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1 Parametrization of five classical plant growth models applied to
2 sugar beet and comparison of their predictive capacities on root
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9 **Abstract**

10 A wide range of models have been proposed and developed for modelling sugar beet
11 growth, each of them with different degrees of complexity and modelling assumptions.
12 Many of them are used to predict crop production or yield, even when they were not
13 originally designed for this purpose, and even though their predictive capacity has never
14 been properly evaluated.

15 In this study, we propose the evaluation and comparison of five plant growth models
16 that rely on a similar energetic concept for the production of biomass, but with different
17 levels of description (individual-based or per square meter) and different ways to describe
18 biomass repartition (empirical or via allocation): Greenlab, LNAS, CERES, PILOTE and
19 STICS. The models were all programmed on the same modelling platform, calibrated on
20 a first set of data, and then their predictive capacities were assessed on an independent
21 data set. First, a sensitivity analysis was carried out on each model to identify a subset
22 of parameters to be estimated, to reduce the variability of the models. We were able
23 to reduce the number of parameters from 10 to 4 for Greenlab, and from 16 to 1 for
24 STICS. Three criteria were then used to compare the predictive capacities of the models:
25 the root mean squared error of prediction and the modelling efficiency for the total dry
26 matter production and the dry matter of root, and the yield prediction error.

27 All the models provided good overall predictions, with high values of the modelling

28 efficiency. The use of sensitivity analysis allowed us to reduce the variability of the
29 models and to enhance their predictive capacities. Models based on an empirical harvest
30 index gave good yield predictions, and similar results compared to allocation models for
31 the total dry matter, but the harvest index might not be very robust. The crucial role
32 of initiation was also pointed out, as well as the need for an accurate estimation and
33 modelling of this early phase of growth.

34 *Keywords:* sugar beet; prediction; model evaluation; model comparison; RMSEP;
35 modelling efficiency

36 1. Introduction

37 A wide range of plant growth models are available in the literature, either generic
38 ones, that can be applied to different species, or more specific ones built for given plants or
39 trees. Some of them are designed to predict yield or biomass production at field scale, and
40 help management decisions, while some others are built for descriptive purposes, to en-
41 hance our understanding of plant functioning and simulate plant architecture (Fourcaud
42 et al., 2008). One can also be confronted with the need to compare and choose between
43 different versions of the same model, corresponding to different biological assumptions,
44 for example, or to decide whether a given biological process should be accounted for or
45 not.

46 Depending on their initial objective, these models can have different levels of com-
47 plexity. For example, descriptive models would tend to be more complex than purely
48 predictive ones as they would integrate more underlying eco-physiological processes (e.g.
49 allocation processes, reaction to environmental stresses, ...). Often, this increase in the
50 model complexity results in a higher number of parameters, and consequently in a de-
51 crease of the predictive capacity of the model due to a higher variability. This is the

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52 well known bias/variance compromise. However, a lot of models are used as prediction
53 tools even though they were not originally designed for this purpose. It is thus necessary,
54 when using a model, to define precisely the context in which it will be used, and even
55 more importantly, to evaluate properly its performance according to the objective of the
56 study.

57 In this context, we propose a methodology to build and evaluate different models in
58 a predictive perspective. We apply this approach to five plant growth models for sugar
59 beet crops, with different levels of description and modelling scales: Greenlab (de Reffye
60 and Hu, 2003; Yan et al., 2004), CERES (Jones and Kiniry, 1986; Leviel, 2000), Pilote
61 (Mailhol et al., 1997; Taky, 2008), STICS (Brisson et al., 1998, 2008) and a fifth model
62 named LNAS (Cournède et al., 2013), based on a global allocation of biomass to the
63 leaves compartment or root. First elements of comparison for Greenlab, CERES and
64 Pilote are available in Lemaire (2010).

65 The five models rely on a similar formulation for the production of biomass, based
66 on Monteith's equation (Monteith, 1977) and on an extension of the Beer-Lambert law.
67 The accumulated dry matter production is linearly related to the fraction of intercepted
68 radiation, which can generally be expressed according to the leaf area index (LAI) or to
69 the leaves biomass. From this common basis, the models then differ in their formulations
70 of the LAI curve, either based on allocation processes (Greenlab, LNAS) or on empirical
71 relationships (PILOTE, CERES). STICS can be seen as an intermediate between these
72 two approaches, since the LAI is computed from an empirical function, but modulated
73 by a source-sink ratio. Two modelling scales were also compared, with either individual-
74 based models (CERES, Greenlab) in which the LAI was computed from the development
75 of each individual leaf, or more classical crop models (PILOTE, STICS, LNAS) where
76 the LAI was computed per square meter at field scale. The differences between the five
77 models are summarized in Table A.1.

78 [Table 1 about here.]

79 All these models have already been tested and calibrated in the case of sugar beet, but

80 the purpose here is to evaluate their predictive capacities. In this perspective, to reduce
81 the variability of the models which included a large number of parameters, a sensitivity
82 analysis was computed for each of them. The parameters were ranked according to their
83 influence on the model outputs, and then, the best subset of parameters to be estimated
84 was identified, according to AIC and BIC criteria. They were first calibrated on the
85 same set of data, and their predictive capacity was then evaluated and compared on
86 an independent data set using three classical criteria: the root mean squared error of
87 prediction (RMSEP), the modelling efficiency (EF), and the yield prediction error.

88 In the second section, we present the five models, along with the data and the criteria
89 used for the calibration and the evaluation of their predictive capacity. The calibration
90 process, and in particular the sensitivity analysis performed on each model, is described
91 in section 2.3. Results from this sensitivity analysis are given in section 3.1, those from
92 the comparison between the different versions of STICS, in section 3.2.1, and between
93 the two data sets (calibration and validation sets), in section 3.2.

94 **2. Material and methods**

95 *2.1. Models*

The five models rely on the same concept for the energetic production of biomass, based on an extension of the Beer-Lambert law (Monteith, 1977). The biomass production in grams per square meter on day t , $Q(t)$ is proportional to the incoming photosynthetically active radiation $PAR(t)$ (in MJ/m^2), to the fraction of intercepted radiation $I(t)$ (which depends on the leaf area index or on the dry matter of leaves) and to the radiation use efficiency RUE (in g/MJ) (Damay and Le Gouis, 1993):

$$Q(t) = 0.95 \cdot RUE \cdot PAR(t) \cdot I(t). \quad (1)$$

96 The leaf area index is defined as the one-sided green leaf area per unit ground surface
97 (Watson, 1947), thus some adjustments were necessary for the two individual-based mod-

98 els Greenlab and CERES. In Greenlab, as the biomass production is computed at the
 99 individual plant level, a ‘local’ LAI (Cournède et al., 2008) was defined, corresponding
 100 to the leaf surface of the plant multiplied by a coefficient related to the two-dimensional
 101 projection of the space occupied by the plant on the ground (see 2.1.1). In CERES,
 102 as the biomass production is computed at the square meter level, a ‘global’ LAI was
 103 constructed from the individual leaf surfaces of the plant, by multiplying by the crop
 104 density (see 2.1.5).

