

## CHAPTER 15

### FUNCTIONAL-STRUCTURAL MODELLING OF GRAMINEAE

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**Abstract.** The Gramineae have been a pioneer group among non-woody plants to be modelled with the approach of functional-structural plant modelling (FSPM). During the past decade, models have focussed on morphological aspects of plant development. They now provide crop scientists with general guidelines for building new cereal models. We present some of them here, considering the different aspects of cereal architectural modelling: plant development, pattern formation and plant geometry. We also review some significant examples that illustrate the different types of uses of these models for agronomic research. We conclude that the next generation of cereal models should be based on a less empirical modelling of the processes that control morphogenesis.

#### INTRODUCTION

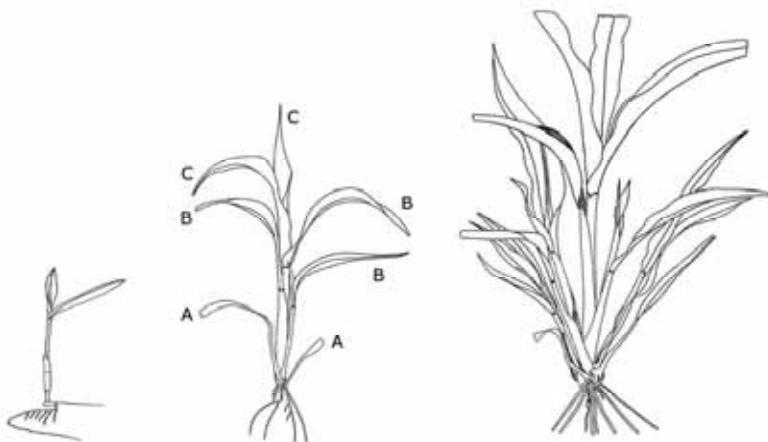
Because of the economic importance of cereals, the Gramineae have long been of interest to crop modellers and were a pioneer group, among non-woody plants, to be modelled with the approach of FSPM (e.g. Goel et al. 1990). Classical crop models greatly increased our understanding of plant–environment interactions, but paid much more attention to mass growth and resource acquisition than to plant morphogenesis. This is changing thanks to the development of numerous cereal architectural models, which mostly focus on morphological aspects of plant development (Fournier and Andrieu 1998; Buck-Sorlin and Bachmann 2000; Kaitaniemi et al. 2000; Wernecke et al. 2000; Fournier et al. 2003; Evers et al. 2005;

Buck-Sorlin et al. 2005; Watanabe et al. 2005), and its regulation by resource availability (Fournier and Andrieu 1999; Drouet and Pagès 2003; Guo et al. 2006). We propose here to give an overview of these advances, together with the new type of issues they bring to cereal crop modellers. We first describe the basics of the architectural development of grasses, and point to the central question of pattern emergence and morphologic plasticity. Second, we give some guidelines on the principal aspects to be addressed when developing a cereal SPM, and finally illustrate, using two different examples, the current applications of this kind of tools.

## BASICS OF GRAMINEAE ARCHITECTURE

### *Description of architectural development*

The architecture of Gramineae results from the repeated formation, expansion and senescence of a basic unit, the phytomer (see McMaster 2005). Phytomers are formed sequentially at the top of each axis by a dedicated structure: the shoot apical meristem (SAM). During the vegetative stage, phytomers usually consist of an axillary bud, an internode, a node, and a leaf that is composed of a sheath and a lamina. The seed already comprises one embryonic axis, composed of a few vegetative phytomers and a SAM that will give rise to the main stem of the plant. Ramification occurs when axillary buds develop into new SAMs, which, if conditions are favourable, will generate lateral axes: the tillers. Externally, the



**Figure 1.** Morphological development of Gramineae as exemplified by first stages of development of sorghum (drawing by C. Loup, INRA 1996). Left: emergence of the first two leaves from the coleoptile. Middle: morphology before tillering stage: (A) older leaves bend down, (B) mature leaves are unrolled and positioned, (C) growing leaves form a more erect structure: the whorl. Right: morphology of the base of the plant during tillering: tillers appear within a sheath, inclined toward the horizontal

accumulation of phytomers at the apex of each shoot leads to the typical nested architecture of grasses, each phytomer being enrolled within the leaf sheaths and blades of the older ones, and rolling in the younger ones (Figure 1). Tillers emerge from the sheaths and develop into lateral axes that first bend towards the horizontal (Figure 1) and later incline towards the vertical.

