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Assessment of Non-Linearity in Functional-Structural Plant Models

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Introduction

Global sensitivity analysis (SA) has known an increasing interest to assess the relative importance of parameters in ecological models [Cariboni et al., 2007] or crop models [Makowski et al., 2006]. Such methods have an important role to play in functional-structural plant growth modeling. The complexity of the underlying biological processes, especially the interaction between functioning and structure [Vos et al., 2009], usually makes parameterization a key step in modeling, and the analysis of model sensitivity to parameters provides useful information in this process. A side result of global SA is that it provides an indicator of the degree of non-linearity of the model by computing the level of interaction between parameters and how this interaction contributes to the variance of the output. Plants are known as complex systems with a strong level of interactions and compensations, and the aim of FSPMs is to describe and understand this complexity. As such, non-linearity is expected to play a key role in the study, since it reveals the interactions between parameters [Cariboni et al., 2007] [Saltelli, 2002]. The knowledge of the intrinsic non-linearity of the model and of its dynamic evolution throughout plant growth is very useful to study model behavior and properties, to underline the occurrence of particular biological phenomena or to improve the statistical analysis when confronting models to experimental data (e.g. statistical properties of estimators or numerical methods to compute the propagation of errors [Julier et al., 2000]).

The objective of this paper is thus to explore the level of linearity of 3 FSPMs with different levels of complexity, and infer in each case what information can be drawn from this analysis. We first introduce the basic principles of Standard Regression Coefficients (SRC) method which is used for the analysis and gives a short overview of the different models addressed. We then analyze the results of the linearity study, particularly stressing on the emergence of non-linearity. We end by discussing the interest and potential extensions of this work.

Materials and Methods

Standardized Regression Coefficients (SRC) Method and Linearity Index

A model is represented by a mapping relating the space of inputs to a chosen output. The input factors are supposed to be random variables described by identified probability distributions which reflect the uncertain knowledge of the system under analysis. The SRC ([Cariboni et al.]) method is based on a global linear approximation of the model. It provides the model coefficient of determination R^2 , which represents the fraction of the output variance explained by the linear regression model itself. When $R^2 = 1$, the system is linear and the SRCs can totally explain the variance of the output affected by each factor. The coefficient of determination can thus be considered as a linearity index and is used as such in what follows, in order to assess the non-linearity of models. Even when models are moderately non-linear (i.e. $R^2 > 0.9$), the SRCs can

provide valid qualitative information. When R^2 gets small, the SRCs are no longer reliable sensitivity representations.

Models

First a simple source-sink model of maize growth, GreenLab (description and parameterization can be found in [Ma et al. 2008]), is used to specifically study the process of carbon (C) allocation among expanding organs during plant growth. The model describes dry biomass production by an extension of Monteith's law at the individual plant level and biomass allocation to expanding organs with a proportional model involving empirical sink functions, whose parameters are estimated by model inversion from experimental data. The model time step, also called Growth Cycle (GC), corresponds to the phyllochron. There are 20 phytomers when the plant is fully developed, and the 15th phytomer bears the cob. The total growth lasts for 33 growth cycles.

Second, we study the GreenLab model of tree growth (applied to poplar tree) characterized by the retroaction of plant functioning on its organogenesis [Mathieu et al. 2009]. This model describes tree structural plasticity in response to trophic competition. At each GC, the ratio of available biomass to organs' demand determines the numbers of new phytomers in growth units, the appearances and types of branches, as well as their life spans.

Finally, we consider a functional-structural model, NEMA [Bertheloot et al., 2009], describing C and nitrogen (N) acquisition by a wheat plant as well as C and N distributions between plant organs after flowering. This model has the specificity to integrate physiological processes governing N economy within plants: root N uptake is modeled following the transport systems HATS and LATS, and N is distributed between plant organs according to the turnover of the proteins associated to the photosynthetic apparatus. C assimilation is predicted from the N content of each photosynthetic organ. Consequently, this model is more mechanistic but also more complex than the two previous ones.

In this study, we follow dynamically the linearity index throughout plant growth. For models of GreenLab type, the output of interest for the SA is the biomass production at each GC, and for the NEMA model, grain dry mass, grain N mass and root N uptake are considered.

Results

GreenLab Maize

The linearity analysis for the biomass production is given in Fig.1.a. A non-linear period is denoted by the minimum around GC17. It is a key step in terms of biophysical processes corresponding to the transition between two allocation phases, the first one corresponding mostly to leaf area increase and the second one to grain filling (as illustrated by Fig.1.b showing the biomass allocation to each kind of organs).

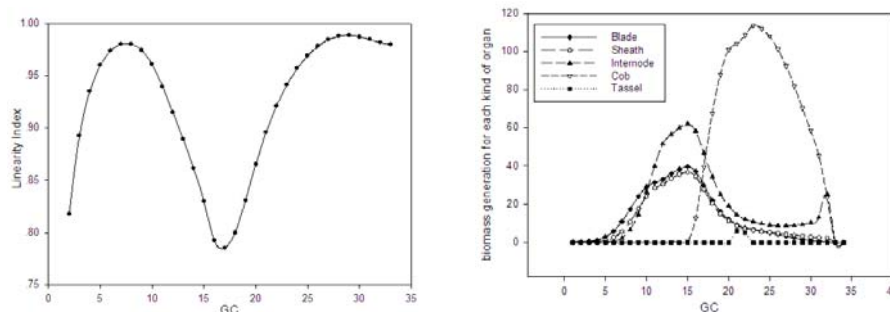


Fig.1 (a) Evolution of the linearity index (b) At each GC, biomass allocation per organ type

Poplar tree model with retroaction of functioning on organogenesis

In Fig.2.a, is shown the evolution of the ratio of biomass production to organs' demand, which is the key variable controlling tree organogenesis in the GreenLab model of tree growth. The linearity index is shown in Fig.2.b. The initial states show the high linearity indices, but it decreases rapidly with the increasing influence of the trophic competition on organogenesis, particularly the appearance of the first branch at growth cycle 5. The linearity index stabilizes at around 0.5, which is quite low, and probably a consequence of the strong level of retroaction in the dynamic system.