105 2.1.1. GreenLab

106 GreenLab is a generic functional-structural plant model (FSPM), combining the de-
 107 scription of the plant architecture and its physiological functioning (Vos et al., 2007;
 108 Sievänen et al., 2000). The model in its discrete version was introduced by de Reffye and
 109 Hu (2003), and was studied in the case of sugar beet by Lemaire et al. (2008).

110 In its first version, the time step chosen to compute the organogenesis and the eco-
 111 physiological processes was the growth cycle (i.e. the thermal time elapsing between the
 112 appearance of two successive metamers). However, for a better accuracy in the handling
 113 of continuous variations of environmental conditions, and consistency with the usual
 114 daily collection of climatic data, a continuous version of the Greenlab model was used,
 115 discretized with a daily time step (Li et al., 2009). Such formulation is also more con-
 116 sistent with the other plant growth models studied in this paper and that provide daily
 117 outputs (Mailhol et al., 1997; Guérif and Duke, 1998; Spitters et al., 1989).

In Greenlab, the biomass production on day t is computed at the individual plant
 level, thus some adjustments were made from equation (1):

$$Q_{pl}(t) = 0.95 \cdot \text{RUE} \cdot \frac{\text{PAR}(t)}{d} \cdot \left(1 - \exp \left(-k_B \frac{Q_b(t)}{e_b \cdot S_p} \right) \right),$$

118 with $Q_{pl}(t)$ the biomass production of an individual plant (in g/pl), d the plant density
 119 (in pl/m^2), k_B the Beer-Lambert law extinction coefficient, $Q_b(t)$ the accumulated blade
 120 mass (in g/pl) at day t , e_b the mass per unit area of blade (in g/m^2), and S_p an empirical

121 coefficient related to the two-dimensional projection of the space occupied by the plant (in
 122 m^2/pl). The biomass production per square meter $Q(t)$ can be obtained by multiplying
 123 $Q_{pl}(t)$ by the crop density d . The biomass is then allocated to the different organs of the
 124 plant according to source-sinks relationships (we refer the reader to Yan et al. (2004);
 125 Lemaire et al. (2008) for more details).

126 2.1.2. LNAS

127 A simplified model called LNAS (Cournède et al., 2013) was elaborated, where the
 128 biomass allocation is done globally for the whole leaves compartment, instead as leaf by
 129 leaf as in the Greenlab model. The leaf area index was obtained by dividing the biomass
 130 of leaves by the mass per unit area. It is a generic daily time-step model, presented here
 131 in the case of sugar-beet, but that can be easily extended to other plants.

The biomass production on day t is given by (1), with:

$$I(t) = 1 - \exp\left(-k_B \cdot \frac{Q_g(t)}{e_g}\right),$$

132 where $Q_g(t)$ is the dry matter of green leaves at day t (in g/m^2), k_B the extinction
 133 coefficient and e_g the mass per unit area of leaf (in g/m^2). Note that here, the quantity
 134 e_g is different from the quantity e_b used in the Greenlab model, as in LNAS we are
 135 dealing with the dry matter of leaves, considering blades and petioles together, whereas
 136 in Greenlab we are only dealing with the dry matter of blade.

137 Then, the produced biomass is allocated to the different organs compartments. Only
 138 two compartments are considered in the case of sugar beet: leaves and root. We denote
 139 by $Q_l(t)$ and $Q_r(t)$ respectively the total mass of leaves and the total mass of root on
 140 day t . At the beginning of day $t + 1$, the masses of leaves and root are given by:

$$\begin{aligned} Q_l(t+1) &= Q_l(t) + \gamma(t) \cdot Q(t) \\ Q_r(t+1) &= Q_r(t) + (1 - \gamma(t)) \cdot Q(t) \end{aligned}$$

where function γ is defined as:

$$\gamma(t) = \gamma_0 + (\gamma_f - \gamma_0) \cdot G_a(\tau(t)),$$

141 with G_a the cumulative distribution function of a log-normal law, parametrized by its
142 median μ_a and its standard deviation σ_a , $\tau(t)$ the thermal time on day t , and γ_0 and γ_f
143 respectively the initial and final proportion of biomass allocated to the leaves.

The proportion of non-senescent leaves is given according to the following equation:

$$Q_g(t) = (1 - G_s(\tau(t) - \tau_{sen})) Q_l(t)$$

144 where G_s is the cumulative distribution function of a log-normal law, parametrized by
145 its median μ_s and its standard deviation σ_s , and τ_{sen} is the thermal time at which the
146 senescence starts.

147 2.1.3. STICS

148 STICS (Simulateur multIdisciplinaire pour les Cultures Standard (Brisson et al.,
149 1998, 2008)) is a generic daily time-step model, which has already been applied to a
150 large variety of crops (maize, tomato, wheat, sugarbeet, ...). It is organized into seven
151 modules corresponding to the different mechanisms involved in plant growth.

152 In the original formulation of STICS, the relation between biomass production and
153 intercepted radiation is not linear as in (1), but quadratic, with the introduction of a
154 saturation coefficient, and a radiation use efficiency that could vary according to the
155 development stage $s(t)$. However, since the main differences between the models con-
156 cern the modelling scale and the biomass repartition, we choose a simplified version of
157 the production function, with a constant RUE and a linear relationship with radiation
158 interception, so that the five models share the same formulation for biomass production.
159 A complementary study is conducted in 3.2.1 in order to check if such simplifications
160 alleviate the predictive capacity of STICS, and actually shows that the simplified version

161 performs better in our case.

The leaf area index is modelled with an empirical function as the net balance between growth and senescence, and is supposed to evolve in three phases: a first phase of logistic growth (from emergence to the maximal LAI point), a stability phase, and a senescent phase in which the LAI decreases linearly (Brisson et al., 2008). We have:

$$I(t) = (1 - \exp(-k_B \text{LAI}(t))),$$

with k_B the Beer-Lambert law extinction coefficient, and:

$$\text{LAI}(t) = \sum_{j=t_e}^t (\Delta\text{LAI}(j) - \Delta\text{LAI}_{\text{sen}}(j))$$

162 where t_e is the day of emergence, $\Delta\text{LAI}(j)$ is the net leaf area growth on day j and
163 $\Delta\text{LAI}_{\text{sen}}(j)$ is the leaf area senescence on day j .