At a given time, the SAMs shift to the reproductive stage and initiate new types of phytomers that will develop into inflorescences and end the annual cycle of the plant. Gramineae exhibit a wide range of morphologies of inflorescences, which will not be described here (see Arber 1965; Weberling 1989 for standard work on the topic). As an example, in wheat and barley, the typical ear is made up of a rachis consisting of short internodes, with one or more spikelets being inserted at each rachis node. Each spikelet is a compressed shoot structure consisting of one (barley) or several (wheat) flowers, at the base of which are two bracts (glumes), marking the limit of the spikelet. The flower as such is hulled by two further membranous, leaf-sheath-like bracts: a lemma at the abaxial side and a palea at the adaxial side.

#### *Coordination of development and pattern formation*

Although plant development and the resulting architecture are highly sensitive to environmental conditions (see e.g. Moulia et al. 1999), it is possible to find, for any Gramineae, conservative traits in their morphology, linked to stable features of developmental processes. For instance, typical patterns are found when the size of an organ (lamina, sheath, internodes) is plotted against phytomer rank. The question of the origin of such regularities, which is central for modelling morphogenesis, has raised the interest of botanists from quite ancient times, especially in cereals (e.g. Arber 1934; Prat 1935). However, there are still a lot of unknowns, and only part of the different aspects of the response can be presented here.

For example, the production of regularities in organ size variations along the shoot is probably linked to the strongly conservative nature of the coordination between the visual appearance of leaf tips and leaf collars at the top of the whorl, the initiation of new phytomers by the SAM, and the duration of extension of individual phytomers (see e.g. Fournier et al. 2005 for details). A plausible mechanism is that tip and collar emergence, defined as the event of the leaf emerging from the encircling sheath tube, could be sensed by the plant, triggering various developmental events that control leaf extension, such as the production of an elongation zone, the differentiation of a collar, or the end of cell extension in a growing zone. Conversely, leaf extension is a major determinant of leaf emergence, so that such a feedback mechanism provides the plant with a robust timer for coordinating its development and stabilizing the proportions between the dimensions of successive organs. For wheat, Fournier et al. (2005) simulated such a loop and were able to reproduce the regular increase of leaf length as a function of phytomer rank together with the regularity of the thermal-time interval between the appearance of successive tips.

Second, the stability of several allometries and important patterns of the botanical organization of the axes within a plant, relates to one major developmental

event: the floral transition. In cultivated Gramineae, such as wheat or maize, floral transition occurs when only a few phytomers are fully developed, and thus affects a significant part of vegetative development. Physiologically, this transition corresponds to a change in the activity of the SAM, which initiates new types of primordia and produces various growth substances with pleiotropic consequences on plant development. For example, in maize (see e.g. Moulia et al. 1999 and references included) floral transition at the apex of the main stem simultaneously determines the number of vegetative phytomers produced, promotes internode elongation, stops the production of axillary buds, thus determines ear position as that of the last-formed bud and changes qualitative properties of the leaves (Lawson and Poethig 1995). This results in the stable relationships found in this species between the final number of leaves, the rank of the phytomer bearing the ear (and the largest leaf) and the rank of the first significantly elongated internode (see e.g. Dwyer et al. 1992; Lizaso et al. 2003).

