

# ADEL-Wheat: a 3D Architectural Model of Wheat Development

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## Abstract

A 3D architectural model of winter wheat development is presented. The model simulates the kinetics of elongation of individual organs, together with their geometric shape. With the inclusion of two additional parameters, it was possible to model the development of tillers using the same parameter values as for the main stem. The duration of organ extension was found to be the same amongst phytomers, and the kinetics of extension of any organ could be simulated from its final length and two parameters. Finally, lengths of mature organs were found to follow simple functions of phytomer position. The resulting model simulates development of the whole plant with a small number of parameters, characterising the size and geometry of mature organs and the timing of collar appearance.

Keywords: Virtual Plant, Wheat, L-System, Architecture, Tiller, Coordination, Development, Elongation Kinetic, Emergence.

## 1 Introduction

Since the pioneer work of [1], on maize, virtual plant models have gained much interest in the context of crop modelling, as shown by the increasing number of species covered: maize [1, 2], sorghum [3], cotton [4], faba bean [5], barley [6], and white clover [7], among others. Compared to usual crop models, virtual plant models focus on plant rather than on canopy functioning, and the interactions between plants are considered as resulting from the changes in local conditions encountered by individual organs due to neighbouring ones. For instance the local phytoclimate of any organ can be calculated explicitly when the 3D structure of a plant population is described [8], so that competition for light can be simulated dynamically by interfacing a individual-based model of a plant population, and a light model [9]. This approach results in higher genericity of plant models, allowing on one hand an easier link with genomics [10], and on the other hand the modelling of cropping systems having a marked level of heterogeneity (mixture of varieties, high-density canopies, intercropping systems...). Here, we present the first version of such a model on wheat. A virtual plant model should incorporate a parameterisation of development that allows for a detailed simulation of the evolution of the plant 3D structure, with a tractable number of parameters. A useful starting point for this is to quantify the degree to which a plant can be considered as a collection of metamers behaving similarly. In the case of wheat, which produces tillers, this question is addressed here at two levels (i) do tillers reproduce the development of main stem? And (ii) do phytomers (elementary units of a plant comprising a node, its axillary bud, an internode and a leaf composed of a blade and a sheath) behave similarly along an axis? We will focus here on major traits of vegetative development, which are: the timing of initiation and extension of organs, and the geometry of mature organs. As it is well

recognised that the rate of plant development depends on temperature (*e.g.* [11]), we expressed kinetics in thermal time units.

## 2 Materials and Methods

### 2.1 Experiments

Two field experiments were organised at INRA Grignon [12], both with winter wheat (*c.v.* Soisson). Experiment 1 focused on kinetics of development and organ extension, whereas experiment 2 focused on the plant 3D geometry.

In the first experiment, wheat was sown on October 15, 1998. Measurements started on December 7, when the plant had three fully developed leaves and finished on June 6, 1999 when plants had achieved architectural maturity. Plants were grown under non-limiting conditions of water and nutrients, and were kept free of disease and weeds by fungicide and herbicide applications. The experiments included two density treatments: 250 pl./m<sup>2</sup>, corresponding to a usual agronomic density, and a low-density treatment (70 pl./m<sup>2</sup>) to allow for the development of additional tillers. Meteorological data (air temperature at 2 meters, global radiation) were registered by a Stevenson screen, 500 meters from the experimental field. Additionally, soil and organ temperatures were monitored directly by thermocouples inserted in the soil and in plant organs. These data were used to compute the thermal time at each sampling date, using a base temperature of 0°C, widely accepted for wheat. Biological data were monitored from observation and dissection of both main stems and tillers every two or three days. The data set includes: (i) developmental state of the shoot apex (number of primordia, time of double ridge stage, and of terminal spikelet initiation); (ii) kinetics of the lengths of leaf laminae, sheaths, and internodes; (iii) final size of all organs.

In the second experiment, wheat was sown on October 15, 1999 at a density of 250 pl./m<sup>2</sup>. Plants were grown in the same way as in experiment 1, in water and nutrient non-limiting, pest- and disease-free conditions. To account for senescence of basal leaves that occurs before full plant development, the geometry of thirty plants was characterised at two periods. The first measurement period was when leaves 1 to 6 were fully developed and no leaves had senesced; the second measurement period was after heading, when stems were fully extended and leaves 7 to 12 were fully developed. Measurements were performed for the main stem and for all tillers as follows: The insertion height of all leaves, and the shape and orientation of the midrib were measured using a 3-D magnetic digitiser; the 2-D shape of the leaves (leaf width as a function of distance to tip) was also measured. Altogether, the data set includes the 3-D shapes of approximately 1000 leaves, representing all axes and leaf positions. This provided the data for parameterising the shape of the organs.

