Simulating maize plasticity in leaf appearance and size using regulation rules

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Highlights: Plants regulate their architecture in response to the growth environment, which challenges us to design models capable of performing well in different conditions. By using self-regulating rules, we reproduced blade and collar emergence time, and organ size distribution along phytomer rank in maize under varying growing conditions. The role of emergence events, e.g. blade tip emergence, collar emergence, in controlling growth phase and elongation duration of different components of one phytomer (blade, sheath and internode) are confirmed.

Keywords: growth regulation, plasticity, blade tip emergence, collar emergence, organ size distribution

INTRODUCTION

Plants react plastically to their environment and to management interventions by adjusting their structure and physiological functions (Sultan, 2010). At the plant level, the main plastic traits are the number of phytomers produced, the size of their organs, the number of branches produced, phyllotaxis, leaf inclination angle, and developmental characteristics such as plastochron (thermal time interval between initiation of successive leaf primordia), phyllochron (time interval between appearance of successive leaves), and leaf elongation rate (Nelson, 2000).

Phyllochron is determined by both timing of leaf initiation at the shoot apical meristem and leaf elongation through the whorl of leaves (Skinner & Nelson, 1995). A stable phyllochron is usually found in most grasses (Fournier *et al.*, 2005; Fournier *et al.*, 2007). Additionally, typical patterns of blade, sheath and internode final size against phytomer rank are found for most Gramineae (Fournier *et al.*, 2007).

However, phyllochron and final organ sizes of an individual plant may change depending on environmental conditions during development (Birch *et al.*, 1998);(Dornbusch *et al.*, 2011). Regulation rules linking organ development within and between phytomers have been reported. For example, there is evidence for a coordination mechanism in which tip emergence, defined as when tip exceeds the highest ligule, of the blade itself controls blade elongation, resulting in a stable phyllochron (Fournier *et al.*, 2005; Verdenal *et al.*, 2008). This idea can also be applied to sheath and internode elongation in which sheath initiation is related to blade tip emergence and fast elongation of internode is related to collar emergence, defined as when collar exceeds the highest ligule (Fournier & Andrieu, 2000; Andrieu *et al.*, 2006). However plant modelers have as yet not succeeded to predict how plant structure and function respond to their environment using such rules.

The aim of this work is (i) to understand how a regular phyllochron emerges from coordination of the dynamic processes of leaf initiation, leaf elongation and whorl construction, as well as (ii) to explain plasticity in leaf appearance in different planting patterns, based on coordination rules between phytomers. Ultimately, we want to predict how phyllochron responds to changes in environment, based on a quantitative model of the regulation rules that govern coordination between the processes of initiation, growth and appearance of plant organs. To this end, we constructed a functional-structural plant model to quantitatively characterize plant responses to growth interaction with neighbors. The model also allows us to simulate plasticity in the patterns of size of blades, sheaths and internodes along the stem, and we expect that it will be useful in understanding the competition for light resources between plants.

HYPOTHESES AND SIMULATIONS

Our model is based on Fournier & Andrieu (2000) and Andrieu et al. (2006), and extends these works with a holistic system view on regulation of whole plant development. The basic hypotheses are as follows:

a. The growth rate of a blade depends on the length of its growing zone, which in turn depends on the length of the sheath tube from which the blade tip emerges.

b. Before tassel initiation, sheath initiation is synchronized with blade tip emergence of the same rank; after tassel initiation, sheaths are initiated at a regular thermal time interval (Andrieu et al., 2006).

c. After ear initiation, collar emergence triggers rapid elongation of the internode of the same rank (Fournier & Andrieu, 2000).

d. Number of initiated leaves and the number of appeared leaves are coordinated with 0.63 appeared leaves per initiated primordia after leaf appearance of rank 3 (Padilla & Otegui, 2005).

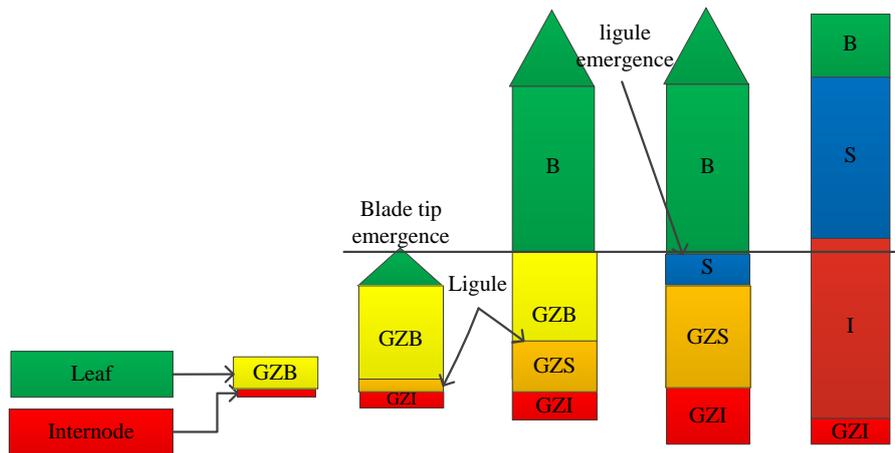The growth scheme of one phytomer, including blade, sheath, internode, is shown in in Fig.1.