#### *Phenotypic plasticity*

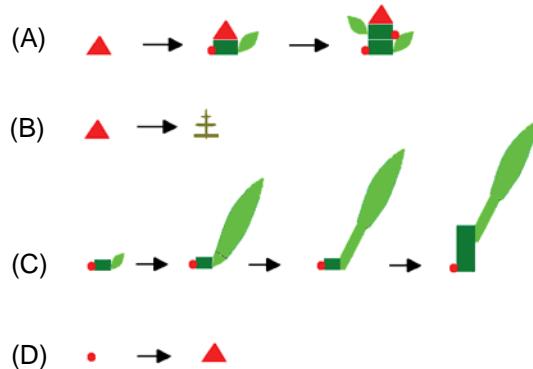
The existence of stable developmental patterns still allows for a great plasticity of plant morphology and development. At the plant level, the main variations concern the number of phytomers produced, their absolute size, the number of tillers produced, the phyllotaxy and the inclination of leaves, and various rates of development such as the plastochnron, the phyllochron or the leaf elongation rate (see e.g. Nelson 2000 for more details). However, especially in the context of FSPM, which describes not only the spatial relations between modules but also in detail the timing of development of individual modules, it is appealing to think of plant plasticity as emerging from the local plasticity and development of the modules the plant is composed of (De Kroon et al. 2005). This led, for example, to the view that intra-plant variation between phytomers (such as the occurrence of branching or the size of organs) arises from identical units having experienced different growth conditions, due to plant development and environmental changes (White 1979). A slightly more elaborate scheme includes the concept of ontogenetic contingency (Diggle 1994), the key point being that modules are not strict repetitions of each other, but that their properties may be determined by the state of other modules at the time they were formed.

### MODELLING GRAMINEAE ARCHITECTURE

#### *Developmental aspects*

Models of Gramineae development are based on the stability of coordinations between developmental events and emergence events at the top of the whorl (see above). Therefore, they generally consist of a qualitative model of plant development, a fixed set of coordination rules, and a scheduling of a few particular sequences of events (generally leaf and collar appearance). The qualitative model defines the developmental events of interest (see, e.g., Figure 2), together with their

timing in plant development. For example, the growth of a phytomer could be modelled as a strict succession of extension of its components: first the blade, then the sheath and finally the internode (Fournier and Andrieu 1998; Fournier et al. 2003). Coordination rules enable the synchronies between the developmental events to be expressed, and thus reduce the parameterization of the whole developmental sequence to the timing of a few events. For example, it is generally assumed that the plastochron, i.e. the time interval between the initiation of two phytomers, is a constant fraction of the phyllochron (the time interval between the appearance of two leaves). In wheat, Fournier et al. (Fournier et al. 2003) also found that the thermal-time duration of the extension of various phytomer components could be considered constant when expressed relative to the thermal-time interval between the appearance of successive collars. Finally the parameterization of the scheduling of a few developmental events enables the question of the rate of plant development in real time to be addressed, together with the synchrony or asynchrony of the different axes of the plant. In wheat and maize, for example, a simple but efficient model is to consider a fixed thermal-time interval between the appearance of two successive leaves on all axes, and tiller-dependant thermal-time delay between the appearance of leaf one on a tiller and leaf one on the main stem (Fournier and Andrieu 1998; Fournier et al. 2003; Evers et al. 2005).



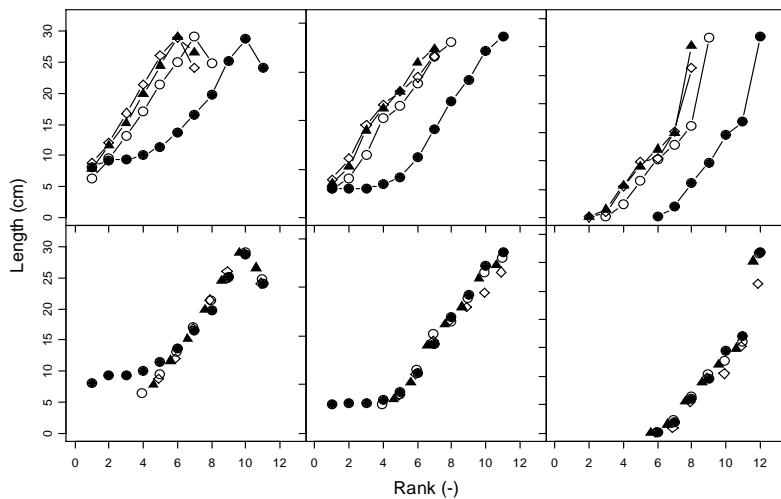
**Figure 2.** Example of a qualitative model of vegetative development of Gramineae. (A) Initiation of phytomers by the apex; (B) transition of apex to reproductive phase; (C) phytomer development showing the succession of rapid elongation phases of blade, sheath and internode; (D) tiller production obtained by transforming an axillary bud into an apex

