

## CHAPTER 17

### A 3D VIRTUAL PLANT-MODELLING STUDY

#### *Tillering in spring wheat*

J.B. EVERS AND J. VOS

*Crop and Weed Ecology Group, Plant Sciences, Wageningen University,  
P.O. Box 430, 6700 AK Wageningen, The Netherlands.  
E-mail: jochem.evers@wur.nl*

**Abstract.** Tillering in wheat (*Triticum aestivum* L.) is influenced by both light intensity and the ratio between the intensities of red and far-red light. The relationships between canopy architecture, light properties within the canopy, and tillering in spring-wheat plants were studied using a 3D virtual plant-modelling approach. The advantage of virtual plant models is that each element in the architecture of the canopy is given an explicit 3D representation, which enables simulation of processes at the level of individual organs.

The model used, called 'ADELwheat', was calibrated for spring wheat. The model was validated for ground cover and leaf area index, using an independent dataset. Experimentally, it was shown that new tillers ceased to appear when the fraction of light intercepted by the canopy exceeded 0.4. That threshold was independent of plant population density, shading, developmental stage of the plants and rank number of the tiller. At the time tillering ceased, the red/far-red ratio (R:FR) was fairly similar across population densities. Cessation of tillering in ADELwheat was therefore made dependent on thresholds of light properties. A light model ('nested radiosity') was coupled to ADELwheat and was used to calculate both PAR interception and R:FR at the level of the individual organ while employing a series of different thresholds. The simulation results show that the virtual plant-modelling approach is useful to simulate global effects of local stimuli. The study demonstrates that the virtual plant-modelling approach can provide insight into the factors that determine the developmental plasticity of wheat in terms of tillering.

#### INTRODUCTION

This chapter presents a 3D virtual plant-modelling study of tillering in spring wheat. A virtual plant (Room et al. 1996) is a three-dimensional representation of the development of a plant or crop, i.e., the geometrical and topological properties of the plant are taken into account. Therefore, in cases in which the research question benefits from analysis at the level of the individual organ, the virtual plant approach has an advantage over less detailed modelling methods.

The subject of this modelling exercise is the phenomenon of tillering (analogous to branching in dicotyledons) in spring wheat, and its determinants. Next to nitrogen availability, which was not taken into account in this study, light properties greatly influence the pattern of tillering in wheat and other Gramineae (Bos and Neuteboom 1998). Two properties of light are especially important:

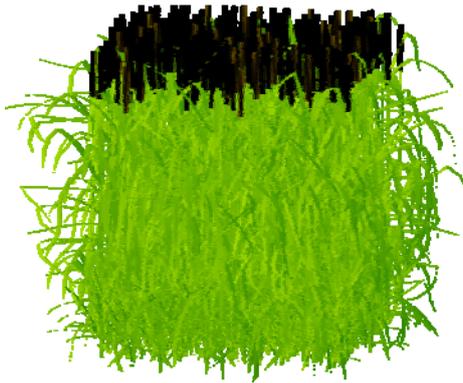
- a) The intensity of photosynthetically active radiation (PAR). It had been hypothesized by Bos (1999), that for tiller bud outgrowth, the PAR intensity incident on the parent leaf of the bud (which is the leaf on the same phytomer as the bud) is an important determinant of bud outgrowth, through its effect on the assimilate production of the parent leaf.
- b) The ratio between the respective intensities of red and far-red light (red/far-red ratio, R:FR). It had been shown that a reduction in R:FR, resulting from the differential scattering properties of plant tissues for red and far-red light (Holmes and Smith 1977), severely reduces tillering in Gramineae (Casal et al. 1987; Casal 1988; Davis and Simmons 1994). Changes in R:FR are perceived by vertically oriented organs such as sheaths and elongating leaves; in general the base of the plant is a site of R:FR perception, especially at early stages of development (Cordukes and Fisher 1974; Skinner and Simmons 1993).

The local nature of the responses to these two determinants of tillering (at the parent leaf and at the base of the plant, respectively) made this problem an ideal candidate to be analysed using a virtual plant-modelling approach. The objectives of the study were (a) to construct and parameterize an architectural model of spring wheat; (b) to evaluate model performance using independent data for contrasting growing conditions; (c) to formulate hypotheses on tiller bud outgrowth in relation to light based on experimental data; and (d) to incorporate these hypotheses into the model and evaluate simulation output.