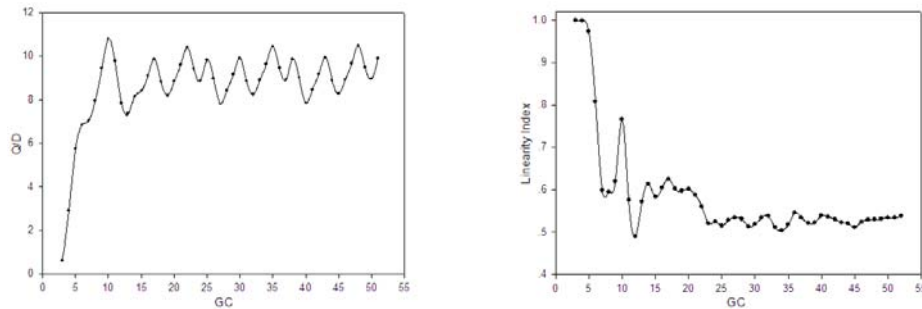


Fig. 2 (a) Evolution of ratio of available biomass to organs' demand (Q/D) (b) Evolution of linearity index

Model of C-N dynamics (NEMA)

The evolutions of the linearity indices for the N mass of the grains, their dry mass and the rate of root N uptake are shown in Fig.3. If the model is highly linear for the grain dry mass Fig.3.a, it is not the case for grain Nitrogen mass Fig.3.b. For N uptake by root Fig.3.c, the evolution of the linearity index is hieratic with a low level of linearity. It seems reasonable when we consider the complex driving forces for N uptake in the model, involving function of the nitrate concentration in the soil modulated by positive and negative feedbacks of respectively C and N in the plant, on root activity.

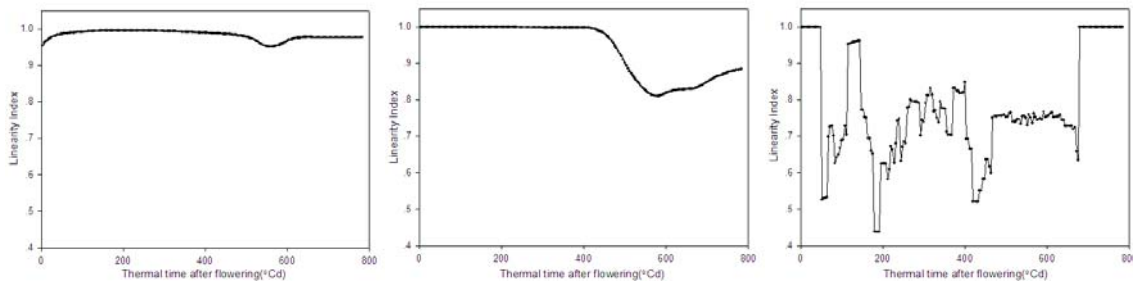


Fig.3 Evolution of the linearity index for different outputs (a) Dry mass of the grains (b) Nitrogen mass of the grains (c) Root N uptake

Discussion

Considering the dynamic evolution of the linearity index throughout plant growth may reveal phases during which linearity is very high, probably showing some stable behavior for which the experimental process for parameter estimation could be lighter in this period. On the contrary, the analysis may show evidence of some moments when a strong non-linearity occurs. Such moments may be characteristic of very specific biological phenomena during plant growth as well as the high level of interactions between parameters, either known by the modeler or unknown, in which case they should probably be investigated more. For non-linear phases, a special care should be taken of in the frequency and details of experimental measures.

For example, since the parametric estimation of GreenLab by model inversion relies on multi-stage observations, the information given by the linearity analysis can be taken advantage of. For

maize, it is important to have detailed and frequent observations between cycles 14 and 20, while the measurements can be lighter after cycle 20. For the poplar tree model, the high level of non-linearity is coupled with the difficulty to get regular observation data (due to the time scale of growth and the weight of experiments). The linearity analysis should thus be coupled with a full SA to help us define a proper strategy for parameter estimation: for example, in two steps as proposed by [Letort et al., 2008], first estimating the functional parameters from the observed topology, then estimating the parameters driving the retroaction of functioning on organogenesis.

For complex bio-physical models like NEMA, we expect a strong genetic determinant of model parameters. One of the interests of assessing the level of model linearity is that non-linear phases are characterized by a high level of interactions between parameters, according to the definition of high-order sensitivity indices, such as Sobol's [Cariboni et al., 2007][Saltelli, 2002]. When model parameters are genetic, understanding and quantifying this interaction is crucial in the objective of using plant models as an intermediate to develop a predictive capacity from genotype to phenotype [Hammer et al., 2006] and design ideotypes. If a parameter has little interaction with others, we can directly concentrate on this trait for the design of ideotypes. If the interaction is strong, it is more complex. If the parameters are strongly genetically related (determination by the same genes), the model parameterization should be improved to take into account this fundamental interaction. If they are not genetically related, breeding strategy should rely on multi-dimensional optimization to handle the interacting processes. The next objective of our study is thus to use Sobol's method [Cariboni et al., 2007] to explore the interactions between processes and parameters for this model.

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