### 2.2 Modelling

Adel-wheat was implemented using the L-system formalism [13-15], which provides facilities for implementation of virtual plants models. Here we use the software Graphtal [16], available for free on the internet (<ftp://ftp.unibe.ch/pub/Graphics/Modelling>). Only minimal information on L-System modelling is given here. One can refer to [17] for more details on this approach, and to [2, 9] for an example of an L-System maize model built similarly to the current project.

In the L-system formalism, the plant is represented as a string of words and characters, some representing the plant organs (e.g. leaves), hereafter called modules, the others coding for topological or geometrical links between modules. Each module has associated parameters, which allow its state (e.g. present length), or geometric characteristics, to be coded. Plant development is coded by a set of substitution rules (the productions), which are applied simultaneously to the whole string. For example the initiation of phytomers by the apex (fig 1) is coded by a substitution of the apex module by an internode module, a leaf module and an apex module with updated parameters. A key feature of the formalism is that the string coding for the plant includes a code that is interpreted through a dedicated step, to produce a 3D representation.

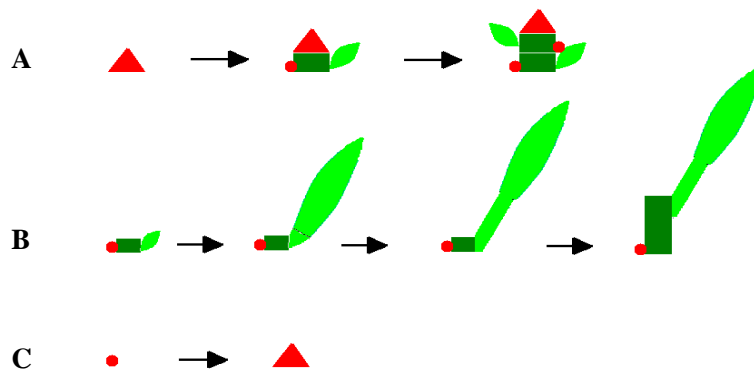


Fig. 1. L-system-like developmental sequences used to model wheat development. (A) Initiation of phytomers by the apex; (B) phytomer development showing the succession of rapid elongation stages of blade, sheath and internode; (C) tiller production obtained by transforming an axillary bud into an apex.

### 3 Results

#### 3.1 Plant development

Plant development could be described simply as the repetition of three sequences of events (Fig. 1). The first sequence occurs at the top of each axis, on a dedicated structure, the apical meristem, on which groups of founding cells successively isolate (initiums), each of it will give rise to a whole phytomer. This sequence interacts with a phase change in the apex, so that lower initiums develop into vegetative phytomers (node, internode, bud, leaf), and higher initiums develop into reproductive organs (spikelets). To simplify this complex behaviour, only the initiation of vegetative phytomers was considered in the model, and was parameterised in terms of the rate of production of initiums and of the total number of phytomers produced. The second sequence is at the level of the vegetative phytomers and says that its components successively enter in a rapid stage of elongation: the leaf blade elongates first, followed by the sheath and then the internode. Simulation of this rapid elongation stage requires information, for each of these components, on the timing of the onset of rapid elongation, and the rate and duration of rapid elongation. We choose to define the timing of rapid elongation based on the emergence of leaf collars, as there exists a

striking synchronism observed experimentally, suggesting that collar emergence is involved in a coordinating process (see below). The third sequence is for the axillary bud, which, after a phase of meristematic development, will either remain dormant (and later possibly abort) or produce a new axis behaving similarly to the mother stem. In the model, these events were coded as a phase of latency, followed by either deletion of the module or its transformation into an apex module. We do not consider here the mechanisms leading to each of these two fates, so the number of buds giving rise to a tiller is a parameter ( $N_t$ ) of the model. Besides the timing of phytomer initiation on all axes, and the number of tillers, the only additional parameter needed to describe the development of a given tiller is the duration of bud latency phase.

To summarise, the development is parameterised with the timing, for all axes, of three developmental events: phytomer initiation by the apex, collar emergence, and end of bud latency phase. Phytomer initiation was found to be a linear function of thermal time for all axes, and parameterised with one parameter, its rate (plastochron). Collar emergence was also found to be a linear function of thermal time for all axes, thus defining a second parameter (phyllochron). The delay between emergence of the collar of the first leaf on a tiller and that of the collar of the axillary leaf on main stem was approximately 3 phyllochrons, but we prefer to keep explicitly one parameter per tiller. Finally, the duration of the bud latency phase was reasonably approximated by a constant duration of four plastochrons for all axes.