#### MODEL CONSTRUCTION AND PARAMETERIZATION

The first objective was to design an architectural model of spring wheat, which would be able to produce a 3D description of a wheat canopy (Figure 1), for the cultivar and growing conditions as prevalent in spring wheat cropping seasons in The Netherlands (Evers et al. 2005). In the initial model, the occurrence of tillers was not dependent on light conditions, as this was a feature to be implemented after the correct functioning and performance of the wheat model had been evaluated. The model, which was implemented in the plant-modelling language CPFG (Měch 2005), was based on an existing architectural model of wheat, called ADELwheat (Fournier et al. 2003). This model, based on the L-system formalism (Lindenmayer 1968a; 1968b; Prusinkiewicz and Lindenmayer 1990), contained explicit descriptions of rates of initiation and extension of organs and final organ dimensions, leaf-geometrical properties (base angle, curvature, azimuth), and tillering kinetics. The model was initially parameterized for winter wheat. Reparameterization therefore provided the opportunity to compare parameters and functions for winter and spring wheat. The reparameterization was based on an outdoor experiment using spring-wheat cultivar Minaret, grown in a regular grid in

containers of  $70 \times 90$  cm, at a low plant population density ( $100 \text{ plants m}^{-2}$ ) to induce extensive tillering. The following sections describe a selection of the components that were reparameterized.



**Figure 1.** An example of the visual output of a simulation run for spring wheat at a population density of  $100 \text{ plants m}^{-2}$

#### *Leaf appearance*

The elapsed time between the appearance of two consecutive leaves (the phyllochron), was found to differ between main stem and tillers. This difference was caused by a high rate of appearance (i.e., a short phyllochron) of main-stem leaves one to four, whereas higher main-stem leaves had phyllochron values similar to those of tiller leaves. A similar distinction between early and late leaves was made by Jamieson et al. (1995) for wheat and by Abeledo et al. (2004) for barley. Therefore, the model was parameterized with two values for phyllochron: one for main-stem leaves one to four ( $52 \text{ }^\circ\text{Cd}$ ) and one for all other leaves ( $92 \text{ }^\circ\text{Cd}$ ).

#### *Relative phytomer number (RPN)*

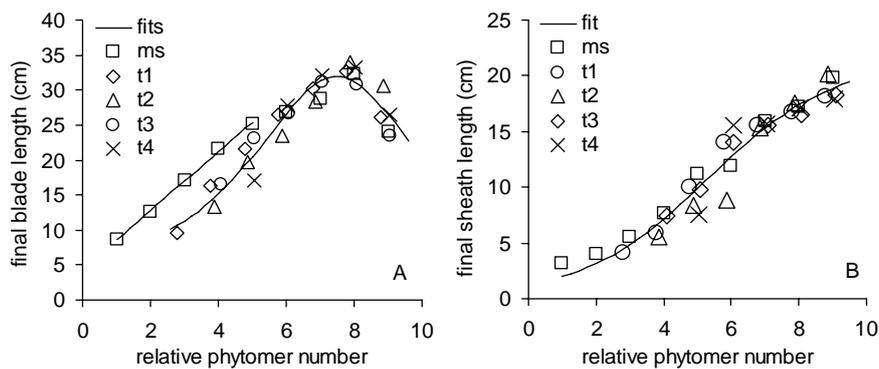
In the original winter-wheat parameterization (Fournier et al. 2003), several properties of tiller organs could be directly derived from those of the main stem using the concept of relative phytomer number (RPN). These properties included leaf blade and sheath dimensions, internode length and final leaf number (see next section for their specific parameterization).

The RPN value of a phytomer is the sum of the rank number of the phytomer on the shoot to which it belongs, and a phytomer shift value. The latter is specific for a particular tiller. For example, if tiller 2 would have shift value 2.7, phytomer 3 on tiller 2 would have an RPN value of 5.7. The components of this phytomer would then have properties similar to an imaginary phytomer 5.7 on the main stem.

The RPN concept appeared applicable to the spring-wheat cultivar used in our study. The shift values differed only slightly between spring and winter varieties.

