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Parametrization of five classical plant growth models applied to sugar beet and comparison of their predictive capacity on root yield and total biomass

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a b s t r a c t

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

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

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

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1. Introduction

A wide range of plant growth models are available in the literature, either generic ones, that can be applied to different species, or more specific ones built for given plants or trees. Some of them are designed to predict yield or biomass production at field scale, and help management decisions, while some others are built for descriptive purposes, to enhance our understanding of plant functioning and simulate plant architecture [\(Fourcaud](#page--1-0) et [al.,](#page--1-0) [2008\).](#page--1-0) One can also be confronted with the need to compare and choose between different versions of the same model, corresponding to different biological assumptions, for example, or to decide whether a given biological process should be accounted for or not.

Depending on their initial objective, these models can have different levels of complexity. For example, descriptive models would tend to be more complex than purely predictive ones as they would integrate more underlying eco-physiological processes (e.g. allocation processes, reaction to environmental stresses, . . .). Often, this increase in the model complexity results in a higher number of parameters, and consequently in a decrease ofthe predictive capacity of the model due to a higher variability. This is the well known bias/variance compromise. However, a lot of models are used as prediction tools even though they were not originally designed for this purpose. It is thus necessary, when using a model, to define

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Table 1

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

precisely the context in which it will be used, and even more importantly, to evaluate properly its performance according to the objective of the study.

In this context, we propose a methodology to build and evaluate different models in a predictive perspective. We apply this approach to five plant growth models for sugar beet crops, with different levels of description and modelling scales: Greenlab [\(de](#page--1-0) [Reffye](#page--1-0) [and](#page--1-0) [Hu,](#page--1-0) [2003;](#page--1-0) [Yan](#page--1-0) et [al.,](#page--1-0) [2004\),](#page--1-0) CERES [\(Jones](#page--1-0) [and](#page--1-0) [Kiniry,](#page--1-0) [1986;](#page--1-0) [Leviel,](#page--1-0) [2000\),](#page--1-0) Pilote ([Mailhol](#page--1-0) et [al.,](#page--1-0) [1997;](#page--1-0) [Taky,](#page--1-0) [2008\),](#page--1-0) STICS ([Brisson](#page--1-0) et [al.,](#page--1-0) [1998,](#page--1-0) [2008\)](#page--1-0) and afifth model named LNAS ([Cournède](#page--1-0) et [al.,](#page--1-0) [2013\),](#page--1-0) based on a global allocation of biomass to the leaves compartment or root. First elements of comparison for Greenlab, CERES and Pilote are available in [Lemaire](#page--1-0) [\(2010\).](#page--1-0)

The five models rely on a similar formulation for the production of biomass, based on Monteith's equation [\(Monteith,](#page--1-0) [1977\)](#page--1-0) and on an extension of the Beer-Lambert law. The accumulated dry matter production is linearly related to the fraction of intercepted radiation, which can generally be expressed according to the leaf area index (LAI) or to the leaves biomass. From this common basis, the models then differ in their formulations of the LAI curve, either based on allocation processes (Greenlab, LNAS) or on empirical relationships (PILOTE, CERES). STICS can be seen as an intermediate between these two approaches, since the LAI is computed from an empirical function, but modulated by a source–sink ratio. Two modelling scales were also compared, with either individual-based models (CERES, Greenlab) in which the LAI was computed from the development of each individual leaf, or more classical crop models (PILOTE, STICS, LNAS) where the LAI was computed per square meter at field scale. The differences between the five models are summarized in Table 1.

All these models have already been tested and calibrated in the case of sugar beet, but the purpose here is to evaluate their predictive capacities. In this perspective, to reduce the variability of the models which included a large number of parameters, a sensitivity analysis was computed for each of them. The parameters were ranked according to their influence on the model outputs, and then, the best subset of parameters to be estimated was identified, according to AIC and BIC criteria. They were first calibrated on the same set of data, and their predictive capacity was then evaluated and compared on an independent data set using three classical criteria: the root mean squared error of prediction (RMSEP), the modelling efficiency (EF), and the yield prediction error. In Section 2, we present the five models, along with the data and the criteria used for the calibration and the evaluation of their predictive capacity. The calibration process, and in particular the sensitivity analysis performed on each model, is described in Section [2.3.](#page--1-0) Results from this sensitivity analysis are given in Section 3.1, those from the comparison between the different versions of STICS, in Section [3.2.1,](#page--1-0) and between the two data sets (calibration and validation sets), in Section [3.2.](#page--1-0)

