

A 3D approach for modelling tillering in wheat (*Triticum aestivum* L.)

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Introduction

In crop science and related disciplines, crop development and growth have been analysed in models that basically describe development in relation to temperature (and in some cases: photoperiod) and in terms of increment of dry matter from light interception. The distribution of dry matter over components (e.g. stems, leaves, roots) and the associated increase in leaf area index are usually functions of development. Such models have been instrumental to provide references for potential crop production in given climates have increased the quantitative insight in crop production and have influenced the agenda of experimental research (van Ittersum et al., 2003).

For wheat (*Triticum aestivum* L.), various advanced crop growth models have been developed (e.g. Jamieson et al., 1998; Ewert et al., 2002). Most of these models do not describe the dynamics of leaf and tiller numbers. Therefore, these models are not particularly suited to analyse and design ideotypes and to explain interactions between canopy architecture and crop performance. To study the dynamics of numbers of organs, their determinants and the consequences of specific physiological responses, models are needed that are capable of describing the morphogenesis and ontogeny of plants in more detail than is done in current crop growth models.

L-systems (Lindenmayer, 1968; Prusinkiewicz, 1999) provide a basically modular approach to modelling, enabling plants and canopies to be described as a collection of modules. In a functional-structural approach, L-systems are combined with environmental models. The virtue is that each next step in the development of the 3D structure can be made dependent of external driving forces, acting on the structure as a whole, but also (and more interestingly) on each individual module. Such an approach is particularly suited for modelling tillering in wheat as influenced by light conditions at the level of the individual organs. For this to be correctly simulated, it is necessary to establish accurate values for the developmental kinetics and geometry of the cultivar of interest.

The current work is based on an L-system of *winter* wheat developed at INRA Grignon (Fournier et al., 2003). The objective of the study is to explain the appearance of a tiller, or conversely: the suppression of tiller growth, from the light regime experienced by the parent leaf in spring wheat. This paper presents the general approach and addresses the parameterisation of the L-system for *spring* wheat

Developmental pattern of the wheat plant and determinants of tillering

The morphological development of wheat is a highly co-ordinated process. Studies such as those by Kirby (1990) and Bos and Neuteboom (1998b) emphasise that the timing of phenological events (initiation and appearance of organs) conform to a fairly fixed pattern. For example, the time of the possible appearance of a specific tiller can be predicted from the stage of development of the main stem or another type of parent tiller.

Tillering is one of the adaptive mechanisms of the wheat plant to keep sources and sinks in balance. The configuration of tillers on a plant (total number and their order, e.g. primary tillers, secondary tillers) reflects the outcome of an adaptive process. Whether particular tillers do appear or not depends on conditions during a window of opportunity for the axillary bud involved. This window is specific in terms of timing and duration. Internal and external conditions that favour growth per plant appear to enhance the number of tillers and the order of tillering that is attained ultimately. These conditions include moderate temperature, high level of incident radiation, high plant nitrogen concentration and low plant density. Unfavourable conditions for growth, e.g. low light level, especially per unit thermal time, and high plant density appear to result in reduced tillering.

Analysis of effects of plant density and radiation (Bos, 1999) led to the hypothesis that the light quantity (Photosynthetically Active Radiation, PAR) received by a parent leaf is decisive for the outgrowth of its bud into a tiller. In this view outgrowth of a tiller is prevented if carbon resources are insufficient to sustain unrestricted growth and functioning of parent plant organs. Furthermore, tillering in wheat appears to be sensitive to changes in light quality, particularly in red/far-red ratio (R:FR) (Casal, 1988; Kasperbauer and Karlen, 1986). These changes in R:FR are the result of selective reflection of light by leaves in the canopy (Holmes and Smith, 1975), and appear to be an environmental cue for impending competition (Ballaré et al., 1987).

The model assembly

To adequately simulate light interception in a wheat canopy and for the calculation of light conditions at the level of the organ (see also Gautier et al., 2000), an L-system of wheat is used in combination with a light interception model. The latter is called the “nested radiosity” model, and is capable of calculating light conditions anywhere in a virtual canopy, taking into account multiple scattering of radiation and changes in its spectral composition (Chelle and Andrieu, 1999).

The wheat L-system is adapted from the ADEL-wheat model (Fournier et al., 2003), using L-Studio (Prusinkiewicz, 2000). It simulates the 3D development of winter wheat plant as a function of thermal time. The simulation of the dynamics of plant architecture requires calculating (1) geometric features such as leaf orientation and midrib curvature, (2) the 2D shape of the leaves, and (3) the kinetics of extension growth of individual organs (blades, sheaths and internodes). An example of a simulated plot is shown in Figure 1. Basically, the architectural wheat model captures the essential features of the temporal and spatial patterns in the formation of plant architecture, which allows simulation of the development of the plant using a limited number of parameters. These parameters are obtained from geometrical measurements characterising the architecture of the mature plant, and the kinetics of collar emergence of successive leaves.