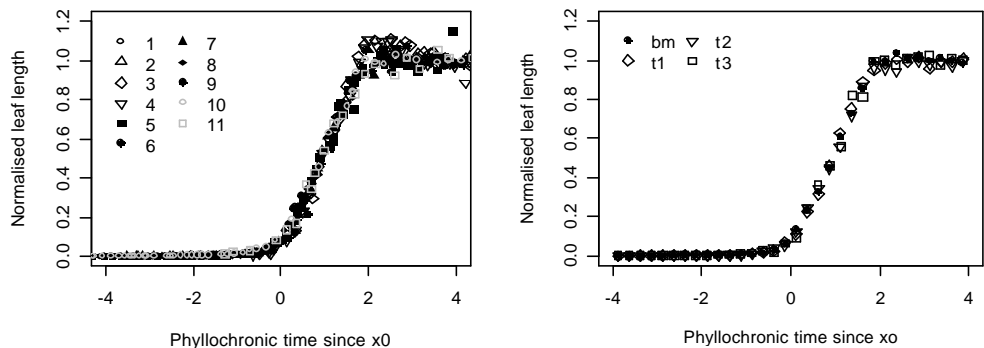


Fig. 2. Normalised kinetics of extension of leaves of wheat grown at 250 pl./m<sup>2</sup>. Left panel is for the different phytomers of main stem (numbered acropetally). Right panel is for the different axes: main stem (bm) and three tillers (t1 to t3). On the right panel, for each axis, data are running-medians averages of all phytomers. Length is normalised with respect to final leaf length and time is counted, for all phytomers, from  $x_0$ , which is the point of intersection of a linear fit of the data with the abscissa.

### 3.2 Phytomer extension

The kinetics of elongation of either leaves or internodes were found to be very similar between axes and between phytomers (Fig 2). Thermal time durations of elongation were the same for all leaves, and for all internodes in the plant, but differed between leaves and internodes. One other striking feature of the elongation curves is the stability of coordination with collar emergence. Collar emergence of phytomer  $n$  was found to be strikingly close to the onset of internode elongation (and thus close to the end of leaf elongation) and to the onset of leaf elongation on phytomer  $n-2$ . For leaves, as collar emergence rate was constant

here, this is equivalent to the observation of a constant duration. However, similar synchronisation patterns with emergence events are also observed on other species [18-20]. This could be interpreted by considering that collar emergence was a trigger of organ extension [21-23]. Therefore, we prefer here to define a constant elongation duration for all internodes and to calculate all other extension parameters (onsets of rapid elongation of leaves and internodes, and duration of leaf extension) using these coordination rules. This would (to be tested) make the model more robust in the case where collar emergence rate varies during development.

### 3.3 Final lengths of organs

The final length of organs varied with position on all axes, but followed similar patterns among axes. More precisely, shifting the numbering of phytomers from a given (optimised) offset, depending on the axis number, makes final lengths follow the same function of phytomer number (Fig 3). Moreover, the shift was the same whatever the type of organ (blade, sheath or internode). This allows defining three functions describing respectively, blade, sheath and internode length as a function of phytomer position on any axis, with only one axis specific parameter (the shift). In total, the number of parameters required to describe the mature length of all organs of a plant is  $10 + N_t$ .

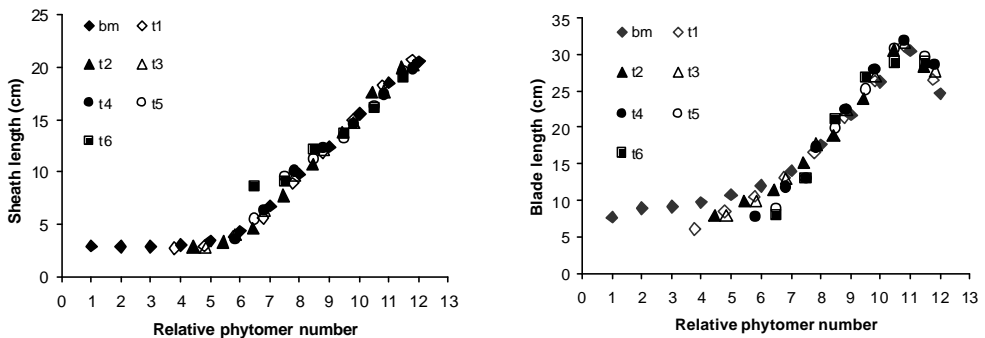


Fig. 3. Measured length of mature leaf sheaths (left) and mature leaf blades (right). The two figures are for the density 70 pl./m<sup>2</sup>: Main stem (bm) and six tillers (t1 to t6). Relative phytomer number is phytomer position for main stem, and is obtained, for tillers, by shifting data on the x-axis to obtain the best superposition with main stem.

