

A simple model simulating the construction of blade and sheath length in maize

Christian Fournier¹ and Bruno Andrieu²

1 INRA, UMR 759 LEPSE, 2 place Viala, 34060 Montpellier cedex 01, France

2 INRA, UMR Environnement et Grandes Cultures, Thiverval Grignon, France 78850

{Christian.Fournier|Bruno.Andrieu}@grignon.inra.fr

Keywords: regulation of architecture, simulation, ecophysiology, L-Systems.

Introduction

Thinking at plant architecture as emerging from a simple set of construction rules is a very appealing feature of L-Systems. In the context of crop modeling, it opens new ways to model the effects of environmental stresses on crop architecture, by pointing to regulation loops that are ignored in usual models (Fournier et al., 2007). As such, the triggering of leaf development by emergence events, which has been for long suggested to exist (Dobrynin 1960, Malvoisin 1984, Skinner and Nelson 1994), offers a simple and elegant frame for re-analysing the regulation by the environment of leaf area development (Durand et al., 1999, Fournier et al., 2005a). This would also explain the persistence of stable patterns in plant architecture, despite the variability of environmental conditions in which plants grow. Here we illustrate that point with a simple model simulating some of the regulation processes likely to be involved in the construction of maize shoot architecture.

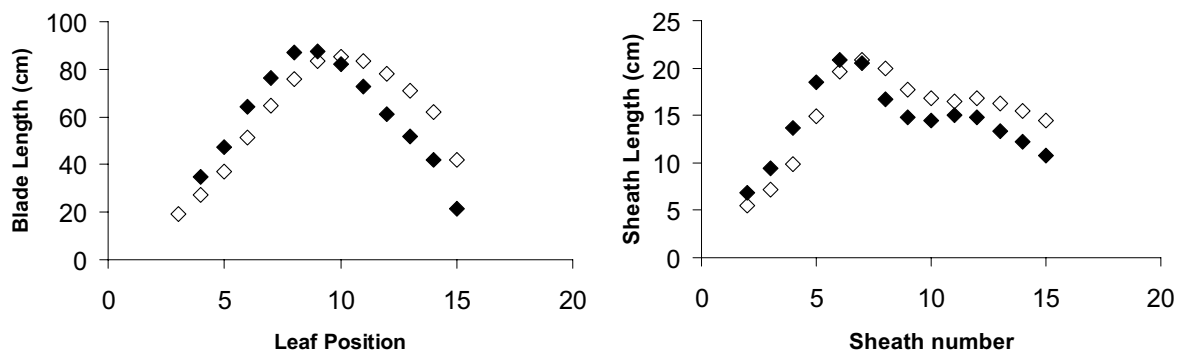


Fig. 1. Patterns of variation of blade (left) and sheath (right) length with leaf position in maize in two contrasted cases : open symbols are for maize grown at normal density, filled symbol are for maize grown at high density

Leaf ontogeny and patterns of leaf length variation in maize

The maize leaf is composed of a sheath, that encircles the stem, and a blade. The leaf appears at the shoot apical meristem as a small protuberance, that will become the blade. During a first stage, which corresponds to the set-up of the growing zone, growth occurs in all part of the blade/leaf. Afterwards, the extension only occurs in the basal zone of the leaf (the growing zone), that dynamically maintains its length, by producing new cells and pushing away mature tissues. At a given time, the leaf sheath boundary appears within the growing zone, defining the onset of sheath extension. This boundary is displaced within the growing zone, and defines, when it overcomes the growing zone, the end of blade extension. Finally, the growing zone collapses and leaf/sheath extension ends. The mature length of sheath and blade therefore reflects the timing of phase changes that occurred at the level of the growing zone during leaf extension. At the plant level, the

patterns relating leaf length and sheath length to leaf position (Fig 1) reflect the coordination of phase changes on successive leaves. The present work aims at explaining how these phase changes are regulated to produce these stable patterns.