Modelling of organ extension requires simulation of extension of both main stem and tillers, using rules with a restricted number of parameters. These rules were extracted from several detailed experiments on winter wheat. Quantification of the coordination of successive events is an important issue. The start of leaf and internode extension is described in rules assuming co-ordination between phytomers: e.g., the emergence of the collar on phytomer n is considered to be a signal that stops the extension of sheath n , and triggers linear extension of internodes n and of blade $n+2$. Another important feature is that the duration of extension of leaves and internodes was found not to vary between phytomers, the rate of extension being proportional to the final length in winter wheat. Finally, the function of blade length vs. phytomer number showed a “developmental shift”, in which all axes are identical except for a parameter describing the developmental state when the bud was initiated; see Figure 2 for an example. Similarity was found for the 2D leaf shape variables as well, and the midrib curvature parameters were found very similar among leaves on the main stem and the tillers.

In the current work the wheat L-system is extended with rules which process the light information provided by nested radiosity, and make tillering dependent on the intercepted radiation. The first objective is the calculation of the cumulative amount of absorbed energy of each parent leaf (that can potentially produce a tiller from its axil) over time. “Over time” has to be defined more closely as being the “window of opportunity” that is decisive for the outgrowth of the tiller bud. It is hypothesised that the cumulative amount of energy absorbed during the window of opportunity has to exceed a minimum value for the growth of a tiller. Once such a model is calibrated it needs to be tested for a range of conditions (plant densities, light regimes, perhaps experimental manipulations of parent leaves). When the model proves capable of predicting tillering consistently, the conclusion can be drawn that the model essentially reflects the behaviour of the real system. Likewise, hypotheses can be tested on effects of light quality on tillering. It can be calculated when the R:FR ratio of light falling on particular organs drops below threshold values, and such information can be confronted with observed tillering patterns.

Parameterisation

The parameterisation of the original winter wheat model required data collection and analysis to extract robust rules that describe co-ordination of successive events and revealed similarities in

properties among phytomers. At present, similar data are collected and processed for spring wheat. It is embedded in the concept of the current L-system that the description of thermal time course of 3D plant architecture can be simulated based on the knowledge of (1) the final size and geometric parameters for successive organs along the main stem, (2) the timing of collar emergence of leaves on the main stem, and (3) the (estimated) developmental delay between a tiller and the main stem. Geometric parameters are derived from 3D scan data (see Figure 3 for an example of a digitised wheat plant). These parameters include leaf orientation (azimuth) and midrib curvature (Fournier et al., 2003).

In wheat, published data suggest that the morphology of tillers resembles that of the main stems in all cultivars. Similarly, the fact that timing of development of successive phytomers along the main stem is highly co-ordinated appears to be a general observation (Kirby, 1990; Bos and Neuteboom, 1998b), both for spring and winter wheat cultivars. The rules incorporated in the architectural wheat model are an economic way of formalizing these patterns, and hopefully will be valid independently of the cultivar. Hence, it is probably true that parameter values determined for one cultivar can be used to simulate the course of development of other cultivars. This is important, because functional-architectural modelling is not helpful as a tool to analyse problems if first substantial time has to be devoted to model parameterisation. In other words, it is essential in architectural modelling to simplify the concept of the system to the largest acceptable degree. In this context it is more important to stress similarities in parameter values across different types of leaves and tillers than to stress what is different.

On the other hand, genetic and environmental variation affects the final size and geometric parameters of organs along the main stem, as well as the rate of collar emergence. Midrib curvature and leaf width are described in the architectural model by purely empirical rules, thus the value of parameters will change according to genotype-environment interactions. The range of variation is difficult to predict a priori and parameters should be estimated from measurements in any given experiment, especially regarding spring and winter wheat. For example, Figure 2 shows the final length of spring wheat blades for the main stem and primary tillers. It appears that the length of the blades on phytomer 1 vary among stems, whereas for winter wheat these values are more or less similar among stems. Therefore, in the architectural wheat model, the blade length function is different for spring wheat compared to winter wheat.

As was mentioned in section 3, the parameterisation of the length of successive organs along the main stem is based on the idea of a developmental shift. This may be general for winter wheat, as our measurements compare well with published data (e.g. Gallagher et al., 1979). Clearly however, the variability is much higher in spring wheat, probably due to conditions of temperature during the vegetative period, and possibly interactions with photoperiod (Pinthus and Meiri, 1979). Whereas the effect of temperature on leaf length has been demonstrated in numerous studies (Friend and Pomeroy, 1968; Dale, 1982), no quantitative model yet exists, thus organ length along the main stem and its determinants should be investigated for spring wheat.