### 3.4 Leaf width

Leaf width varies as a function of the curvilinear abscise counted from the base of the blade along the midrib. However, the function describing these variations appears to be the same for all leaves, when the distance is normalised by blade length and leaf width normalised by maximum leaf width [24]. Similarly to [25], we used a second order polynomial to model the leaf width as a function of maximum leaf width. Maximum leaf width was found to be well correlated to either sheath length or blade length (depending on the rank), and the same allometric relationships were found for all axes. This allows, with the use of four additional parameters, modelling of the leaf width.

### 3.5 Plant Geometry

Geometry was analysed for azimuth of leaves and curvature of leaf midribs. The analysis of midrib curvature was performed similar to [25] for maize leaves: the midrib is assumed to be in one plane (no twisting is taken into account) and is described by a parabolic arc for the ascending part and an elliptic arc for the descending part. Two categories of leaves were found, for all axes: basal leaves and the 3 topmost leaves (Fig 4). Basal leaves are almost always strictly ascending and followed an opposite phyllotactic pattern, whereas top leaves have both an ascending and a descending part, with both opposite and spiral phyllotactic pattern and with a narrower phyllotactic angle. This permitted the establishment of two sets of distribution functions for the representation of leaves in 3D.

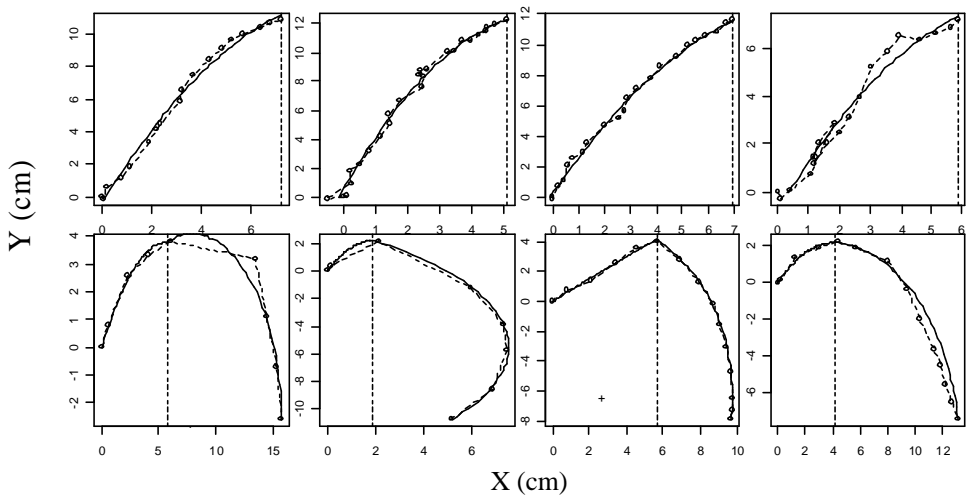


Fig. 4. Examples of measured (dots) and modelled (lines) leaf laminae curvature. X and Y are respectively the horizontal and vertical distance to the base of the leaf laminae (“insertion point”). The first line shows five example leaves of the base of the plant. An ascending parabolic arc can model such leaves. The second line shows five examples of leaves of the top of the plant. Such leaves are modelled as a parabolic portion followed by an elliptic portion.

### 3.6 Simulation of 3D Development

Altogether, 29 parameters were used to simulate wheat development, with the addition of two sets of tables for the geometry of leaves. Simulations were realistic (Fig 5), and we also checked that the model correctly reproduced important agronomic features such as kinetics of LAI and of plant height.

## 4 Discussion

The first aim of this work was to obtain an operational 3D model covering the principal aspects of wheat development. Because relatively few data are published with the required level of detail, this first version relies mainly on the analysis of a single experiment, corresponding to one and two densities. Moreover, not all aspects were studied with the same level of detail, and thus are not expected to have the same degree of genericity.