#### Architectural patterns

The parameterization of architectural patterns generally consists of finding a simple, yet flexible, mathematical expression that relates a phytomer-dependent variable (such as length or width) to phytomer rank. It is worthwhile to choose parameters with a biological meaning related to the developmental process that produced the pattern. For example, in the case of wheat, the variations in the size of modules

along an axis were found to follow quite simple broken line patterns, with one or two breakpoints (Figure 3). The first breakpoint was at a similar rank for all organ types, and corresponds to the rank of the phytomer that was the first to grow after the SAM changed from vegetative to reproductive phase. The second breakpoint was found for laminae and internodes only, and its position close to the top of the axis suggests a change related to floral development.

It is also worthwhile to detect and model similarities among axes. For example, in wheat (Fournier et al. 2003; Evers et al. 2005), rice (Tivet et al. 2001) or barley (Buck-Sorlin 2002) tillers reproduce the patterns of the main stem, for all organ types (laminae, sheath and internode), provided a given offset (or shift), which may be non-integer, is added to the phytomer rank (Figure 3).



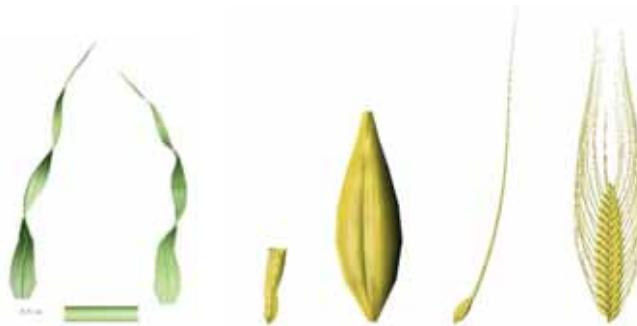
**Figure 3.** Patterns and similarities of organ length variation as a function of phytomer position and axis number. Upper panels show the variation of lengths of laminae (left), sheaths (middle) and internodes (right) for different types of axes: • main stem, ○ first tiller, ▲ second tiller, ◇ third tiller. Lower panels represent the same data after applying a shift to the numbering of the phytomers on each tiller, illustrating that properties of phytomer 'n' on a tiller are the same as on phytomer 'n + s' of the main stem, where 's' is the phytomer shift (number of ranks) that was needed to superimpose the curve of the tiller on the curve of the main stem (after Fournier et al. 2003)

#### Geometrical aspects

Geometrical aspects concern the modelling of individual 3D shapes of organs and the dynamics of shape change during the development of the structures, including unrolling of leaves, geometry of the whorl, bending of axes and azimuthal positioning of leaves. The parameterization and the coding of the geometry of even

complex objects is now within reach thanks to advanced graphical features included in the specialized platforms (Figure 4).

However, relatively little is known about the processes that regulate plant geometry. Therefore, geometrical models rely on empirical functions, with statistical distributions of their parameters. Such models have been developed for, e.g., the shape and inclination of blades (Prévet et al. 1991; Stewart and Dwyer 1999), or the dynamics of inclination of leaves and tillers (España et al. 1998; Watanabe et al. 2005). A limitation here is that the adaptation of plant morphology to the local environment may result in correlations between parameters that are not generally taken into account by this statistical approach. Finally this may induce bias between the properties predicted from these representations and the properties of an actual plant canopy. For example, Gramineae are known to have shade avoidance behaviours (Drouet et al. 1999; Maddonni et al. 2002; Pierik et al. 2005), and the shape of leaves is very sensitive to water stress (Moulia 2000). In the future, these stochastic models may benefit from the integration of more mechanistic approaches.