#### *Organ dimensions and final leaf number*

Final length and width of the leaf blade and final length of the leaf sheath were parameterized by fitting appropriate functions. For blade length, a linear relationship with RPN was used for main-stem leaves one to five, and the Lorentz Peak Distribution function (Buck-Sorlin 2002) was used for all other leaves (Figure 2A). For blade width, a linear relationship of sheath length data with RPN appeared appropriate (not shown). For sheath length, a logistic relationship with RPN was used (Figure 2B). The functions were all slightly different from the ones used for winter wheat, and were discussed to be more applicable for Gramineae in general in Evers et al. (2005).



**Figure 2.** Final blade (A) and sheath (B) length vs. relative phytomer number of the main stem (ms) and primary tillers t1 to t4. The lines indicate in (A) the linear and Lorentz Peak Distribution fits, and in (B) the sigmoidal fit.  $N = 33$  in both cases

#### *Leaf blade geometry*

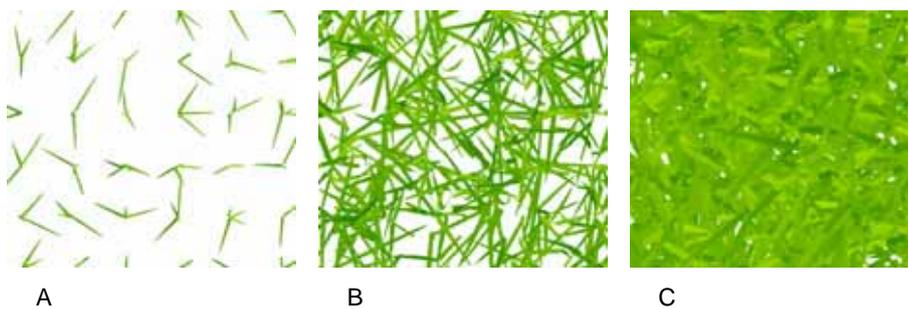
To parameterize the geometrical properties of leaf blades, a Polhemus Fastrak magnetic digitizer was used (Polhemus, Colchester, USA). This method records the coordinates (x, y, z) of a point in space relative to a reference point. For each leaf blade, several points along the midrib were digitized. From these data, the base angle and the curvature of the leaf blades were derived (based on a model by Prévot et al. 1991) as well as the azimuth of the leaves (the angle between consecutive leaves, when viewed from the top). These were all stochastic components in the model: during a simulation, for each individual leaf the coefficients defining its base angle, curvature and azimuth were drawn from observed distributions. This stochasticity reflected the variation as experimentally observed.

## MODEL EVALUATION

To evaluate the parameterization and the performance of ADELwheat, a second outdoor experiment was performed. Three plant population densities were used (100, 262 and 508 plants  $m^{-2}$ , square grid), and the plants were subjected to two light regimes (0% and 75% shading). To obtain additional data, an indoor (growth chamber) experiment was conducted with plants grown at 100 plants  $m^{-2}$ ; light intensity was set at ca. 425  $\mu mol m^{-2} s^{-1}$  at the top of the canopy.

Various components of the model parameterization were evaluated. Generally, phyllochron, tiller appearance delay and the final number of produced leaves were not significantly affected by population density in the full-light treatments. Shade generally increased phyllochron by 13–46% and reduced final number of leaves by 4–25%. The relationships of final blade length and width, sheath length and internode length with RPN were basically similar to the parameterized relationships. However, the coefficient values of these relationships depended on the light regimes and plant population density. The phytomer shift values were similar to those obtained from the parameterization experiment.

The performance of ADELwheat was evaluated using the (logistic) time courses of both ground cover (Figure 3) and gLAI (gross leaf area index, i.e., leaf death not taken into account) as test variables. Both are global characteristics of leaf production and their values integrate effects of several important model parameters and functions such as phyllochron and blade dimensions. ADELwheat appeared capable of simulating development of wheat in growth conditions for which the model was not calibrated (Evers 2006); however, refitting some key coefficients accounting for the effects of population density and shading yielded still better results. A sensitivity analysis of changes in blade length, width, phyllochron and tiller appearance delay showed that phyllochron needs to be parameterized accurately as small changes can have significant effects on the model output. A full description of the model validation and sensitivity analysis can be found in Evers (2006).