Fig.1. Growth scheme of one phytomer. GZ is growing zone where cells divide and elongate. B, S and I represent blade, sheath and internode, respectively. Internode initiation occurs half a plastochron after blade initiation. Before tassel initiation, the ligule appears at the bottom of the growing zone, synchronized with the time of blade tip emergence. After tassel initiation, ligule appears in GZB with a regular thermal time interval (Andrieu et al., 2006). The length of the GZB is linked with time when ligule appears in it, and growth activity gradually shifts from blade to sheath after this. Ligule emergence triggers the growth activity transition between sheath and internode.
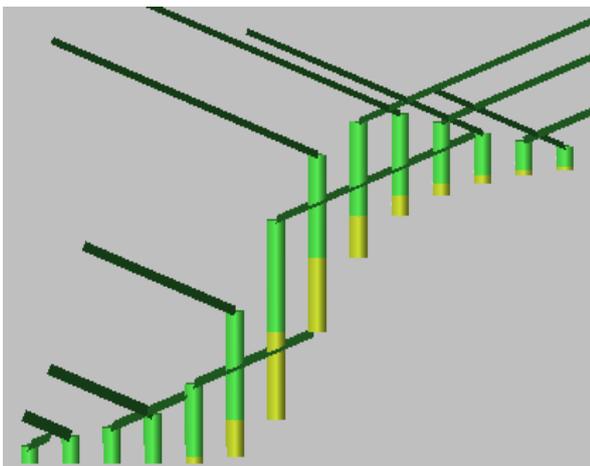

Fig.2 Snapshot of simulation of internode (light green), sheath (green), blade (dark green) extension of different phytomers (count from left right: 1 to 14) at collar emergence of rank 10 in GroIMP
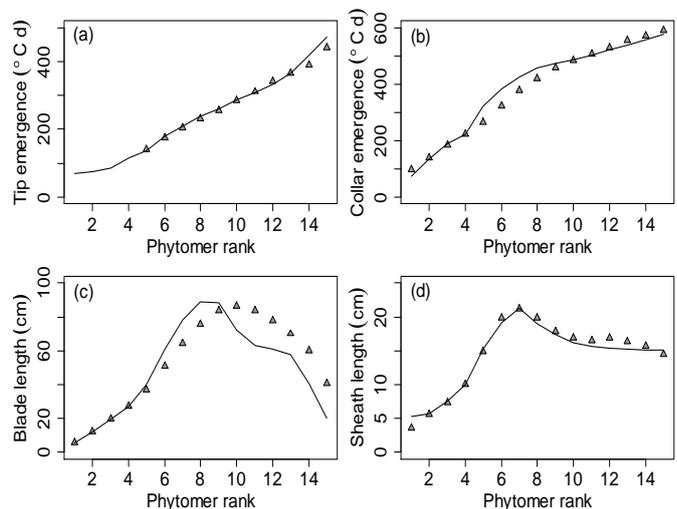

Fig.3: (a) tip emergence, (b) collar emergence, (c) final blade length, (d) final sheath length versus phytomer rank, observed (triangle) and simulated (line). Observed data: Andrieu et al., 2006.

We implemented the model using the GroIMP platform based on Java language and L-system (Hemmerling *et al.*, 2008). The whole plant growth was simulated at phytomer level (Fig. 2). Each element of the phytomer (blade, sheath, and internode) was characterized by several state variables: length and growth phase, e.g. has tip (collar) emerged. The length and growth phase together determine the growth rate of each component. Summed length of blade, sheath and internode determines tip emergence and collar

emergence time by comparing with the sheath length with highest ligule. Subsequently, such events trigger the growth transition from blade to sheath and from sheath to internode.

The relative growth rate at normal population density for blade and sheath of maize (cultivar 'Déa') from Andrieu et al. (2006) and for internode from Fournier and Andrieu (2000) were used to parameterize the model. The growth phases, growth rates, and growth durations were controlled by the regulation rules as mentioned above. Properties of phytomers 1 to 4 were forced as an input.

RESULTS AND DISCUSSION

Simulated tip and collar emergence were consistent with obervations in Andrieu et al (2006) (Fig. 3a). Collar emergence was slightly overestimated for ranks 5-8 (Fig. 3b) The model underestimated final blade length for high ranks (Fig. 3c). Overall, the model reproduced organ emergence and organ size distribution well, based on simple regulation rules that control the growth shift between blade, sheath and internode. The role of emergence events, e.g. blade tip emergence and collar emergence, in controlling growth phase and elongation duration of different components of one phytomer (blade, sheath and internode) are confirmed.

This method enables complex features of architectural development to emerge from a small number of parameters and interactions between different phytomers, which makes it easy to predict correctly how a plant responds to a change in morphology. Therefore, we will use this model to study the shade avoidance response of maize at high population density and in wheat-maize intercropping condtions, aiming at better understanding the performance of maize in competitive environments such as crop species mixtures.

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