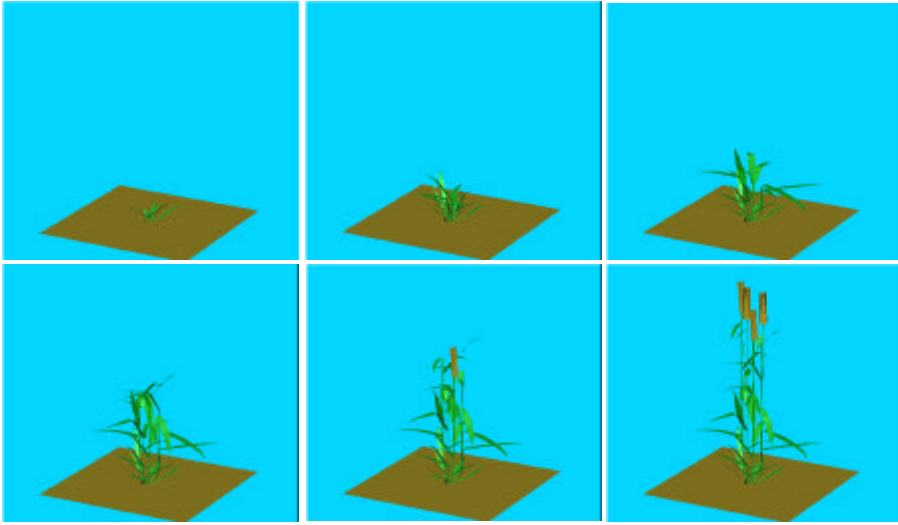


Fig. 5. Sequence of 6 images illustrating the 3D architectural development of wheat simulated with ADEL.

To a large extent, the geometric description of organs (leaf width and midrib curvature) is thought to be only empirical, and expected to vary according to genotype–environment conditions. It is expected to hold generally that dimensions of components of a given phytomer on one hand and the length of organs of successive phytomers on the other hand are highly correlated. This is because our data strongly support the idea that the length of organs are to a large amount controlled by the length of the whorl at the time of elongation [26–28, 23]. That such correlations can result in a rigid parametrisation of the variation of organ lengths with position is based on the idea that the relation between length of successive phytomers reflects a developmental gradient, expressed similarly on all axes (but with an axis-specific delay). Published data (e.g. [29]) suggests that this may be general for winter wheat. However, data published for spring wheat or for winter wheat grown in spring, and data we collected for winter wheat in a glass-house experiment, show a higher variability in the length of successive organs. This suggests that in general the length of one organ is linked to the length of the whorl by a function depending both on the ontogeny and the environment, but that there exists a range of environmental conditions (that encountered in winter sowing) where ontogenetic factor dominate, leading to the stereotyped progression of organ length with phytomer encountered in this study and in the literature for winter wheat. Obviously, more experimental data are required to explore these ideas. Finally, we also believe to be general the fact that the emergence of organs triggers phases changes in the kinetics of organ extension. This idea was also supported in the study of maize internode elongation, by the greater stability of the developmental timing when based on emergence events rather than on thermal time (e.g. [23]), and by the correlations observed by several authors [21, 22, 18, 19, 23, 20]. Moreover, although it may be fortuitous, [30] showed that, on wheat, during the vascularisation of a leaf, the vessels of leaf  $n$  connect themselves to phytomer  $n-2$ , that is to the phytomer that was found here to be involved in the onset of leaf extension. Finally

environmental triggering at organ emergence may be an essential process resulting in formation of both time and size patterns characterizing plant growth.

## 5 Conclusion

An L-system based model simulating the thermal time course of the 3D architectural development of a wheat plant was implemented. The use of similarities among phytomers allows a concise parameterisation that requires only: (i) the calibration of simple functions that describe the final size and the geometry of successive organs along the main stem; (ii) the timing of collar emergence on all axes; and (iii) a (estimated) developmental delay between main stem and every reproductive tiller. This model provides a tool for applications where simulations of plant 3D development are required, after having performed a calibration procedure. Such applications include simulation of satellite signal during crop development, and the simulation of agronomic experiments together with phytoclimate, to investigate processes at a local scale [31, 32]. Other applications, such as the prediction of crop development would obviously require further work. The experimental results on which this model is based support the speculation that the emergences of organs act as triggers allowing the emergence of a stable schedule of organ extension. We propose that a more detailed investigation of the nature of this trigger, and how the response to this trigger is modulated by environmental conditions, is a key to understanding the combination of regularity and plasticity that characterizes the building of plant architecture.

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