**Figure 3.** Top view of ground cover of simulated wheat plots at a population density of 100 plants  $m^{-2}$ , at (A) 183 °Cd, (B) 365 °Cd, (C) 620 °Cd after emergence

## ANALYSIS OF TILLERING BEHAVIOUR

The outdoor experiment that was used for model evaluation was also used to analyse the mechanisms that determine the tillering pattern of spring wheat (Evers et al. 2006). To this end, data were gathered on the tillering dynamics of the plants grown in the different treatments; simultaneously, changes over time were measured in the fraction of PAR intercepted by the canopy and R:FR (both measured at soil surface).

Both population density and shading affected the time course of the number of tillers per plant: a higher population density resulted in fewer tillers per plant than a lower population density, and shading dramatically decreased the number of tillers per plant (Table 1). Tiller appearance was hardly affected by population density, but shading delayed tiller appearance by 0.52 phyllochrons on average. The maximum number of tillers produced per plant differed between treatments, as was the stage of development at which this maximum number was reached (i.e., cessation of tiller appearance). However, the fraction of PAR intercepted by the canopy at the moment of cessation of tiller appearance was identical in five out of six treatments, independent of the rank number of the last emerging tiller, the population density or the shading treatment. Also R:FR at soil level at the moment of tillering cessation was independent of the rank number of the last emerging tiller and the population density, but differed between light regimes. The probability of a bud to grow out was shown to be related to the leaf mass per unit leaf area (LMA, in  $\text{mg cm}^{-2}$ ) of its parent leaf: a low LMA was related to bud dormancy, and a high LMA to bud outgrowth.

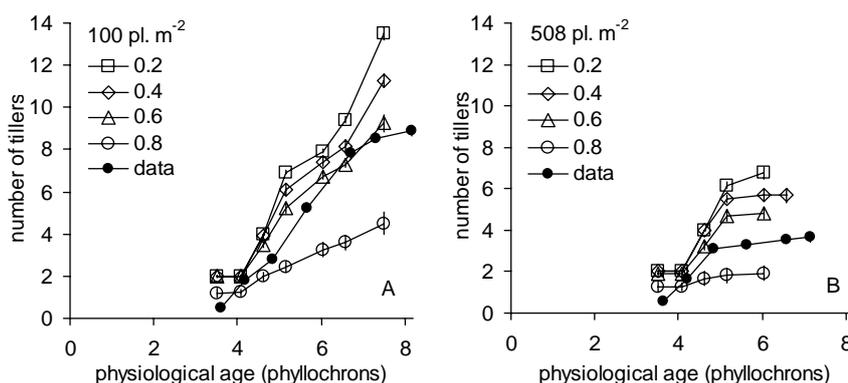
It was concluded that cessation of tiller appearance was primarily regulated by the fraction of PAR intercepted by the canopy, and/or R:FR (taking into account that these two variables are highly correlated) rather than the absolute amount of intercepted light by the parent leaf, confirming suggestions by Simon and Lemaire (1987) and Lafarge and Hammer (2002), and corroborating the results of Sparkes et al. (2006). Only the appearance of the first primary tiller (the coleoptile tiller) seemed related to absolute PAR intensity. A threshold value of fraction of PAR intercepted (0.40) or R:FR (0.32 in full-light situations and 0.51 in shade) was considered to be the trigger of tiller bud outgrowth. It was hypothesized that the relation between bud dormancy and LMA was caused by the photomorphogenetic effects R:FR has on both bud outgrowth and LMA of the parent leaves.

**Table 1.** Maximum and final number of tillers reached per plant, for plants grown at 0% or 75% shade, at a population density of 100, 262 or 508 plants  $\text{m}^{-2}$  (D100, D262 and D508, respectively)

	0% shade			75% shade		
	D100	D262	D508	D100	D262	D508
Maximum tiller number	8.90	5.65	3.65	2.95	1.25	0.65
Final tiller number	3.80	1.90	0.10	2.55	1.00	0.06