The net leaf area growth on day j depends on the leaf development unit on day j , $u(j)$, which varies from 1 at emergence to 3 when the leaf area index is maximal. From emergence to the maximal LAI point, the LAI growth follows a logistic curve:

$$\Delta\text{LAI}(j) = \frac{\alpha}{1 + \exp(\beta(u_{\text{mat}} - u(j)))} \cdot d \cdot f_d(j) \cdot f_T(j) \cdot s(j), \quad \text{for } 1 \leq u(j) \leq 3$$

164 where u_{mat} is the leaf development unit at the end of the juvenile stage, d is the
165 plant density and f_d a density factor related to the competition between plants, f_T
166 is the effective crop temperature, and s is a trophic stress index. This trophic stress
167 is determined by a source-sink ratio, and thus induces a retroaction of the allocation
168 process on the LAI curve. With this formulation, the leaf area index stops growing all at
169 once after having reached its maximal point, but it is possible to introduce a progressive
170 decline of the LAI. We refer the reader to Brisson et al. (2008) for more detailed equations.

171 A lot of parameters are required for the model, but a list of recommended values for
172 different crops are available in Brisson et al. (2008).

173 As explained previously, in the original formulation of STICS, the relationship be-
 174 tween biomass production and intercepted radiation is quadratic and not linear. More-
 175 over, among the several modules available in STICS, some of them are dedicated to the
 176 management of environmental stresses, so that these processes can be easily implemented
 177 in the model. As a consequence, a complementary study was carried out on STICS to
 178 evaluate the effect of these different modelling assumptions, and four versions of STICS
 179 were compared (see section 3.2.1):

- 180 1. the initial version of STICS, with a varying radiation use efficiency and a quadratic
 181 relationship between biomass production and intercepted radiation, but no stresses
- 182 2. a linear version, with a varying radiation use efficiency but a linear relationship
 183 between production and radiation
- 184 3. a linear version with a constant radiation use efficiency (this version is the standard
 185 one used in the comparison with the other models)
- 186 4. the linear and constant RUE version, with the addition of thermal stress

187 The thermal stress was added in the modified version of the model because, as it will
 188 be shown latter in the paper, this modified version performed better than the initial one.

189 2.1.4. *Pilote*

Pilote is a crop-soil interaction model, which was first built for sorghum and sunflower (Mailhol et al., 1996, 1997), but that can be applied to a large variety of crops. It has been developed for sugar beet by Taky (2008). It is designed to predict the actual evapotranspiration and the yield of crops, through the modelling of the leaf area index. In this paper, we considered the version of Pilote without hydric stress. In such case, the biomass production per square meter at day t is given by (1), with:

$$I(t) = 1 - \exp(-k_B \cdot \text{LAI}(t))$$

$$\text{LAI}(t) = \text{LAI}_{\max} \left(\frac{\tau(t) - \tau_e}{\tau_{\max}} \right)^{\beta} \exp \left[\frac{\beta}{\alpha} \left(1 - \left(\frac{\tau(t) - \tau_e}{\tau_{\max}} \right)^{\alpha} \right) \right]$$

190 with k_B the Beer-Lambert law extinction coefficient, LAI_{\max} the potential maximum
 191 value of LAI in non-limiting conditions, τ_{\max} the thermal time (in °Cday) necessary to
 192 reach this maximal LAI, τ_e the thermal time (in °Cday) of emergence, and α and β two
 193 parameters. It is also possible to model growth and senescence separately, using two
 194 different values α_1 and α_2 depending on whether we are before or after τ_{\max} . Then, the
 195 biomass repartition to root and leaves is done with an empirical harvest index.

196 2.1.5. CERES

CERES (Crop Environment REsource Synthesis) was originally built on maize by
 Jones and Kiniry (1986), but a sugar beet version was developed by Leviel (2000). Ef-
 fects of irrigation or nitrogen uptake can also be integrated in the model. In CERES,
 the biomass production is done at the square meter level from equation (1), from the
 individual foliar surfaces of the plant:

$$I(t) = 1 - \exp\left(-k_B \cdot d \cdot \sum_k S_k(t)\right),$$

197 with k_B the Beer-Lambert law extinction coefficient, d the plant density (in pl/ m^2), and
 198 S_k the foliar surface of leaf k at time t (in m^2).

The foliar surface of leaf k , S_k is supposed to grow linearly from the thermal time
 of appearance of leaf k to the end of its expansion, then stay at its maximum surface
 $S_{k,\max}$ until the end of its lifetime:

$$S_k(t) = \begin{cases} 0 & \text{if } \tau(t) \in [0, \tau_k^i[\\ \frac{S_{k,\max}}{\tau_k^e - \tau_k^i} (\tau(t) - \tau_k^i) & \text{if } \tau(t) \in [\tau_k^i, \tau_k^e[\\ S_{k,\max} & \text{if } \tau(t) \in [\tau_k^e, \tau_k^i + \tau_k^s[\\ 0 & \text{otherwise} \end{cases}$$

199 with $\tau(t)$ the thermal time at time t , and τ_k^i , τ_k^e and τ_k^s respectively the thermal time

200 of initiation, the thermal time of end of expansion and the lifespan in thermal time of
201 leaf k . The maximum foliar surfaces $S_{k,\max}$, as well as the thermal times of initiation,
202 expansion and senescence, are thus needed to calibrate the model.

203 The biomass is then distributed to root and leaves thanks to an empirical harvest
204 index, corresponding to the ratio between the dry matter of root and the total dry
205 matter at harvest.

206 2.2. Data

207 We used a first dataset from 2010 experiments to calibrate the models. Field ex-
208 periments took place at La Selve, France, N49°34'22", E3°59'24", on a sandy loam soil.
209 A commercial variety, Python, was sown on April 15, with 45 cm between rows and
210 18 cm between seed-plots, and fertilized with 136 kg N ha⁻¹. The final plant density
211 was estimated at 11.82 plants per square meter (pl/m²). Dry matter of root and leaves
212 (blades and petioles separately or altogether) were collected on 50 plants at fifteen dif-
213 ferent dates, and dry matter of individual blades and petioles, as well as blade surface
214 areas, were measured on 10 plants at five different dates. Mean values were then used
215 for the calibration process. The LAI was not measured directly on the field, but could
216 be computed from the blade mass Q_b , the mass per unit area e_b and the plant density d :
217 $\text{LAI}_{\text{exp}} = \frac{Q_b}{e_b} d$. The mass per unit area of blade e_b was obtained from a linear regression
218 between leaf areas and blade masses on the five dates of individual measurements. The
219 observed maximum surfaces of leaves were used for CERES model.

