



Comparing an empirical crop model with a functional structural plant model to account for individual variability



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ARTICLE INFO

Article history:

Received 27 January 2012

Received in revised form 5 November 2013

Accepted 7 November 2013

Keywords:

Empirical crop model

Functional structural plant model

Plant variability

Plant architecture

Visualization

Zea mays L.

ABSTRACT

Individual variability generally exists in crop fields. It increases with an increase in plant population density, water or nutrient deficiency, or spatio-temporal irregularity, and often results in a reduction in yield. As individual variability exists in a community but is expressed through individuals, we studied it by applying two models, one at the stand level and the other at the individual level.

The crop model PILOTE and the functional structural plant model (FSPM) GreenLab were applied to a field of maize (*Zea mays* L.) to provide a numerical description of the crop at different levels. The delay and slower increase in LAI and in total dry matter at stand level compared to individual level, led us to hypothesize that uneven emergence could have an effect on variability. We derived a theoretical distribution of germination dates, which supported this hypothesis. In parallel, we used GreenLab to analyze possible sources of variability in accumulated biomass within a dynamic system, and to estimate possible parameters from experimental data.

Using PILOTE and GreenLab, we successfully identified two typical types of individual variability in the maize field: variability in development over time and variability in competition for space during growth. Our method could be used in future research on the cause and influence of individual variability on performance, and to identify the link between an FSPM based on individual plants and a crop model at stand level.

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1. Introduction

In agronomic management and agricultural research, a monoculture crop is normally considered as a uniform whole, even though differences between individual plants are common in the field. In addition to genetic plasticity, the expression of individual phenotype variability reflects varying levels of stress in the local environment of the plant, or caused by neighbouring competitors. Previous studies demonstrated that variability increases with an increase in plant population density (Edmeades and Daynard, 1979; Rossini et al., 2011; Sangoi, 2000), in the case of a water deficit or nutrient deficiency (Tollenaar and Wu, 1999), in the case of irregular plant spacing (Lauer and Rankin, 2004; Liu et al.,

2004b; Maddonni and Otegui, 2004; Pommel and Bonhomme, 1998; Tollenaar et al., 2006) and irregular emergence (Ford and Hicks, 1992; Nafziger, 1996; Nafziger et al., 1991; Tollenaar et al., 2006), and often leads to a reduction in crop yield (Liu et al., 2004a; Muldoon and Daynard, 1981; Tollenaar and Wu, 1999).

Individual variability exists in a plant community but is expressed through the performance of individual plants. Researchers typically sample individual plants from a field and measure the size and weight of each plant to identify variability (e.g. Edmeades and Daynard, 1979). We propose here that models could advantageously replace conventional means, and consequently we used a crop model and a functional structural plant model (FSPM) to test this hypothesis.

Crop models and FSPMs analyze plant growth at different scales. A crop model considers a crop as an object located within the surface area of a field. It can answer questions about how the stand responds to temperature, light, water dynamics, and human factors (e.g. planting density, irrigation) (Bouman et al., 1996; Marcelis et al., 1998). The resulting simulations and predictions therefore provide information that is useful to agronomists, farmers and agricultural operators. However, crop models are strongly dependent

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on the empirical value of certain key variables, such as the leaf area index (*LAI*), and the harvest index (*HI*) (Vos et al., 2007). On the other hand FSPMs consider an individual plant together with its different organs as the research object. FSPMs answer questions about how the structure of the plant evolves through organ build-up, how the plant captures resources (e.g. water, light, *N*) from its environment, and how plant growth interacts with development. Internal processes, such as biomass production and partitioning, are described through organ behaviour (Marcelis and Heuvelink, 2007; Vos et al., 2007). Explicit organic dynamics (i.e. genesis, expansion, activation, abortion or senescence) are established (Werneck et al., 2007). FSPMs play an important role in increasing our knowledge of plant internal activities and how the plant reacts to environmental constraints (Fourcaud et al., 2008). On the other hand, the rapid calculation of a complex architecture and its extension from an individual to the stand are major challenges to the use of FSPMs in the field of agricultural industrial applications.

In this work, we combined the use of the PILOTE crop model and the FSPM GreenLab to study both the stand and the individual plants in a field of maize with the aim of generating numerical representations of the crop at both stand and individual levels. By comparing the outputs of the two models, we expected to identify individual variability and the pattern created by the individuals which build the stand.

2. Materials and methods

2.1. Field experiment

The experiment was conducted in 2009 at the Irstea experimental station in Montpellier, France (43°40' N, 3°50' E) on a loamy soil (18% clay, 47% silt, 35% sand) in the framework of a study dealing with the impact of irrigation systems and irrigation strategies on water productivity (Mailhol et al., 2011). Meteorological data including precipitation, global radiation, and air temperature were recorded at the station. Maize (*Zea mays* L., Pioneer PR35Y65) was sown on April 23 and established at 75,000 plants/ha, where the average density per m² was $d = 1333$ plants/m². Irrigation was by surface drip irrigation; irrigation dates were adjusted on the basis of tensiometer monitoring and neutron probe measurements to avoid drainage problems and to supply 350 mm/m² (see Mailhol et al., 2011 for details), so no water stress was expected in our experiment.

