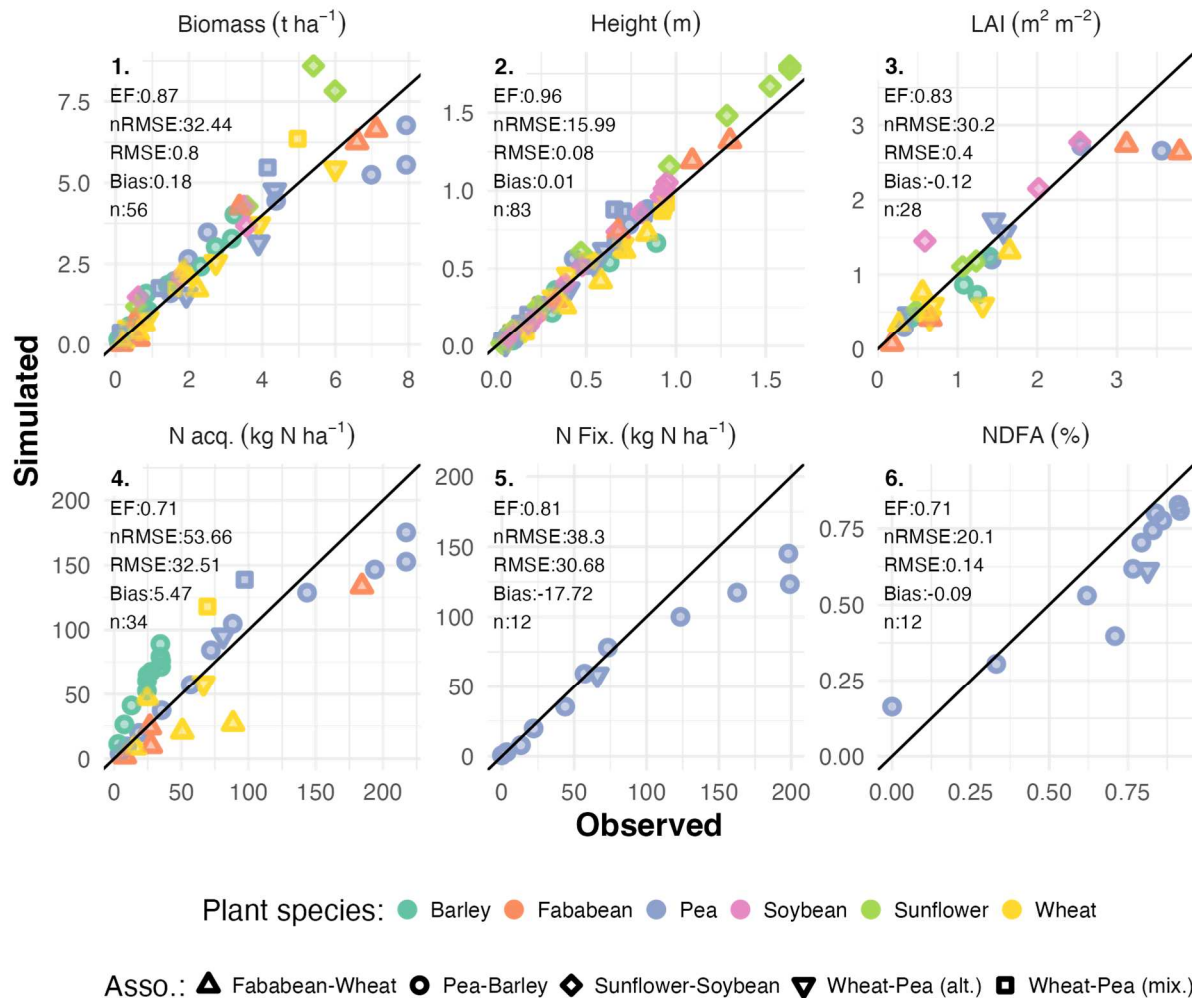
458 The simulations showed that the improved version of STICS could simulate niche complementarity for
459 N (Figure 4) with a significant increase in N acquisition per plant in wheat crops and in the N₂ fixation
460 rate (NDFA) in pea crops. This increase leads to a higher overall N content in the intercrop 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,