## SIMULATION OF TILLERING PATTERN UNDER THE INFLUENCE OF LIGHT PROPERTIES

The light conditions for suppression of tiller bud outgrowth, described above, were adopted for use in the virtual plant model. ADELwheat was interfaced with a light model called Nested Radiosity (Chelle and Andrieu 1998), using the L-systems communication functionality (Měch and Prusinkiewicz 1996; Měch 2005). The Nested Radiosity model is capable of calculating PAR interception and R:FR perception at the level of the individual organ, and was therefore highly suitable for our purpose. ADELwheat was modified to make tiller bud outgrowth dependent on the fraction of PAR intercepted by the bud's parent-leaf blade (analogous to the hypothesis by Bos (1999) mentioned above) and on the R:FR perceived by the tube of sheaths (the pseudostem); sheaths are known to act as an R:FR sensor (Cordukes and Fisher 1974; Skinner and Simmons 1993). Simulations were done using a threshold of fraction of PAR intercepted by the parent leaf for tillering cessation of 0.2, 0.4, 0.6 and 0.8, or using a R:FR threshold of 0.32 with either the sheaths or the parent-leaf blades as the sites of R:FR perception.



**Figure 4.** Number of tillers per plant versus the physiological age of the plants for population densities of (A) 100 and (B) 508 plants m<sup>-2</sup>, from simulations using threshold values for PAR intercepted by the parent leaf of 0.2 (squares), 0.4 (diamonds), 0.6 (triangles), 0.8 (circles), and from experimental data (dots). Error bars show 2 × SE

Plant population density affected the degree of tillering in accordance with expectations: a higher population density resulted in fewer tillers produced per plant. A higher threshold value for PAR interception resulted in reduced tillering (Figure 4) and a lower production of leaf area (not shown). When compared to experimental data, the fraction of PAR intercepted at the parent leaf blade appeared to be a good indicator for outgrowth of tillers of a low rank, but outgrowth of tillers of a high rank was overestimated. Perception of R:FR by the pseudostem resulted in an overestimation of tiller production at any of the three population densities. These overestimations suggested that photo-morphogenetic effects alone may not be

sufficient to predict tiller production; introduction of photosynthesis and carbon distribution through the plant may enhance model performance in terms of appropriate simulation of tiller production. Nevertheless, the study shows that the L-system approach is a powerful tool to analyse crop-morphological/ecological research questions in which the determinants act on the level of the individual plant organ.

### CONCLUSIONS

Overall, this study has shown that (a) most of the functions in the spring-wheat parameterization in ADELwheat can be regarded as generic for Gramineae; (b) in our experiment, cessation of tiller appearance occurred at fixed light conditions within the canopy; and (c) hypotheses on local stimuli affecting global characteristics of crop development can be tested using a 3D virtual plant-modelling approach.

### REFERENCES

- Abeledo, L.G., Calderini, D.F. and Slafer, G.A., 2004. Leaf appearance, tillering and their coordination in old and modern barleys from Argentina. *Field Crops Research*, 86 (1), 23-32.
- Bos, H.J., 1999. *Plant morphology, environment, and leaf area growth in wheat and maize*. PhD Thesis, Wageningen University, Wageningen.
- Bos, H.J. and Neuteboom, J.H., 1998. Morphological analysis of leaf and tiller number dynamics of wheat (*Triticum aestivum* L.): responses to temperature and light intensity. *Annals of Botany*, 81 (1), 131-139.
- Buck-Sorlin, G.H., 2002. L-system model of the vegetative growth of winter barley (*Hordeum vulgare* L.). In: Polani, D., Kim, J. and Martinetz, T. eds. *Fifth German workshop on artificial life, March 18-20, 2002, Lübeck, Germany*. Akademische Verlagsgesellschaft Aka GmbH, Berlin, 53-64. [<http://taxon.ipk-gatersleben.de/homepage/Bucksorlin-GWAL5.pdf>]
- Casal, J.J., 1988. Light quality effects on the appearance of tillers of different order in wheat (*Triticum aestivum*). *Annals of Applied Biology*, 112 (1), 167-173.
- Casal, J.J., Sanchez, R.A. and Deregibus, V.A., 1987. Tillering responses of *Lolium multiflorum* plants to changes of red/far-red ratio typical of sparse canopies. *Journal of Experimental Botany*, 38 (194), 1432-1439.
- Chelle, M. and Andrieu, B., 1998. The nested radiosity model for the distribution of light within plant canopies. *Ecological Modelling*, 111 (1), 75-91.
- Cordukes, W.E. and Fisher, J.E., 1974. Effects of shading of the leaf sheath on the growth and development of the tiller stems of Kentucky bluegrass. *Canadian Journal of Plant Science*, 54 (1), 47-53.
- Davis, M.H. and Simmons, S.R., 1994. Tillering response of barley to shifts in light quality caused by neighbouring plants. *Crop Science*, 34 (6), 1604-1610.
- Evers, J.B., 2006. *Tillering in spring wheat: a 3D virtual plant modelling study*. PhD Thesis, Wageningen University, Wageningen.
- Evers, J.B., Vos, J., Fournier, C., et al., 2005. Towards a generic architectural model of tillering in Gramineae, as exemplified by spring wheat (*Triticum aestivum*). *New Phytologist*, 166 (3), 801-812.
- Evers, J.B., Vos, J., Andrieu, B., et al., 2006. Cessation of tillering in spring wheat in relation to light interception and red:far-red ratio. *Annals of Botany*, 97 (4), 649-658.
- Fournier, C., Andrieu, B., Ljutovac, S., et al., 2003. ADEL-wheat: a 3D architectural model of wheat development. In: Hu, B.-G. and Jaeger, M. eds. *Plant growth modeling and applications: proceedings-PMA03: international symposium on plant growth modeling, simulation, visualization and their applications, Beijing, China, October 13-16, 2003*. Tsinghua University Press, Beijing, 54-66.

