

Understanding shoot branching by modelling form and function

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Shoot branching plays a pivotal role in the development of the aboveground plant structure. Therefore, to understand branching in relation to the environment, it is not only necessary to integrate the knowledge on mechanisms that regulate branching at multiple levels of biological organisation, but also to include plant structure explicitly. To this end, we propose the application of an established methodology called functional–structural plant modelling.

Significance of shoot branching

Shoot branching (hereafter referred to as ‘branching’) is the collective term for all processes leading to the formation of side shoots (branches, tillers and stolons; see [Glossary](#)) from axillary buds on the shoots of a plant. Branching is a key determinant of plant shape. Because of sensitivity to environmental factors, branching is highly plastic: when grown in a dense stand, a plant can produce a single branchless stem, whereas when grown solitarily, the same plant can produce numerous branches, resulting in a bushy habit. This plastic response to population density can be observed in wild plants such as *Arabidopsis* (*Arabidopsis thaliana*) [1] and is conserved in cultivated species such as wheat (*Triticum aestivum*) [2].

At any time, the number of branches formed and their size determine the total area of the plant, the spatial distribution of leaf area in the canopy and, thus, the amount of light absorbed. Therefore, plasticity in branching determines the competitive strength of the plant in relation to neighbouring plants in terms of capture of light and other resources. Plasticity in branching is a key element of the so-called ‘shade avoidance syndrome’ [3]. Shade avoidance enables a plant to anticipate future competition for light by reducing resource investment in branching and investing more in height growth. This strategy has a trade-off in biomass production, reducing the mechanical stability and fecundity of the plant. Therefore, it is of critical importance for a plant to monitor continuously the potential competitive capacity of the surrounding vegetation to regulate its branching and growth patterns to match future conditions.

Branching is also a significant trait in the domain of agriculture and horticulture. The ability of a plant to respond to the environment in terms of branching and to create a proper balance between production and storage organs are important breeding targets, for example in

cereals [4]. Depending on the plant population density, a low number of tillers can result in suboptimal use of light, space and other resources early in the growing season and increased opportunities for weeds to grow, whereas a high number of tillers can reduce kernel size and induce lodging owing to insufficient resources per culm. Branching is also actively manipulated through pruning and harvesting, for example in kiwifruit (*Actinidia deliciosa*) vines [5] and tree orchards [6]: removal of main branches induces outgrowth of dormant axillary buds, creating new branches. The location and quality of these new shoots determine future crop production. In a crop such as tomato (*Solanum lycopersicum*), suppression of axillary bud outgrowth is weak and production of marketable tomatoes can increase when branches are removed to allocate assimilates to a limited number of fruits per plant [7].

Recently, valuable new insights into the regulation of branching, both in qualitative and in quantitative terms, have been obtained. Extensive studies have been performed on hormone-regulated bud break at the level of the organs (e.g. [8]), and on light-regulated branch growth at the whole-plant level (e.g. [2,9]). Each of these efforts was restricted to only a part of the total regulatory system and did not link processes from different levels of biological organisation (i.e. cell, tissue, organ, whole plant and plant population), although the branching behaviour observed in plants is the result of interacting processes occurring at those different levels. Therefore, to understand fully competitive relations between plants in natural and crop situations, branching needs to be described as a behaviour emerging from interaction of processes both within and between plants. Integration of knowledge on mechanisms that regulate branching at different levels of biological

Glossary

Apical dominance: The control exerted by the shoot apex over the outgrowth of axillary buds.

Functional–structural plant model (FSPM): a simulation model explicitly describing the development over time of the 3D architecture or structure of plants as governed by physiological processes that, in turn, depend on environmental factors

Plant plasticity: the ability of a plant to adapt its structure and functioning in response to environmental factors.

R:FR: the ratio between the intensity of red light (660 nm) and far-red light (730 nm).

Shade avoidance: the response of a plant to maximise its light capture by perceiving and responding to signals indicating future competition for light.

Stolon: a branch growing horizontally along the ground, arising from an axillary bud at the base of the plant, and capable of producing clones of the parent plant.

