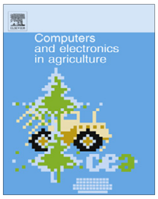
Computers and Electronics in Agriculture 138 (2017) 105–116

Contents lists available at ScienceDirect

Computers and Electronics in Agriculture

journal homepage: www.elsevier.com/locate/compag



Original papers

Yield analysis as a function of stochastic plant architecture: Case of *Spilanthes acmella* in the wet and dry season

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ARTICLE INFO

Article history:
Received 24 January 2017
Received in revised form 14 April 2017
Accepted 17 April 2017
Available online 2 May 2017

Keywords:
GreenLab
Plant architecture
Source-sink parameters
Model calibration
Stochastic method
Functional-structural plant model

ABSTRACT

The number of organs produced by a plant varies among the individuals of a population. Taking these variations into account is an important step in understanding phenotypic variability. The aim of this study was to simulate stochastic development and growth in response to environmental change using GreenLab, an organ level functional-structural model. An annual herbaceous species, *Spilanthes acmella* L., was grown in pots in two climatic conditions corresponding to a wet and a dry season. Detailed records of plant development, plant architecture and organ growth were kept throughout the growing period. The concept of simple and compound organic series was introduced to target data for fitting. The model was calibrated using a mathematical model of stochastic plant development and growth. Here we describe (1) how a stochastic Functional Structural Plant Model is calibrated in two steps by first assessing the functioning parameters of meristems, and second the source-sink parameters of organs by fitting them on average organic series; (2) how dry conditions trigger the response of the plant both in the development of the inflorescence and in the allocation of biomass, quantified by model parameters. The calibration of a stochastic plant model opens a large window of opportunity to capture the common features of plant development and growth among stochastic individuals in a plant population, especially those with a branching structure. This extends the area of application of FSPM to analyzing food plants, or assisting breeding.

1. Introduction

Yield prediction has been the target of process based models (PBM), e.g. APSIM (Keating et al., 2003), STICS (Brisson et al., 2003), CERES (Jones et al., 1986), and PILOTE (Mailhol et al., 2011). PBMs mainly focus on plant population per unit area rather than on individual plants; biomass partitioning is based on organs (leaves, internodes, fruits), and usually total biomass and the compartment representing yield (fruit, tap root, or stem) are taken into account. The basic equation of biomass production relies on light use efficiency (LUE), photosynthetic active radiation (PAR), light interception by the crop at the m^2 level (using the leaf area index, LAI).

The majority of PBMs can predict yield when the components of the plant architecture are simple, such as the plants with a single stem (*e.g.* sunflower, maize). This ensures that the HI does not vary too much in different experiments, an important condition for the satisfactory prediction of yield (Ma et al., 2008). In the case of environmental stress (water, light), or plant architectures with stochastic traits (branching patterns, abortion of organs), problems with PBMs occur because the harvest index (i.e. dry mass of harvested component/the total shoot dry mass) can vary significantly, mainly because biomass partitioning is modified depending on the behavior of the organ abortions during plant development (Marcelis, 1994).

With no precise identification of the origin of variation at the level of organs (abortion, etc.) working with PBMs requires correction of the model using the empirical functions of the organ. The

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http://dx.doi.org/10.1016/j.compag.2017.04.012
0168-1699/

Pilote model (Mailhol et al., 2011) can modify the LAI thanks to an empirical function depending on water shortage. On the other hand, if the plant architecture is simple as in sunflower, PBMs can integrate plant development traits. For example, Sunflow (Casadebaig et al., 2011) computes the size of each leaf along the stem to assess the LAI.

The allocation of biomass to the different organs changes in a complex way depending on the interaction between source-sink organs (Mathieu et al., 2008) and triggers meristem and organ abortion, which is at the origin of the stochastic behavior of plant development.

For a better understanding of the mechanisms that drive biomass production and partitioning, it is useful to consider both plant growth and plant architecture, as well as its phenotypic plasticity, *i.e.* the phenotypic diversity that a given genotype can generate in response to environmental variations (Bradshaw, 1965). This is the domain of functional structural plant models (FSPM), whose goal is to mimic physiological functioning during the growth process in a given environment in the framework of plant architecture. In FSPMs, organs play the role of sources and sinks. The action of light on individual leaves produces biomass that is distributed among competing organs. The drawback of most FSPMs (Allen et al., 2005; Eschenbach, 2005) is that they provide a deterministic description of the meristem functioning at phytomer level.

Stochastic processes have been developed to account for variability in plant architecture. Originally, only plant development was concerned, coupled with fixed organ dimensions, i.e. plants with continuous growth like cotton, (de Reffye et al., 1988), and plants with rhythmic development like poplar (de Reffye et al., 1991). Complex branching patterns interacting with gravity effects have been developed based on Maple tree (Costes et al., 2008).