- Holmes, M.G. and Smith, H., 1977. The function of phytochrome in the natural environment. 2. The influence of vegetation canopies on the spectral energy distribution of natural daylight. *Photochemistry and Photobiology*, 25 (6), 539-545.
- Jamieson, P.D., Brooking, I.R., Porter, J.R., et al., 1995. Prediction of leaf appearance in wheat: a question of temperature. *Field Crops Research*, 41 (1), 35-44.
- Lafarge, T.A. and Hammer, G.L., 2002. Tillering in grain sorghum over a wide range of population densities: modelling dynamics of tiller fertility. *Annals of Botany*, 90 (1), 99-110.
- Lindenmayer, A., 1968a. Mathematical models for cellular interactions in development. I. Filaments with one-sided inputs. *Journal of Theoretical Biology*, 18 (3), 280-299.
- Lindenmayer, A., 1968b. Mathematical models for cellular interactions in development. II. Simple and branching filaments with two-sided inputs. *Journal of Theoretical Biology*, 18 (3), 300-315.
- Mêch, R., 2005. *CPFG version 4.0 user's manual*. University of Calgary, Alberta. [<http://algorithmicbotany.org/lstudio/CPFGman.pdf>]
- Mêch, R. and Prusinkiewicz, P., 1996. Visual models of plants interacting with their environment. In: *SIGGRAPH 96, New Orleans, Louisiana, August 4-9, 1996: proceedings of the 23rd annual conference on computer graphics and interactive techniques*. ACM Press, New York, 397-410. [<http://algorithmicbotany.org/papers/enviro.sig96.pdf>]
- Prévot, L., Aries, F. and Monestiez, P., 1991. Modélisation de la structure géométrique du maïs [Modelling the geometric structure of maize]. *Agronomie*, 11 (6), 491-503.
- Prusinkiewicz, P. and Lindenmayer, A. (eds.), 1990. *The algorithmic beauty of plants*. Springer, New York.
- Room, P., Hanan, J. and Prusinkiewicz, P., 1996. Virtual plants: new perspectives for ecologists, pathologists and agricultural scientists. *Trends in Plant Science*, 1 (1), 33-39.
- Simon, J.C. and Lemaire, G., 1987. Tillering and leaf area index in grasses in the vegetative phase. *Grass and Forage Science*, 42 (4), 373-380.
- Skinner, R.H. and Simmons, S.R., 1993. Modulation of leaf elongation, tiller appearance and tiller senescence in spring barley by far-red light. *Plant, Cell and Environment*, 16 (5), 555-562.
- Sparkes, D.L., Holme, S.J. and Gaju, O., 2006. Does light quality initiate tiller death in wheat? *European Journal of Agronomy*, 24 (3), 212-217.