Leaf area index (*LAI*) was measured weekly during the cropping cycle using a LAI2000 (LI-COR). An average of 10 measurements was made in each plot for a given date. Plants from 10 sub-plots (10 plants per row at approximately 2 m length, by 1.5 m width) were collected after maturity to measure total aboveground dry matter and grain yield according to the protocol described by Mailhol et al. (1997).

Organs were observed at five dates during crop development. On each occasion, six plants at the same stage of development (i.e. the same number of metamers) were harvested. The fresh weight of aboveground organs (blade, sheath, internode, ear and tassel) was measured rank by rank to characterize organogenesis and organ expansion.

2.2. Model description

2.2.1. Crop model PILOTE

PILOTE (Mailhol et al., 1997; Khaledian et al., 2009) was designed to simulate crop growth at a daily time step under the assumption that water is the only limiting condition. PILOTE contains a soil module to simulate the soil water balance and a crop module to estimate the resulting crop yield.

In the present study, the soil module was a three-reservoir system (Mailhol et al., 1996, 1997) ranging from the surface of the soil to the maximum root depth. Evaporation was determined by the effect of the current *LAI* on the partitioning coefficient between transpiration and soil evaporation. The soil water balance among reservoirs was calculated on the basis of field capacity (*FC*) and wilting point (*WP*), and the resulting instantaneous water stress index (*WSI*) was exported to the crop module as an environmental coefficient.

The crop module focused on simulating the *LAI* and its response to *WSI* (Eq. (3)). The simulation involved two shape parameters and one vegetative stage parameter (T_m) corresponding to the effective accumulated temperature (effective temperature denotes daily mean air temperature above a cultivar-specific base temperature T_b , $T_b = 6$ °C for maize in the present work) when the maximum *LAI* (LAI_X) was reached. T_m and LAI_X were measured in the field. Total dry matter (Q_p) was calculated based on Beer's Law (Eq. (1) in Table 1), according to which *LAI* was affected by *WSI* (Mailhol and Merot, 2008). Grain yield was evaluated as the product of Q_p and a harvest index (*HI*). The *HI* was set to a potential value (corresponding to the value unaffected by water stress) if the average *LAI* from the 'grain filling' stage to the 'pasty grain' stage was greater than a defined threshold value; otherwise it decreased linearly (see Mailhol et al., 2004; Khaledian et al., 2009).

Except for the *LAI* shape parameters, which required calibration for the fully irrigated treatment (Mailhol et al., 1997), the other model parameters were derived from the literature and measured in the field when a new crop was to be simulated. The climatic data required were precipitation, global radiation, average temperature, and the reference evapotranspiration. In this experiment, as the irrigation guaranteed adequate water supply, no correction of *LAI* was required.

2.2.2. FSPM GreenLab

GreenLab (De Reffye and Hu, 2003; Yan et al., 2004) simulates individual plant growth as a cyclic process of ecophysiological functions in interaction with the developing plant structure.

The model for structural development, which took over the "AMAP" methodology (De Reffye et al., 1988; Jaeger and de Reffye, 1992), was developed on the basis of comprehensive botanical knowledge and architectural concepts (Barthélémy and Caraglio, 2007). A metamer is the basic architectural unit, which denotes an internode with its attached leaf and axillary buds. Physiological age (*PA*) indicates homogenous metamers in morphogenesis and physiological capacity, which enable structural factorization of the plant (De Reffye et al., 2003; Cournède et al., 2006). The growth cycle (*GC*) is the usual temporal unit used for discretized simulation; it corresponds to the rate of appearance of leaves (phyllonchroon), measured by effective accumulated temperature (Yan et al., 2004). An automaton based on botanical concepts (Zhao et al., 2001; Hu et al., 2003) was used to construct the topological structure of the plant. The dynamics of organ production could thus be derived and were available for the functional simulation.

We adapted an empirical equation based on Beer's law to an individual plant (Eq. (2) in Table 1) to enable rapid estimation of biomass production (Guo et al., 2006; Cournède et al., 2008). Sink-source regulation (Marcelis, 1996) was the main principle used to formulate the balance between the supply of biomass and allocation among organs. The initial source was a seed. We used a green blade as the only source organ; all organs including blade (*b*), petiole or sheath (*p*), internode (*i*), female (*f*) and male (*m*) reproductive organs were the sinks. Each expanding sink organ was in competition for biomass, equivalent to the proportion of its demand (P_o , $o = b, p, i, m$ or *f*) to the total demand (*D*) of all organs. Organ demand was characterized by a sink strength factor (p_o) and a variation curve captured by a beta distribution function (Yan et al., 2004).

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