Concluding remarks

Morphological modelling involves many parameters, of which values need to be specified. Because of the complexity of the various processes and their interactions, creating a complete simulation of a crop (i.e. a complete *virtual plant*) is a very ambitious and time-consuming task. Yet, investigating particular well-defined problems using the advantages a 3D approach appears the most promising way to go. Using an approach to model tillering behaviour in plants as affected by the light environment seems to be very promising, as light interception at the organ level can clearly benefit from an approach that considers the 3D aspects of organs, their relation to other parts of the crop and to the light microclimate.

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Figure 1: Example of a simulated winter wheat plot.

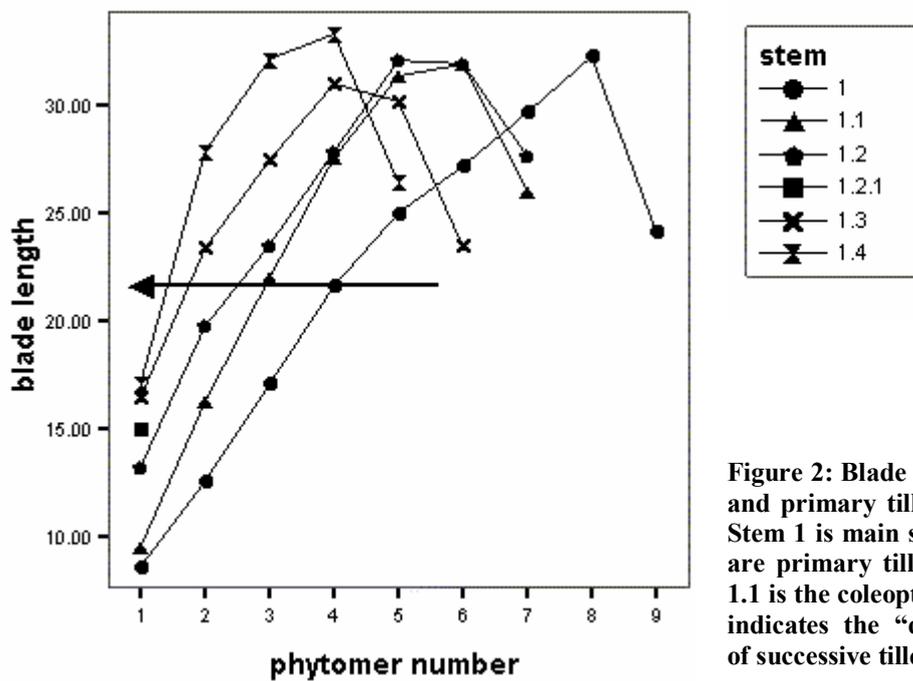


Figure 2: Blade length for main stem and primary tillers of spring wheat. Stem 1 is main stem, stems 1.1 to 1.4 are primary tillers 1 to 4 (of which 1.1 is the coleoptile tiller). The arrow indicates the “developmental shift” of successive tillers.

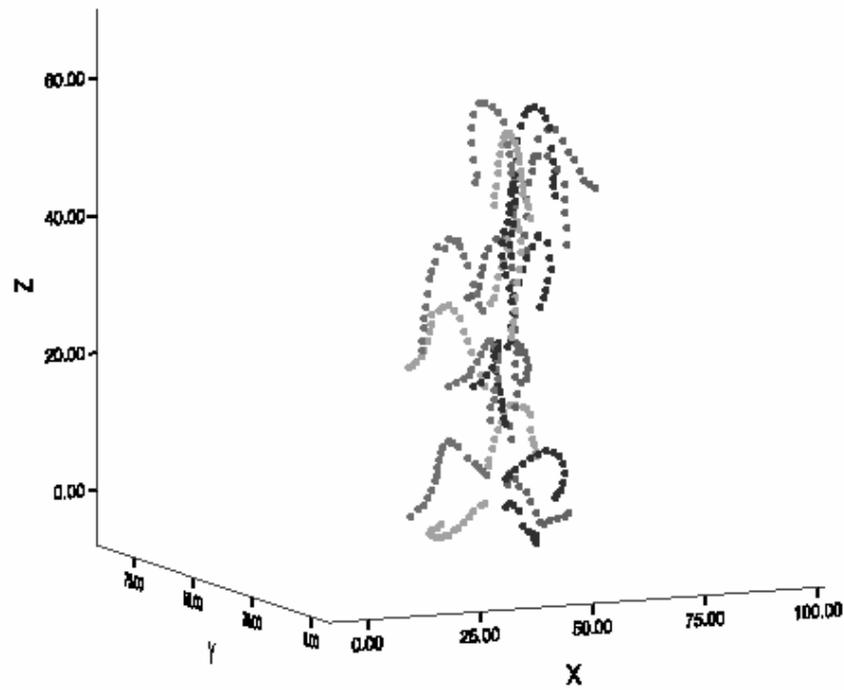


Figure 3: Visualised 3D scanning data (X, Y and Z co-ordinates expressed in distance (cm) to the scanning reference point) for the leaves of one spring wheat plant in booting stage.