220 At first, the predictive capacity of the models was supposed to be tested on 2011
221 experiments, conducted on the same genotype near the 2010 site, at Bourgogne, France,
222 N49°21'18", E4°4'12" on a calcareous loam soil. However, a hail episode occurred this year
223 around day 100, and caused a lot of damages on leaves, with partial or total destruction
224 of blades and petioles, and thus a much lower biomass production than in 2010, leading
225 to over-estimated predictions for this variable. As a consequence, a second dataset was
226 used to evaluate the predictive capacity of the models in the absence of any perturbing
227 event. The field experiments in 2008 were conducted around 200km away from the 2010

228 site, in the Beauce plain near Bazainville, France, N48°11'15", E2°5'50" on a clay loam
229 soil. A commercial variety, very similar to the Python genotype, Radar, was sown on
230 March 11, with 50 cm between rows and 20 cm between seed-plots. The final measured
231 density was 10.9 pl/m². Dry matter of root and leaves were measured at fifteen different
232 dates on 30 plants.

233 Daily mean values of air temperature (°C) and solar radiation (MJ.m⁻²) were ob-
234 tained from French meteorological advisory services (Météo France) near the experimen-
235 tal site. Thermal time was computed using a base temperature of 0°C (Lemaire et al.,
236 2008). All the experiments were conducted in non-limiting water conditions.

237 *2.3. Calibration*

238 *2.3.1. Reduction of the variability*

239 A very important part of this work consisted in the calibration of the five models.
240 Indeed, parametric estimation is a crucial and yet tricky task, especially when the number
241 of parameters is high compared to the amount of data available for the estimation. It
242 can also be impossible to estimate simultaneously all the parameters of a model, due
243 for example to numerical issues or high correlations between parameters (Wallach et al.,
244 2006, Chapter 4). Moreover, estimating too many parameters can have an obnoxious
245 effect on the predictive capacity of the model, due to overparametrization. If it is true
246 that the estimation of a parameter can enhance the goodness of fit of the model, especially
247 when the estimated value is far from the one given in the literature, or when no reliable
248 information is available, the estimation process is also marred with errors, leading to
249 a higher variance of the model. A good compromise has therefore to be made on the
250 number of parameters to estimate.

251 A classical two-step approach to this issue is first to rank the parameters according
252 to their importance, and then, to select the number of parameters to estimate. In the
253 first step, parameters can be ordered for example according to their influence on the
254 model outputs, or their ability to enhance the goodness of fit measured by a given
255 criterion (Campolongo et al., 2007). In the second step, the final number of parameters to

256 estimate is determined using another appropriate criterion like the mean squared error
257 of prediction (Wallach et al., 2001, 2006). In this paper, we adopted a very similar
258 approach, with the use of sensitivity analysis (SA) to rank the parameters and model
259 selection criteria such as AIC and BIC to choose the number of parameters that would be
260 estimated, the others being set to recommended values given in the literature. A similar
261 study has already been carried out for STICS, on wheat and maize, based on response
262 surface method (Ruget et al., 2002).

263 A review on the role of sensitivity analysis can be found in Cariboni et al. (2007) or
264 Saltelli et al. (2008). A first prerequisite to the use of SA is the definition of appropriate
265 distributions for the parameters. Such information can be found in the literature, but
266 may also not be easily available, in particular when a model is used for a species on
267 which it has rarely or never been tested, or when a new model is considered. Uniform
268 distributions were used in this study, and the corresponding variation intervals were
269 defined according to the information available for each model as follow: (i) for STICS,
270 we took a 10% variation around the recommended values given in the literature (Brisson
271 et al., 2008), (ii) for Greenlab, we defined the variation intervals from a combination of the
272 reference values given by Lemaire et al. (2008) for the discrete version of the model and
273 results from previous fittings with the continuous version, (iii) for PILOTE, we defined
274 variation intervals taking into account the different values of the parameters for different
275 crops, including sugar beet (Mailhol et al., 1996, 1997; Taky, 2008), (iv) for LNAS, we
276 built variation intervals using the similarities between LNAS and SUCROS (Guérif and
277 Duke, 1998) or Greenlab, and the relationship between some of the parameters and well-
278 known biological processes. Sensitivity analysis was not used on CERES, as there is only
279 one parameter to calibrate in this model.

280 Sobol's method was used to compute the sensitivity indices for each parameter, each
281 output, and each time of observation, with the estimator proposed by Wu et al. (2011).
282 Then, sensitivity indices (SI) for each parameter and each output were obtained with a
283 weighted sum over each time of observation using the variance of the outputs at each

284 time of observation, and finally, a global SI for each parameter was computed, taking into
285 account all the model outputs. Parameters were ranked according to their global SI, and
286 then, the models were calibrated with a growing number of parameters, introduced in the
287 calibration process in the order determined by SA. AICc and BIC were then computed for
288 each calibrated models. We used the corrected version of AIC, as it lessen the probability
289 of overfitting when the sample size is too small, and as it converges towards AIC when
290 the sample size gets large (Burnham and Anderson, 2002). These two criteria are defined
291 as: $AICc = -2\log L + 2kn/(n - k - 1)$ and $BIC = -2\log L + k \log n$, where L is the
292 estimated log-likelihood of the model, k is the number of parameters and n the sample
293 size. It is worth noting that, if these criteria are not relevant to assess the predictive
294 capacity of a model, leading to the use of appropriate criteria as defined in section 2.4,
295 there are nonetheless suitable for goodness-of-fit evaluations and can therefore be used
296 in this calibration step.

297 A summary of the variation intervals adopted for each parameter can be found in
298 Table A.2. To lighten the table, intervals are not shown for STICS, we thus refer the
299 reader to Brisson et al. (2008) for a list of recommended values for the parameters on
300 sugar beet.

301 [Table 2 about here.]

302 2.3.2. Fixed parameters

303 A first set of fixed parameters was identified, corresponding to those than can be
304 measured directly or for which well documented values are given in the literature. These
305 parameters included: the extinction coefficient of the Beer-Lambert law ($k_B = 0.7$ ac-
306 cording to Andrieu et al. (1997), except for STICS when the relationship between biomass
307 production and intercepted radiation was nonlinear, in which case $k_B = 0.58$), the mass
308 per unit area in Greenlab (deduced from our field experiments, $e_b = 83 \text{ g.m}^{-2}$), and the
309 maximum leaf surfaces for CERES (deduced from the individual measurements). The
310 harvest index for Pilote and CERES was computed as the ratio between dry matter of

311 root (including crown) and total dry matter at harvest, and was estimated at 70% on
312 2010 data. This value is lower than the one found by Leviel (2000) for sugar beet (root
313 + crown: 85%).