Hypothesis

The model is based on the interpretation scheme discussed Andrieu et al. (2006), completed with hypothesis concerning the functioning of the growing zone presented in Fournier et al (2005a,b). It combines three main ideas. The first idea is that for the basal leaves of the plant, the emergence of leaf tips and leaf collars regulates both the transition from blade to sheath extension and the ontogeny of the growth zone, that is the phase changes of leaf extension. Tip emergence triggers the end of spatial extension of the division zone and of the elongation zone, and set-up sheath extension. The emergence of collars triggers the regression of the growing zone, and thus controls the duration of extension. The second idea is that for upper phytomers (those that elongate after floral transition) the dependence of leaf ontogeny to emergence events changes (Andrieu et al, 2006). For these leaves, the set-up of sheath extension occurs at a constant age after leaf initiation (when expressed in thermal time) and the timing of the installation of the growing zone is no longer related to tip emergence, but occurs at constant leaf length. Given the observed concurrent variation of the rate of extension during the installation of the growth zone, it is proposed that this corresponds to a stable number of division events since leaf initiation. Finally, the end of leaf extension remains correlated to collar emergence. The third idea is to use a model of the functioning of the growth zone to build correlations between variables and to predict the time-course of the elongation rate. Here, we consider the growth zone as composed of a division zone that produces a cell flux proportionally to its length, and an extension zone made of cells following an exponential cell extension pattern, whose duration correspond to a constant number of cell doubling periods (Fournier 2005b). As a result, in the model, the variation of the extension rate with leaf stage, leaf position or during stress is related to only two parameters : the length of the division zone and the relative extension rate of cells. Conversely, when, for example, the rate of cell extension is changed, it affects the growth rate of all phases of leaf extension in a coherent way. That model also allows to predict the time course of sheath extension, by simulating the trajectory of a transverse cell wall within the zone.

Model implementation and parameterisation

We implement the model in the L+C modeling language, which provides a good interactivity and a visualization of how the system is constructing the patterns. The computation of the plant according to its topology (from the base to the top) also offers a simple solution for the calculation of emergence events and the triggering of phase changes of young leaves by older leaves. We used the normal density sowing of the detailed dataset of Andrieu et al (2006) to parameterise our equations. We then modified a few parameters to simulate other scenarios and interpret the effects of stresses. In results presented here, we used simplified rules and a simplified model for the functioning of the growth zone. This allows to use directly the data of the original paper of Andrieu et al (2006), but produces some artifacts in the simulations. A re-parameterisation of the model is in progress, that relies on a more realistic description of the functioning of the growth zone. Currently, the model has 5 global parameters, and uses the relative extension rate of each leaf during the first stage (as calculated in Andrieu et al 2006) to calibrate the parameter of the growing zone. We also use exponential extension curves to have an estimation of internode extension, that is required to compute emergence events.

First results

Our first results indicate that the model is able to correctly simulate the kinetic of leaf extension (Fig 2), using a concise set of parameter and a common set of rules for triggering phase changes and the onset of sheath extension. The simulated variations of final length with leaf position are not completely realistic (Fig 2), but the model is able to reproduce the principal traits : leaf length is

increasing exponentially in a first stage, and then decreases with leaf position. To simulate the effects of density, we simply change the dimensions of the first three sheaths and reduce by 20% the relative extension rate of leaves that grow after floral transition (as proposed in Andrieu et al 2006). The resulting pattern reproduces qualitatively the observations, although it tends to amplify the effects of density (upper leaves are too much reduced) and produces some discontinuities. We think that these defaults are linked to the simplifications of the present model.

