



# Parameterising wheat leaf and tiller dynamics for faithful reconstruction of wheat plants by structural plant models

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## ABSTRACT

Structural 3D plant models aim at mimicking the dynamics of plant and crop structure based on experimental data. Such models can be interfaced with physical models to investigate plant-environment interactions. This work aimed at defining functions that represent the leaf and tiller development of individual wheat plants, and that could be fitted to the specific traits produced in a broad range of situations.

A dataset of the dynamics of wheat plant (*Triticum aestivum*) architecture was collected for 55 experimental situations, including 11 growing seasons, three sowing densities, three sowing dates, and 13 commercial cultivars. Data were analysed to identify conserved patterns in the dynamics of leaf emergence and of tiller emergence and senescence.

The broad range of conditions tested allowed us to evaluate the robustness of relationships proposed in previous studies and to identify novel patterns. Amongst them, we observed: (i) that leaf emergence dynamics may follow either a linear or a bilinear pattern for the same genotype. When a change in phyllochron occurred, it coincided with the initiation of the flag leaf; (ii) the delay between leaf and tiller emergence was not constant, but increased very regularly for successive phytomers; (iii) the number of leaves emerged at tillering cessation decreased with plant density but depended also on the final number of leaves on the main stem (MS) and marked differences existed between cultivars. Finally, we defined functions representing leaf and tiller dynamics with parameters that have a simple botanical interpretation and are easy to derive from field measurements. Assessing plant density, crop leaf stage at 5–6 dates and tiller population at 2 dates during the cycle provide the required data.

This study defines a rationale to analyse and represent the dynamics of the architecture of individual wheat plants. The method can be used to determine the dynamics of architecture in 3D models and should be transposable to a wide range of cereal species.

## 1. Introduction

Architectural crop models aim at realistically representing the dynamics of the 3D architecture of a set of plants. These models make it possible to simulate the interactions between plants and their environment such as the interception of light (Chelle and Andrieu, 1998), water (Saint-Jean et al., 2008) and spores (Robert et al., 2008) and thus to investigate how plant architectural traits modulate these interactions. The interplay between the dynamics of architecture and the dynamics of environmental conditions governs the conditions perceived by each plant component. This is particularly important when

investigating the outcome of short impacting events, e.g. the propagation of rain-dispersed fungi or the efficiency of pesticide application are critically dependent on which leaves are exposed at the specific time of the rain or the pesticide application. Accurately reconstructing the plant development for specific cultivars and growth conditions, by representing the timing of development along and between plant axes and accounting for plant–plant variability is important so that simulations with 3D plant models can be used to investigate these types of interactions. Since regulatory mechanisms that define these dynamics are not fully understood, representing them accurately requires the use of empirical relationships.

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Three components together build the leaf dynamics in the plant architecture: (i) the rate of emergence of leaves on an axis; (ii) the final number of leaves produced on each axis; and (iii) the tillering dynamics (emergence and growth arrest). In the following section, we present an overview of the state of knowledge about these aspects and define the specific objectives that we aimed to achieve.

### 1.1. Phyllochron and leaf stage progress

In wheat and numerous other cereals, the progress of vegetative development is often measured by the fractional number of expanding leaves at a given time, to which we will refer as leaf stage. The phyllochron is defined as the thermal time required for the leaf stage to progress by one unit. In several models, the progress of leaf stage is also used to determine the extension, i.e. the increase in length, of other plant organs (laminae, sheaths, internodes) and the timing of emergence of tillers using coordination schemes, as presented by Fournier et al. (2016). The phyllochron has been extensively investigated in wheat. When the phyllochron is expressed in thermal time, it is often approximated as being constant during plant ontogeny, whereas its value depends on the sowing date (Kirby et al., 1985a; Baker et al., 1980). In wheat, the phyllochron is only slightly affected by abiotic stresses such as low nitrogen and water availability (McMaster, 1997; Kirby et al., 1985a; Cao and Moss, 1991). A number of authors (Cao and Moss, 1991; Miralles et al., 2001; Slafer and Rawson, 1995, 1997; Miralles and Richards, 2000; Baker et al., 1986; Boone et al., 1990; Hay and Delecolle, 1989) reported ontogenic changes within the course of plant development. Boone et al. (1990) provided evidence that such a change in the phyllochron may mark the occurrence of an early event related to floral transition of the shoot apical meristem. On the other hand, the apex first develops in the soil and emerges only with stem extension while most authors calculate thermal time based on air temperature; there has been some debate about whether the reported change of phyllochron is real or is an artefact caused by referring to air temperature in the early stages, when the apex actually senses soil temperature (Jamieson et al., 1995).