314 A very important parameter of the five models was the thermal time of initiation
315 (or emergence, depending on the model). Indeed, as these models (except STICS) are
316 not designed to predict the initiation time, this parameter must be given as an input.
317 We used a nonlinear mixed model (Baey et al., 2013) to estimate it, along with the
318 two phyllochrons and the rupture thermal time (Milford et al., 1985; Lemaire et al.,
319 2008), to describe the rhythm of leaf appearance. They were estimated using two datasets
320 to ensure a more robust estimation (2010 and 2011 experiments, driven on the same
321 genotype), as the data available for the estimation of these parameters in 2010 were
322 not satisfying (small number of plants, and few measures before the rupture point).
323 Indeed, as noticed by Lemaire et al. (2008) and Lemaire (2010), the phyllochrons and
324 the duration of the first phase of development in sugar beet remain stable for a given
325 genotype, and only the thermal time of initiation is subject to change, due for example
326 to environmental conditions. A shift was thus progressively introduced between the two
327 datasets, corresponding to the difference between the thermal times of initiation in the
328 two different years, until the same values were obtained for the two phyllochrons and the
329 rupture thermal time. The smallest AIC was obtained with a shift of 140°Cday.

330 The other parameters were included in the sensitivity analysis.

331 *2.4. Criteria for evaluating the predictive capacity*

332 The mean squared error of prediction (MSEP) is the standard criterion for evaluating
333 the predictive capacity of a model (Wallach and Goffinet, 1987; Wallach et al., 2006). It
334 measures the distance between observations and predictions, and its square root is used
335 to obtain the same units as the observed and predicted values.

A first dataset is used for the model calibration, and a second one is used to compute

the criterion:

$$\text{RM}\hat{\text{SEP}}(\hat{\theta}) = \sqrt{\frac{1}{n} \sum_{i=1}^n (Y_i - \hat{Y}_i)^2}$$

336 where Y_i are the observed values, \hat{Y}_i are the predicted values and n is the number of
337 observations in the second dataset.

The modelling efficiency (EF), as defined by Mayer and Butler (1993), is a dimensionless quantity which measures the overall goodness of fit between predictions and observations. It is similar to the coefficient of determination in linear regression.

$$\text{EF} = 1 - \frac{\sum_{i=1}^n (Y_i - \hat{Y}_i)^2}{\sum_{i=1}^n (Y_i - \bar{Y}_i)^2}$$

338 where \bar{Y}_i is the mean of observed values. The modelling efficiency ranges from $-\infty$ to 1.
339 In case of a perfect fit, i.e. when predicted and observed values are equal, the modelling
340 efficiency is equal to 1. A value of 0 corresponds to the case where the model predictions
341 are not better than the mean of the observed values, and a negative value is obtained
342 when the predictions perform worse than the mean.

343 The two criteria defined above give a ranking of the models, the best model being the
344 one with the smallest RMSEP and a modelling efficiency EF as close to 1 as possible.
345 However, as the RMSEP share the same units as the observations, it can be difficult to
346 compare the predictive capacity of a model on variables with different units, whereas the
347 use of EF makes these comparisons easier.

The models were compared on two variables: the dry matter of root and the total dry matter. This allowed for a comparison of biomass production, and a comparison of the biomass allocation to the root. However, for the two models that rely on a constant harvest index for the biomass repartition (Pilote and CERES), the computation of the criteria for the whole time period for the dry matter of root did not make sense, as the harvest index is not supposed to be valid throughout the plant development, but only at harvest. Thus, a third criterion was introduced for the dry matter of root: the yield

prediction error. It is defined as follows:

$$YPE = \frac{|Y_{r,n} - \hat{Y}_{r,n}|}{Y_{r,n}}$$

348 where $Y_{r,n}$ is the observed root biomass and $\hat{Y}_{r,n}$ the predicted root biomass at harvest.

349 The criteria were calculated using the vectors of parameters found at the calibration
350 stage for each model. Only the plant density and the thermal time of crop initiation were
351 adapted to 2008 data.

352 *2.5. Modelling platform*

353 The five models presented above were programmed on the C++ modelling platform
354 PyGMAIion (Cournède et al., 2013) developed in the team. It contains all the necessary
355 tools for parametric estimation, sensitivity analysis, and model selection.

356 **3. Results**

357 *3.1. Sensitivity analysis and parameter selection*

358 Table A.3 gives the results of the parameter selection procedure. AICc and BIC
359 are provided for the four models included in the analysis. They both selected the same
360 number of parameters, except for Greenlab, where AICc included more parameters than
361 BIC. We finally chose to include 7 parameters in the calibration process, as the fitted
362 values were closer from the corresponding biological values found in the literature. In
363 particular, the RUE was estimated at 5.93 g/MJ when only 4 parameters were included
364 in the calibration process, which is higher than all reference values of RUE for sugar beet
365 reported in the literature.

366 [Table 3 about here.]

367 The list of parameters finally estimated for each model is given in Table A.4. The
368 remaining parameters were fixed to the mean value of their corresponding variation
369 interval in the sensitivity analysis (see Table A.2). Expectedly, the radiation use efficiency

370 had the biggest influence on the model outputs, and was top-ranked by the sensitivity
371 analyses for all models. For LNAS and STICS, calibrating only this parameter was
372 enough to ensure a satisfying goodness of fit, and the calibration of more parameters
373 did not allow for a sufficient decrease of the likelihood. For Greenlab and Pilote, more
374 parameters were necessary to calibrate the models, but we were able to reduce the total
375 number of parameters from 10 to 7 for Greenlab.

376 [Table 4 about here.]

377 *3.2. Predictive capacity*

378 As stated previously, different versions of a given model can be available, correspond-
379 ing to different modelling assumptions and their corresponding biological interpretations.
380 It is the case of the STICS model, in our study, where we are using a modified version of
381 the original published STICS model. It is therefore necessary to compare these different
382 models to check whether the simplifications adopted in the paper lessen the predictive
383 capacity of the model.

384 *3.2.1. Comparison of different versions of STICS*

385 As detailed in section 2.1.3, we adopted in this paper a version of STICS, where the
386 relationship between intercepted radiation and biomass production is linear instead of
387 quadratic, and with a constant efficiency coefficient. We provide here a comparison of
388 the predictive capacity of the different versions of STICS listed in section 2.1.3 (see Table
389 A.5).