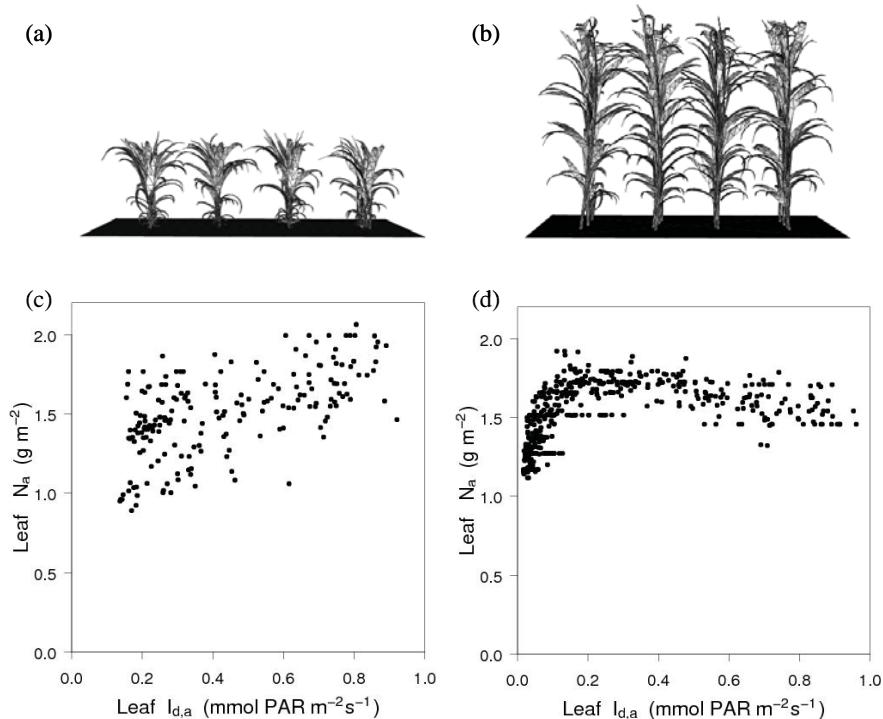
**Figure 4.** Some capabilities of advanced graphical techniques applied to the modelling of various complex shapes in barley. Left: model of a spiralled barley blade with generalized cylinders (L-Studio), Right: textured Bezier surfaces used for a barley inflorescence model (from left to right): rachis element, fertile grain, awn and the resulting spike (after Buck-Sorlin 2002, and unpubl.)

## EXAMPLE OF USES

### *Simulation of experiments*

The ability of morphological models to reproduce *in silico* the 3D development of plants has a direct interest for visualization in the context of, e.g., educational or illustrative purposes (Buck-Sorlin and Bachmann 2000). In ecophysiology, a major interest of these models is the possibility to use them in association with models that compute the microclimate on 3D structures, (like 3D radiative models such as Sinoquet 1993; Chelle and Andrieu, this volume). These tools allow to determine the phytoclimate at the plant organ level, which would be impractical to perform *in vivo*. For example, it is known that in canopies, leaves adapt their photosynthetic activity

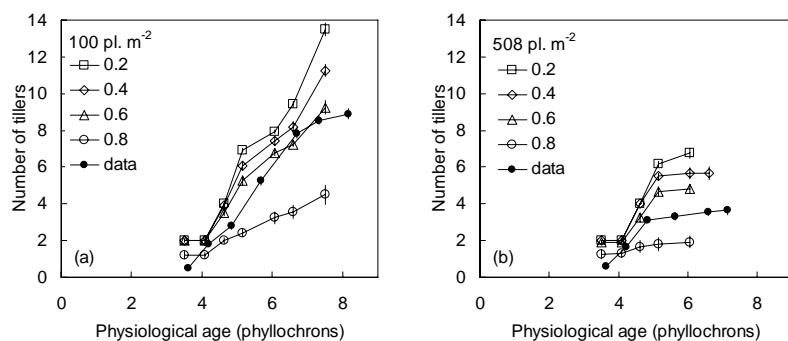
to local light conditions by making nitrogen distribution parallel to light distribution (e.g. Drouet and Bonhomme 1999; Drecer et al. 2000). Processes involved relate to the control of leaf lifespan, nitrogen turnover (see Hikosaka 2005 for a review) and dry-mass accumulation (e.g. Drouet and Bonhomme 2004). Using a reconstruction of 3D description of plant structure at successive developmental stages (Fig. 5a and b, Drouet 2003), it is possible to establish the relationships over time between leaf nitrogen content and light interception at the level of individual leaves (Fig. 5c and d, Drouet et al. 1999). This kind of relationship could not have been obtained experimentally, and is the basis for a mechanistic functional model of acclimation to light.