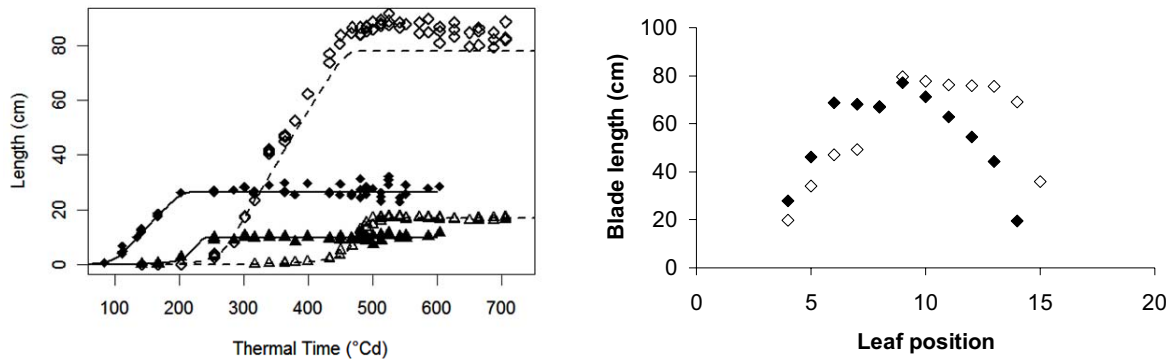


Fig2: Left : Thermal time courses of blade (diamonds) and sheath (triangles) length of leaf 4 (filled symbols) and 10 (open symbols), observed (symbols) and simulated (lines). Right : mature length of leaf blades as a function of leaf position, at normal (open symbols) and high density (filled symbols) with the model

Conclusion

Putting together, with simplifications, three type of ideas of how a maize plant constructs its shoot architecture allows us to reproduce important features of shoot plasticity with density. The role of the sheath tube in regulating plant architecture is confirmed, but this studies also points to the importance of the relative elongation rate of cells in that process. The model unifies three levels of description of shoot development used in ecophysiology : the functioning of the growing zone, the growth curve analysis of leaf extension and the analysis of pattern of mature dimension along the shoot. This open new opportunities to link and interpret the effect of stresses, for which we have details at several levels, but lack of an integrated view. In particular, the present model could help at predicting the consequences of a transient stress on subsequent leaves. This ability to reason phenotypic plasticity would greatly increase the range of application of FSPM in agronomy.

References

- Andrieu B., Hillier J. & Birch C. (2006) Onset of Sheath Extension and Duration of Lamina Extension are Major Determinants of the Response of Maize Lamina Length to Plant Density. *Annals of Botany*, 98, 1005-1016.
- Dobrynin G.M. (1960) Lois régissant la formation de la pousse chez certaines graminées. *Doklady Akademii Nauk SSSR*, 130, 223-226 (French translation, original in Russian).
- Durand J.L., Schauffele R. & Gastal F. (1999) Grass leaf elongation rate as a function of developmental stage and temperature: Morphological analysis and modelling. *Annals of Botany*, 83, 577-588.
- Fournier C., Durand J.L., Ljutovac S., Schauffele R., Gastal F. & Andrieu B. (2005a) A functional-structural model of elongation of the grass leaf and its relationships with the phyllochron. *New Phytologist*, 166, 881-894.
- Fournier C., Muller B. & Tardieu F. (2005b) Which characteristics of the division and of the expansion of maize epidermal leaf cells are intrinsic to the genotype ? Paper presented at the XVII International Botanical Congress, 17 - 23 July, Vienna, Austria.

- Fournier C, Andrieu B, Buck-Sorlin GH, Evers JB, Drouet J-L, Escobar-Gutierrez A, Vos J. 2007. Functional structural modelling of gramineae. In: Vos J, Marcelis LFM, Visser PHBd, Struik PC, Evers JB, eds. Functional-Structural Plant Modelling in Crop Production. The Netherlands: Springer, 175-186.
- Malvoisin P. (1984) Organogenèse et croissance du maître-brin du blé tendre (*Triticum aestivum*) du semis à la floraison.II.- Contrôle des relations entre la croissance et la vascularisation de la tige et des feuilles. Essai de modélisation. *Agronomie*, 4, 587-596.
- Skinner R.H. & Nelson C.J. (1994) Epidermal cell division and the coordination of leaf and tiller development. *Annals of Botany*, 74, 9-15.