390 [Table 5 about here.]

391 Interestingly, the modified versions of STICS performed better than the original one,
392 suggesting that the linear formulation of biomass production and the use of a constant
393 efficiency coefficient is more appropriate for prediction in the case of sugar beet. The
394 introduction of thermal stress in the model slightly improved the performances for the
395 dry matter of root prediction, but not for the total dry matter. These results supported

396 our use of the STICS version with a linear biomass production, a constant efficiency and
397 no consideration of thermal stress for the comparison with the other models.

398 *3.2.2. Comparison on 2008 data*

399 In this section, we present the results for the comparison of the predictive capacity of
400 the five models on 2008 data. We used for STICS the modified version defined in section
401 2.1.3. A comparison of the different versions of STICS is available in 3.2.1.

402 The best predictions for the total dry matter were given by LNAS (see Table A.6),
403 followed by CERES. The five models provided good overall predictions, as indicated by
404 the high values of modelling efficiency (above 0.95 for each of them). However, predictions
405 were less accurate at the end of the growth period, as it can be seen on Figure A.1. In
406 the two empirical models Pilote and CERES, the initiation began earlier than in the
407 other models, or more specifically, the produced biomass grew faster, leading to better
408 predictions during the first growth period (until 1000°Cday approximately), compared
409 with other models. However, due to a higher RUE value than in LNAS for example
410 (see Table A.4), they tended to produce overestimated predictions from approximately
411 1000°Cday. In LNAS, STICS and Greenlab, the initiation was slower, especially for
412 Greenlab, which resulted in underestimated predictions, at least at the beginning of the
413 plant growth. For STICS though, this effect was partly compensated by a very high
414 RUE, and the model provided overestimated predictions from approximately 1500°Cday.
415 LNAS, for its part, was able to better predict the total biomass all along the growth
416 thanks to a lower RUE, even if we observed a decreasing trend at the end. For Greenlab,
417 the underestimations provided by the model seemed to be partly due to a slower initiation
418 that delayed the growth of the simulated plant.

419 The models performed well also for the root biomass prediction, with high modelling
420 efficiency values. We recall that for Pilote and CERES, the comparison of observed
421 and simulated data throughout the plant development did not make sense as there are
422 no dynamic allocation processes in these models. The empirical harvest index which
423 is used is only supposed to be valid at harvest. However, for the sake of illustration,

424 we plotted the simulations of these two models according to thermal time, to have an
425 idea of their behaviours. STICS performed outstandingly well on this variable, which
426 means, given its performance on the total dry matter, that the dry matter of leaves was
427 highly underestimated by the model. For LNAS and Greenlab, the dry matter of leaves
428 is certainly over-estimated by these models, given the fact that root biomass was largely
429 under-estimated while total dry matter was only slightly under-estimated. These two
430 models provided highly biased yield predictions, around 15%.

431 [Table 6 about here.]

432 [Figure 1 about here.]

433 [Figure 2 about here.]

434 4. Discussion

435 This study is a first attempt to develop a benchmarking approach in a research domain
436 where a lot of models coexist. In this paper, we compared five plant growth models for
437 sugar beet on their capacities to predict the total dry matter and the dry matter of root.
438 The five models shared a comparable energetic production of biomass, but differed in
439 complexity level, modelling scale and handling of biomass repartition.

440 More generally, the approach developed in this paper can be used not only for the
441 comparison of different models, but also for the comparison of different versions of the
442 same model as presented for STICS, and help to choose between different formulations.

443 The use of sensitivity analysis allowed us to reduce the variability and to enhance
444 the predictive capacity of the models. They all provided good overall predictions for the
445 total dry matter and the root biomass, with high modelling efficiency values. For Pilote
446 and CERES, a relatively good handling of the plant initiation, coupled with a slightly
447 too high RUE (for Pilote and CERES) resulted in good also overestimated predictions on
448 this data set. For LNAS and Greenlab, a later initiation and a slower RUE also resulted
449 in good but overestimated predictions for the total biomass. In STICS the initiation was

450 also delayed, even if in a less obvious way than LNAS and Greenlab, but it was partly
451 compensated by a very high RUE value.

452 Models that relied on a harvest index for the repartition of biomass to root and leaves
453 provided good yield predictions, and total dry matter predictions in the same range as
454 the allocation models. However, the harvest index was deduced from 2010 measurements
455 and estimated around 70%, which is lower than the recommended values found in the
456 literature for these models, around 85%, and slightly lower than the value measured in
457 2011 of 75%, suggesting that this index might not be very robust. It should also be noted
458 that for Pilote, the LAI curve used for model calibration in 2010 was constructed from
459 mass measurements, while it is normally based on Licor LAI-2000 measurements. This
460 could have probably improved its performance regarding total dry matter production.
461 For CERES, the maximal surfaces $S_{k,\max}$ were computed from individual blade masses
462 and mass per unit area, and may therefore be very variable from one year to another.
463 Moreover, these data are not always available, which can prevent from using this model.

464 From a practical point of view, if one is only interested in yield and root biomass
465 prediction (which is coherent in the case of sugar beet), STICS can be seen as a good
466 candidate. Only one parameter needs to be estimated after a sensitivity analysis, and
467 moreover, reliable recommended values are available in the literature (Brisson et al.,
468 2008). Environmental stresses can also be easily introduced in the model. Current
469 work on a modified version of STICS based on source-sink relationships suggests that
470 this model is indeed very robust. However, if STICS provided good results for the root
471 biomass in our study, its performance was less good on the total dry matter, due to a
472 high underestimation of leaf biomass.

473 Results on the total dry matter also suggested that the initiation is a very crucial phase
474 of the plant growth, as a too early or a too fast initiation could lead to overestimated
475 predictions, whereas a too late or a too slow initiation could produce underestimated
476 predictions. More accurate estimations of this parameter can be found using models
477 designed to predict seed germination and seedling emergence (Forcella et al., 2000), or

478 by introducing the corresponding processes directly in the plant growth models. In any
479 case, a careful attention must be paid to the simulation of this delicate growth phase, both
480 by estimating precisely the thermal time of initiation or emergence, and by modelling
481 adequately the dynamics of the plant during its early phase of growth.

482 This study is only a first attempt to evaluate the predictive capacities of plant growth
483 models for sugar beet, and these results should be confirmed on other datasets, corre-
484 sponding for example to more various situations (different genotypes, stressed environ-
485 mental conditions, . . .). Intuitively, we could imagine that the parameters of more mech-
486 anistic models would be more genotype-dependent than that of more empirical models
487 (Tardieu, 2003; Letort, 2008; Yin et al., 2004).