2. Materials and methods

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 [\(Monteith,](#page--1-0) [1977\).](#page--1-0) 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/m²), 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 $g M$ J⁻¹) ([Damay](#page--1-0) [and](#page--1-0) [Le](#page--1-0) [Gouis,](#page--1-0) [1993\):](#page--1-0)

$$
Q(t) = 0.95 \cdot RUE \cdot PAR(t) \cdot I(t). \tag{1}
$$

The leaf area index is defined as the one-sided green leaf area per unit ground surface [\(Watson,](#page--1-0) [1947\),](#page--1-0) thus some adjustments were necessary for the two individual-based models Greenlab and CERES. In Greenlab, as the biomass production is computed at the individual plant level, a 'local' LAI ([Cournède](#page--1-0) et [al.,](#page--1-0) [2008\)](#page--1-0) was defined, corresponding to the leaf surface of the plant multiplied by a coefficient related to the two-dimensional projection of the space occupied by the plant on the ground (see Section 2.1.1). In CERES, as the biomass production is computed at the square meter level, a 'global' LAI was constructed from the individual leaf surfaces of the plant, by multiplying by the crop density (see Section $2.1.5$).

2.1.1. GreenLab

GreenLab is a generic functional-structural plant model (FSPM), combining the description of the plant architecture and its physiological functioning [\(Vos](#page--1-0) et [al.,](#page--1-0) [2007;](#page--1-0) [Sievänen](#page--1-0) et [al.,](#page--1-0) [2000\).](#page--1-0) The model in its discrete version was introduced by [de](#page--1-0) [Reffye](#page--1-0) [and](#page--1-0) [Hu](#page--1-0) [\(2003\),](#page--1-0) and was studied in the case of sugar beet by [Lemaire](#page--1-0) et [al.](#page--1-0) [\(2008\).](#page--1-0)

In its first version, the time step chosen to compute the organogenesis and the ecophysiological processes was the growth cycle (i.e. the thermal time elapsing between the appearance of two successive metamers). However, for a better accuracy in the handling of continuous variations of environmental conditions, and consistency with the usual daily collection of climatic data, a continuous version of the Greenlab model was used, discretized with a daily time step [\(Li](#page--1-0) et [al.,](#page--1-0) [2009\).](#page--1-0) Such formulation is also more consistent with the other plant growth models studied in this paper and that provide daily outputs ([Mailhol](#page--1-0) et [al.,](#page--1-0) [1997;](#page--1-0) [Guérif](#page--1-0) [and](#page--1-0) [Duke,](#page--1-0) [1998;](#page--1-0) [Spitters](#page--1-0) et [al.,](#page--1-0) [1989\).](#page--1-0)

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

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

with $Q_{pl}(t)$ the biomass production of an individual plant (in g/pl), *d* the plant density (in $pl/m²$), k_B the Beer–Lambert law extinction coefficient, $Q_b(t)$ the accumulated blade 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 coefficient related to the two-dimensional projection of the space occupied by the plant (in m^2 /pl). The biomass production per square meter $Q(t)$ can be obtained by multiplying $Q_{pl}(t)$ by the crop density d. The biomass is then allocated to the different organs of the plant according to source-sinks relationships (we refer the reader to [Yan](#page--1-0) et [al.,](#page--1-0) [2004;](#page--1-0) [Lemaire](#page--1-0) et [al.,](#page--1-0) [2008](#page--1-0) for more details).

2.1.2. LNAS

A simplified model called LNAS ([Cournède](#page--1-0) et [al.,](#page--1-0) [2013\)](#page--1-0) was elaborated, where the biomass allocation is done globally for the whole leaves compartment, instead as leaf by leaf as in the Greenlab model. The leaf area index was obtained by dividing the biomass of leaves by the mass per unit area. It is a generic daily time-step model, presented here in the case of sugar-beet, but that can be easily extended to other plants.

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