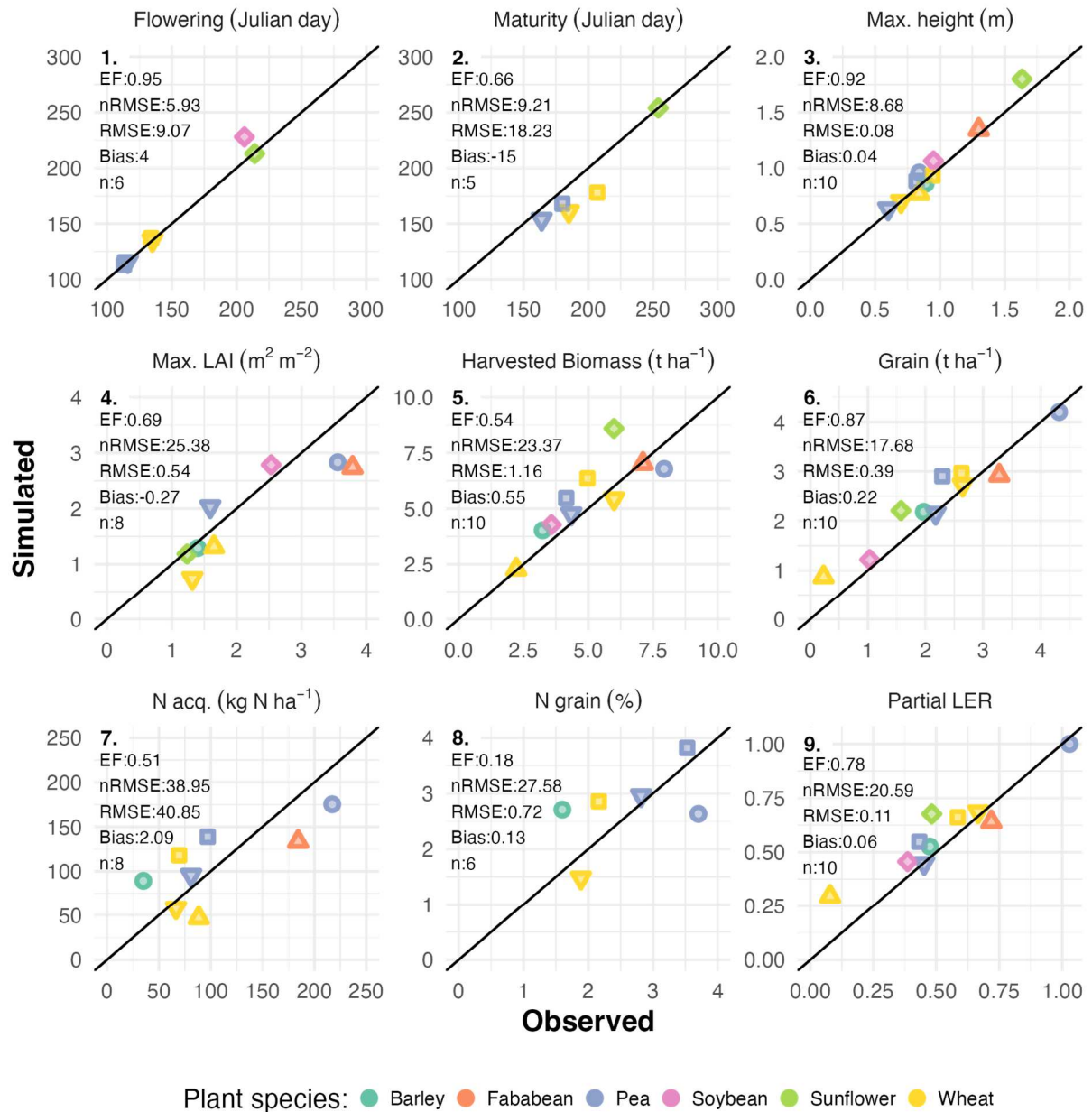
510 with an EF of 0.78, an nRMSE of 21% and a bias close to zero. Furthermore, the total LER of intercrops
 511 presents a relatively low error of 14% in average over all systems, with a minimum at 0.8% for wheat–
 512 pea (alternate rows) intercrops, and a maximum error of 30% for sunflower-soybean (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⁻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).



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⁻¹, 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 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, NO₃ leaching, CO₂ and N₂O 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.

634 **Acknowledgements**

635 We thank Mme Tilly Gaillard for her professional English reviewing of the manuscript.

636 **Declarations**

637 **Funding**

638 This research was supported by the European Research Council under the European Union's Horizon
639 2020 research and innovation program in the framework of the ReMIX (Redesigning European cropping
640 systems based on species mixtures, <https://www.remix-intercrops.eu/>) project from 2017 to 2021 [grant
641 number 727217], and the IntercropValuES (Developing Intercropping for agrifood Value chains and
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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