488 Moreover, the biological validity of our results must be further explored. Indeed, the
489 fitted RUE are quite different from one model to another, and slightly higher than the
490 ones that can be found in the literature and that rarely exceed 4 g.MJ^{-1} : Damay and
491 Le Gouis (1993), between 2.96 and 3.76 g.MJ^{-1} , Milford and Riley (1980), between 3.16
492 and 4.12 g.MJ^{-1} , Biscoe and Gallagher (1977), 3.5 g.MJ^{-1} , . . . even if in their book on
493 STICS, Brisson et al. (2008) provided a value of 4.8 g.MJ^{-1} for sugar beet, which is closer
494 from the values that we obtained. This ‘overestimation’ of the RUE parameters can be
495 due to the fact that not all of the models parameters were estimated in the end, thanks
496 to the sensitivity analysis that allowed us to reduce the dimension of the parameter
497 space, but that also lead to some compensations between the parameter values. This
498 compensation can also arise when the initiation time is not properly estimated, as it can
499 lead to a too high RUE value, as detailed above. In our study, the calibration of more
500 parameters in the Greenlab model allowed us to obtain a more biologically sound value
501 for this parameter. More generally, one should bear in mind that results from sensitivity
502 analysis and model selection as proposed in the first part of our paper are only a guide
503 for the modeller, and the biological interpretation of the fitted models should be checked
504 for carefully.

505 Finally, the proposed approach is an illustration of “the good modelling practice” (Vos

506 et al., 2007) that should be implemented in plant growth modelling. When modelling
507 complex systems like plants, it is important to rely on a rigorous methodology and par-
508 ticularly, to define quantitative or qualitative objectives to the models, to find the proper
509 balance between model complexity and robustness, and to rely on objective criteria to
510 evaluate (and compare) the models.

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613 **AppendixA. Parameters**

614 The models presented in this paper involve a lot of different parameters, that are
615 presented in the table below.

616 [Table 7 about here.]

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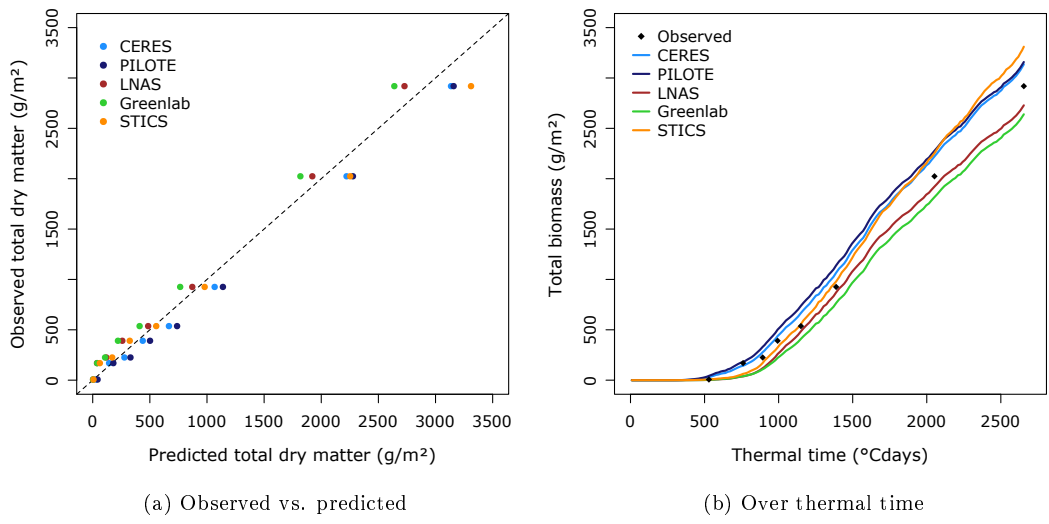
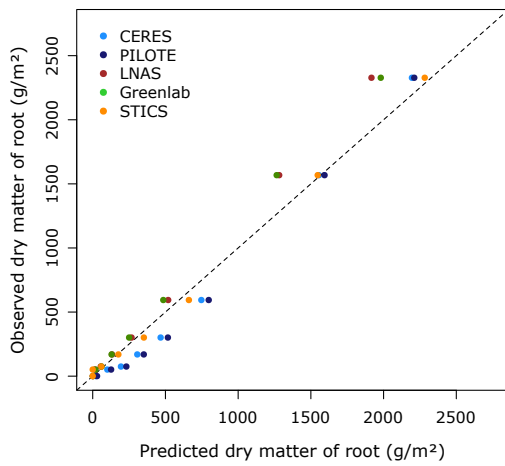
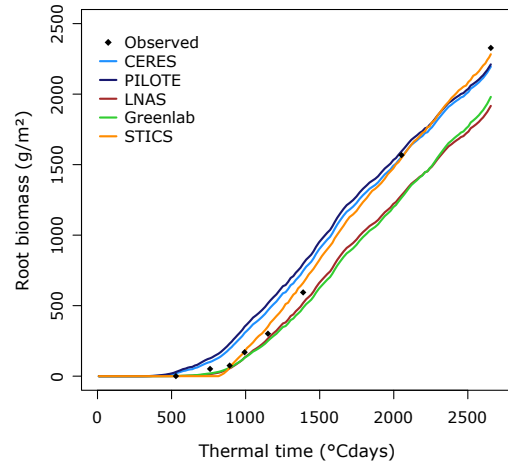


Figure A.1: Models' predictions for the total dry matter in 2008



(a) Observed vs. predicted



(b) Over thermal time

Figure A.2: Models' predictions for the dry matter of root in 2008

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Table A.1: Classification of the five models according to the modelling scale and the presence or absence of allocation processes.

| | Modelling scale (per m²) | Modelling scale (per plant) |
|----------------------|--|------------------------------------|
| No allocation | Pilote | CERES |
| Allocation | STICS LNAS | Greenlab |

| Greenlab | Pilote | LNAS |
|--------------------------|----------------------------|--------------------------|
| $\mu : [5;6]$ | RUE : [3;4] | RUE : [3;4] |
| $S_p : [0.05;0.10]$ | $\alpha : [1;2]$ | $e_g : [50;70]$ |
| $p' : [0.3;0.45]$ | $\beta : [0.5;3.5]$ | $\mu_a : [400;800]$ |
| $p'' : [1.35;1.65]$ | $\tau_{max} : [800;1200]$ | $\sigma_a : [200;2000]$ |
| $\alpha_b : [3.38;3.55]$ | LAI _{max} : [4;6] | $\mu_s : [2000;3000]$ |
| $\beta_b : [5;5.45]$ | | $\sigma_s : [3000;6000]$ |
| $\alpha_p : [3.7;3.8]$ | | $\gamma_o : [0.7;1]$ |
| $\beta_p : [5.25;5.40]$ | | $\gamma_f : [0;0.3]$ |
| $\alpha_r : [4;4.6]$ | | |
| $\beta_r : [2.1;2.8]$ | | |