The works cited above aimed at representing the crop level and were mainly based on the characterisation of the main stem behaviour, whereas our intention here was to address the individual plant level and represent differences between individual plants and between axes when needed. Few parameterisations of leaf stage dynamics have been developed that consider both the main stem and tillers. A simple framework frequently used is that tillers emerge in coordination with the leaves on the main stem and their leaves subsequently emerge at the same rate as that of the main stem (Masle-Meynard, 1982; Klepper et al., 1982; Fournier et al., 2003; Evers et al., 2006). However, these similarities were based on observations of a restricted range of conditions and cultivars, and noticeable differences between the phyllochron of the main stem and the tillers have been reported (Kirby et al., 1985b).

### 1.2. Final leaf number

The main factors that regulate the floral transition and, consequently, the final number of leaves on the main stem are the accumulated thermal-time, the vernalisation requirement and day length sensitivity (Miglietta, 1989, 1991; Hay and Kirby, 1991; Kirby, 1992). For tillers that complete their development, the final number of leaves of a tiller at a given rank is strongly related to that of the main stem (Friend, 1965), which arises from the quasi-synchrony of their floral transition (Friend, 1965; Hay and Kirby 1991). Several authors reported a difference of three leaves between the main stem and the tiller axiled by leaf one ( $T_1$ ), followed by a decrease of one leaf for tillers of successive ranks (Masle-Meynard and Sebillotte, 1981b). However, various published results show some departure from this relationship (e.g. Friend, 1965), and we did not find any quantitative assessment based on a large

experimental dataset.

### 1.3. Tillering

During the vegetative phase, each phytomer initiated by the shoot meristems bears a bud. The buds may remain dormant or may grow and form tillers. Buds on phytomers of the main stem produce first-order tillers, which produce second-order tillers and so on until tillering is stopped. The tiller emergence phase is followed, immediately or after some delay, by a phase of senescence during which a proportion of tillers die while the others complete their cycle and produce an ear. The death of a tiller is the outcome of a gradual process, in which the arrest of leaf extension precedes the gradual senescence of the leaves. If leaf stage is frequently monitored, the arrest of the progress of leaf stage is thus an early marker indicating that a tiller will die before completing its cycle.

A large number of observations exist that can be used to build a descriptive model. For winter wheat, the lowest tiller that emerges is most often the tiller that emerges in the axil of leaf one ( $T_1$ ). However, in favourable conditions, the coleoptile tiller ( $T_0$ ) may emerge, whereas in unfavourable conditions, the first tiller to emerge may be  $T_2$  or  $T_3$ . Once the first tiller has emerged, the next tillers generally emerge with a high probability until the end of the tillering phase (Spink et al., 2000; Whaley et al., 2000). The end of tillering generally occurs before the competition between plants significantly reduces light availability, and it seems that both phytochrome signalling and stem extension are able to trigger the end of tillering (Kirby et al., 1985a; Miralles and Richards, 2000; Sparkes et al., 2006; Vos, 2010). Once tillering has stopped, the number of active tillers per plant remains constant until the onset of the senescence phase. The interval between cessation of tillering and the start of tiller senescence is generally short, and these events may or may not be distinguishable in time. The senescence phase corresponds to a period of strong competition between plants and among plant axes, which may continue until ear emergence (Alzueta et al., 2012). The senescence of tillers in a plant reveals a well-established time pattern in which the first tiller that starts to regress is the least developed tiller, which is generally the last one that emerged. The rate (tillers. $^{\circ}\text{C}^{-1}$ ) at which new tillers start to regress and thus the number of tillers that complete their cycle is highly influenced by the availability of light, water and nutrients (Alzueta et al., 2012; Davidson and Chevalier, 1990; Fraser et al., 1982; Power and Alessi, 1978; Sparkes et al., 2006). Within the same plot, plant-to-plant competition and local heterogeneity in terms of density and resources usually results in a large variability of tillering between individual plants (Masle-Meynard and Sebillotte, 1981a).

Despite the importance of the dynamics of tillering in wheat, relatively few experimental studies with a detailed characterisation for each tiller exist and generally they cover a limited range of conditions. A robust empirical model able to describe the tillering dynamics for a wide range of conditions is therefore needed.

### 1.4. Objectives

In this study, our aim was to define parametric functions that describe the key variables of wheat architecture dynamics from emergence to flowering, as required in 3D plant models: (a) the progress of the leaf emergence on all plant axes; (b) the relationship between the final leaf number on the MS and on fertile tillers; and (c) the dynamics of tiller emergence and arrest of growth.

The three components together describe the dynamics of formation of new phytomers on wheat plants, but they do not suffice to simulate the dynamics of plant architecture. For this, they should be combined with parameterization of the size of phytomer components, as well as the progress of leaf senescence. For a 3D representation, the geometry of stems and leaves is required too. Such elements are integrated in the Adel-wheat model (Fournier et al., 2003) and the development of the

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