**Figure 5.** Three-dimensional (3D) description of the aerial structure of maize plants from digitizing (Polhemus, Inc.) within a 10-plant  $\text{m}^{-2}$  canopy at two developmental stages: (a) 60 and (b) 90 days after sowing. (c,d): relationship between leaf nitrogen content per unit area ( $N_a$ ) and daily average leaf irradiance ( $I_{d,a}$ ). Each point corresponds to values of  $N_a$  and  $I_{d,a}$  for any leaf part (after Drouet et al. 1999)

### Test of hypotheses

Empirical morphological models could also be used to test mechanisms and feedback loops that control development, thus catalysing the evolution towards more mechanistic and realistic SPM. For example, the outgrowth of tiller buds in Gramineae is influenced by the flux density of photosynthetically (PAR) and morphogenetically active radiation (MAR) (Varlet-Grancher and Gautier 1995; Bos and Neuteboom 1998), in particular the ratio of the intensities of red and far-red light (R:FR) (Casal et al. 1987). At each point in the plant canopy volume, PAR and MAR levels are affected by surrounding plant tissues (shading and multiple scattering, respectively). It was shown for spring wheat (*Triticum aestivum* L.) that tiller appearance ceased abruptly at specific values of fraction of incident PAR intercepted by the canopy and R:FR at soil level (Evers et al. 2006). Evidence exists that these light properties operate on a local level (Skinner and Simmons 1993; Bos 1999), i.e. the ‘parent’ leaf blade of the tiller bud (this is the leaf blade of the same phytomer as the bud) and the pseudostem (the tube of sheaths), respectively.



**Figure 6.** Number of tillers per plant versus the physiological age of the plants for a population density of (a) 100 and (b) 508 plants  $m^{-2}$ , from simulations using threshold values of PAR intercepted of 0.2 to 0.8, and from experimental data. Error bars show  $2 \times SE$  (after Evers 2006)

A structural plant model of spring wheat (ADELwheat) (Fournier et al. 2003; Evers et al. 2005) was interfaced with a light model (Nested Radiosity) (Chelle and Andrieu 1998) capable of calculating the distribution of PAR and R:FR in the 3D architecture. The empirical model for tiller bud outgrowth was then replaced by more mechanistic rules that depended on (a) the fraction of PAR intercepted by the parent leaf blade of the bud, or (b) R:FR perceived by the pseudostem (composed of sheaths, which are known to act as a R:FR sensor (Skinner and Simmons 1993). Simulations were done for three plant population densities. Bud outgrowth was expressed as a ‘go / no go’ process (according to Kirby and Faris 1972; Evers et al. 2006), depending on threshold values of the fraction of PAR intercepted by the parent leaf blade (a), and on R:FR at the pseudostem (b). These mechanisms were

used to simulate tiller numbers and frequencies of occurrence of tillers at specific positions. It appeared that both simple assumptions on the control of bud outgrowth could result in an adequate simulation of the global tillering behaviour, but with some imprecision in quantitative predictions. An example, corresponding to situation (a), is shown in Figure 6: in accordance with reality, fewer tillers per plant were simulated for a higher plant population density. However, it was not possible to simulate with a unique threshold value the exact number of tillers at the two densities. To improve model performance, other simulations (not shown) suggest the need to incorporate both photomorphogenic effects and the effects of shading on carbon assimilation.

## CONCLUSION

Currently, SPMs of Gramineae are mainly based on empirical parameterization of the emergent properties of morphogenesis: to a large extent, they capture with mathematical relationships the conservative patterns of architectural development, instead of simulating the local processes by which these patterns are built. This is already a valuable step, as it enables complex features of architectural development to be described with few parameters, and brings new simulation capabilities to researchers. However, this makes it more difficult to predict correctly how a plant responds to a change in the environmental conditions, and will be a key issue to think correctly about how morphogenesis interacts with plant functioning.

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