Table A.2: Variation intervals for the model parameters. We refer to Brisson et al. (2008) for recommended values for STICS. The variation intervals were then defined with a 10% variation around these reference values.

| Number of parameters | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
|----------------------|------|-------------|-------|-------|--------------|--------------|-------|--------------|-------|-------|--------|
| STICS | AICc | 4.63 | 6.77 | 8.29 | 10.82 | 13.55 | 16.48 | 19.63 | 23.02 | 26.68 | 30.65 |
| | BIC | 6.06 | 9.50 | 12.18 | 15.70 | 19.26 | 22.81 | 26.37 | 29.92 | 33.48 | 37.03 |
| Greenlab | AICc | 166.91 | 74.40 | 74.10 | 59.46 | 60.77 | 62.54 | 50.83 | 51.20 | 53.25 | 55.31 |
| | BIC | 171.46 | 83.48 | 87.71 | 77.59 | 83.42 | 89.71 | 82.51 | 87.37 | 93.92 | 100.47 |
| LNAS | AICc | 5.05 | 7.12 | 9.44 | 11.77 | 14.34 | 17.05 | 19.92 | 22.95 | - | - |
| | BIC | 6.71 | 10.35 | 14.11 | 17.76 | 21.52 | 25.29 | 29.05 | 32.81 | - | - |
| PILOTE | AICc | 47.08 | 45.50 | 16.15 | 17.63 | 15.19 | - | - | - | - | - |
| | BIC | 48.26 | 47.68 | 19.14 | 21.22 | 19.13 | - | - | - | - | - |

Table A.3: AICc and BIC according to the number of parameters in the model. Results for STICS for more than 10 parameters are not shown as the log-likelihood is constant, and the two criteria are increasing.

| Model | Data used for the calibration | Estimated parameters |
|----------|--|--|
| Greenlab | Dry matter of root, blades and petioles | RUE = 4.03 <i>g/MJ</i> |
| | Individual masses of blades and petioles | $\alpha_r = 3.16$ $\beta_r = 1.04$ $p_p = 0.0039$ $\alpha_b = 3.08$ $q_p = 1.70$ |
| LNAS | Dry matter of root | RUE = 3.53 <i>g/MJ</i> |
| | Dry matter of green leaves | |
| | Dry matter of senescent leaves | |
| PILOTE | Total dry matter | RUE = 4.12 <i>g/MJ</i> |
| | Leaf area index | $\alpha = 1.54$ $\beta = 1.92$ $\tau_{max} = 1830$ °Cday $LAI_{max} = 3.99$ |
| | | |
| | | |
| CERES | Total dry matter | RUE = 4.37 <i>g/MJ</i> |
| STICS | Dry matter of root | RUE = 4.76 <i>g/MJ</i> |
| | Dry matter of green blades | |
| | Total dry matter | |

Table A.4: Data used in the calibration step for the five models, and list of the parameters finally estimated.

| STICS version | Total dry matter | | Dry matter of root | |
|----------------------|-------------------------|-----------|---------------------------|-----------|
| | RMSEP | EF | RMSEP | EF |
| Initial | 271.24 | 0.9217 | 59.26 | 0.9945 |
| Linear | 192.3 | 0.9606 | 39.05 | 0.9976 |
| Linear and cst RUE | 168.87 | 0.9696 | 39.49 | 0.9976 |
| Thermal stress | 171.73 | 0.9686 | 38.61 | 0.9977 |

Table A.5: Evaluation criteria for the different versions of STICS on 2008 data

Table A.6: Evaluation criteria for the five models on 2008 data.

| Model | Total dry matter | | Dry matter of root | | |
|--------------|-------------------------|-----------|---------------------------|-----------|------------|
| | RMSEP | EF | RMSEP | EF | YPE |
| Greenlab | 166.61 | 0.970 | 169.34 | 0.955 | 14.91% |
| LNAS | 110.85 | 0.987 | 180.5 | 0.949 | 17.66% |
| CERES | 127.02 | 0.983 | - | - | 5.70% |
| PILOTE | 170.51 | 0.969 | - | - | 5.02% |
| STICS | 168.87 | 0.970 | 39.5 | 0.998 | 1.92% |

| Model | Parameter | Unit | Meaning |
|----------|---------------------|---------------------|--|
| All | RUE | $g.MJ^{-1}$ | Radiation use efficiency |
| | PAR | $MJ.m^{-2}$ | Photosynthetically active radiation |
| | k_B | - | Extinction coefficient of the Beer-Lambert law |
| Greenlab | μ | $g.MJ^{-1}.pl^{-1}$ | Efficiency coefficient per plant related to the RUE in the following way : $RUE = \mu \cdot S_p \cdot d$ |
| | S_p | m^2 | Parameter related to the 2-D projection of the space occupied by the plant on the floor |
| | e_b | $g.m^{-2}$ | Mass of blade per unit area of blade |
| | p' | - | Sink strength of petioles |
| | p'' | - | Correction of p' according to a competition index between blades and petioles |
| | α_o, β_o | - | Parameters of beta law for the sink function of organ o ($o = b$ for blades, $o = p$ for petioles and $o = r$ for root) |
| LNAS | e_g | $g.m^{-2}$ | Mass of leaf per unit area of leaf |
| | μ_a | - | Median of the lognormal law assumed for the allocation process |
| | σ_a | - | Standard error of the lognormal law assumed for the allocation process |
| | μ_s | - | Median of the lognormal law assumed for the senescence process |
| | σ_s | - | Standard error of the lognormal law assumed for the senescence process |
| | γ_0 | - | Initial proportion of biomass allocated to leaves |
| | γ_f | - | Final proportion of biomass allocated to leaves |
| PILOTE | α, β | - | Empirical parameters for the LAI curve |
| | τ_{max} | $^{\circ}Cday$ | Thermal time at which the LAI is maximal |
| | LAI_{max} | - | Maximal value of the LAI |
| | τ_e | $^{\circ}Cday$ | Thermal time of emergence |
| STICS | α, β | - | Parameters of the logistic curve for the LAI growth |
| | u_{mat} | - | Leaf development unit at the inflexion point of the logistic curve |