The both stochastic plant development using meristem activity and plant growth using source sink functioning of organs were integrated in FSPMs. Models like L_peach (Lopez et al., 2008) or Lkiwi (Ciestak et al., 2011), use full simulations for a detailed understanding of the functioning of individual organs according to their position in the plant architecture. Many parameters are needed and their values are preset according to direct measurement made on the plants or values reported in the literature. Simulations are run to illustrate the model's potential to reproduce the major features of the plant's behavior.

Inverse methods that calibrate the functions of individual organs as sources and sinks in real plants are rare, hence only a limited number of computer simulation experiments are available to provide insights into plant behavior (Cournède et al., 2011). The GreenLab model (Kang et al., 2011; Guo et al., 2006; Letort et al., 2008) is one of the few FSPMs that includes an inverse method to calibrate both growth and development from experiments that produced field data on plant organs. Herbaceous plants have specific growth and development features: the young plant exhibit a leaf rosette while the adult plant exhibit a basipetal or acropetal flowering gradient during the stem elongation. So the herbaceous plant as *Brassica napus* L. (Jullien et al., 2011), *Arabidopsis thaliana* (L.) Heynh. (Christophe et al., 2008), *Chrysanthemum* sp (Kang et al., 2012) have been calibrated using software like Digiplant or GreenScilab included the GreenLab model. However, stochastic development was not included in these studies and only average plants built from the statistical distributions were taken into consideration. In addition, while environmental constraints modulate plant architecture (Barthélémy and Caraglio, 2007), few studies produced using the GreenLab model were focused on plasticity in contrasting environments such as that caused by seasonality. In Mongolian Scots Pine, Wang et al. (2012) reported that variation in rainfall affects the biomass increment more than architecture. Under drought conditions, plant growth is generally more limited by organogenesis and organ expansion than by C assimilation (Pallas et al., 2013).

The aim of the present study was to model the relationship between biomass production and plant architecture using a stochastic GreenLab model. The effect of drought on phenotypic variability is revealed through model calibration. *Spilanthes* plants were grown in wet and dry season using a similar experimental design. *Spilanthes acmella* was chosen because of its many food and medicinal uses in Madagascar and of a need to improve the crop (Gockowski et al., 2003). The GreenLab model was used to simulate the stochastic development and growth process with a specific module dedicated to the acropetal flowering sequence.

2. Material and methods

2.1. Experimental setup and data collection

The study was conducted at west Madagascar in Mahajanga (15°41′30.28″S; 46°20′21.86″E). The seeds of *Psilanthes acmella* L. (Asteraceae) came from Mahajanga, a plain with a hot dry climate. After germination, single plants were cultivated in large pots without irrigation and without inter-individual competition. The first experiment lasted from February to May 2012, and corresponded to the wet season. The second experiment lasted from June to August 2012, and corresponded to the dry season (see Fig. 1 for climatic data).

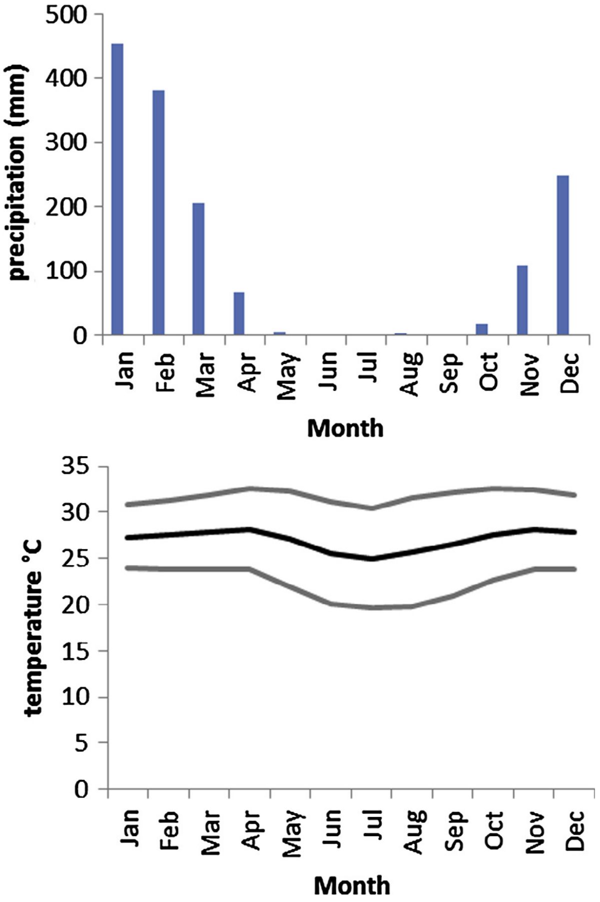

Fig. 1. Climate diagrams (observed precipitations and mean temperature with minimum and maximum curves) were built using data from nearby meteorological stations. From February to May for experimental wet period and from June to August for experimental dry period.