Tiller: a branch that arises from an axillary bud at the base of the stem in the Poaceae family (grasses) and grows vertically.

organisation is therefore important. Computational modelling has great potential as a tool for understanding the complex interactions occurring in branching, as concluded in [8,10]. Here, we discuss how integration of knowledge in a computational model of branching can be achieved.

Shoot branching control

Here, we focus on two prime aspects of shoot branching: breaking of bud dormancy and subsequent branch growth. A stem contains buds that can grow into first-order branches, which can give rise to second-order branches, and so on. In principle, the plant could enter into an almost unlimited, exponential branching process. However, this is not what is observed: sooner or later, further branching ceases [2]. That regulation arises from internal factors responding to environmental cues. Internal and environmental factors do not operate independently, but are part of a complex system with feedbacks that operate at the level of the cell, the organ and the whole plant, up to the level of plant populations.

Regarding internal factors, branching depends on assimilate availability: if the assimilate source:sink ratio is low (e.g. when the number of active buds is high, or the plant leaf area is relatively low), insufficient assimilates might be available and some active buds might not grow a branch. Additionally, bud break and subsequent branch growth are actively regulated by a hormone signalling network. The plant hormones auxin and strigolactones suppress branching, whereas cytokinin promotes branching, and the three types of hormone influence each other in various ways [10].

Environmental control of branching occurs through: (i) light signalling: a low red:far-red intensity ratio (R:FR) is indicative of surrounding vegetation because red light is mainly absorbed by green plant parts, and far-red light is mainly scattered. A low R:FR is one of the signals that elicit shade avoidance responses in plants, leading to suppression of bud break; (ii) light intensity: a high intensity of photosynthetically active radiation results in high assimilation rate and, consequently, a high source:sink ratio, which leads to increased import of assimilates in vascularised buds and, therefore, stimulation of branch growth; (iii) nutrient status of the soil: the nitrogen and phosphorus status of the plant influences auxin, cytokinin and strigolactone synthesis and transport, thereby affecting branching; (iv) manipulation of plant structure through, for example, herbivory, mowing, pruning and harvesting, as a result of effects on hormone balance, light signalling and assimilate status. Current knowledge and hypotheses on internal and environmental branching control are comprehensively reviewed in [11].

Understanding shoot branching through modelling

The branching pattern of a plant depends on the number of buds that were exposed to conditions that allowed bud break and subsequent branch growth. The conditions experienced by a bud depend on the position of the bud in the plant structure (e.g. transport distance to an apex exerting apical dominance). Therefore, to understand branching in relation to the environment, it is not only necessary to integrate the knowledge on mechanisms that

regulate branching at multiple levels of biological organisation, but also to include plant structure explicitly. To that end, we propose the application of an established methodology called functional–structural plant modelling (FSPM) [12,13]. An FSP model is a simulation model ‘... explicitly describing the development over time of the 3D architecture or structure of plants as governed by physiological processes that, in turn, depend on environmental factors’ [13]. As such, an FSP model is typically defined at the level of the plant organ, and contains detailed information about the plant in terms of the number, kind, size, location and orientation of all plant organs, as well as the biophysical connections between them. All that information is updated in every time step of the model. In such FSP models, physiological and physical processes occur within organs (e.g. photosynthesis within a leaf) and between organs (e.g. transport of assimilates), interaction with the environment occurs at the interface of organ and environment (e.g. light absorption by a leaf), and the organs together make up a whole plant. Figure 1 depicts the visual output of an FSP model of wheat, in which the organs intercept light and produce assimilates, which are transported through the plant structure to other growing organs. Alternatively, an FSP model can be defined at lower levels of biological organisation, such as the tissue, cell or subcellular level. In such cases, the output of the model typically is not an entire plant but a plant part, such as a developing meristem producing leaf primordia [14].

In the case of branching control, the key components of the system to be modelled are: (i) acquisition and synthesis of compounds (assimilates, nutrients and hormones); (ii) signalling by compounds (hormones, assimilates and nutrients); (iii) transport of compounds through the plant structure; (iv) plant growth and phenological development; (v) light interception, scattering and signalling; (vi) manipulation of plant structure; and (vii) interactions between individual plants. These different aspects, which occur at multiple levels of biological organisation, can be integrated in an FSP model (Figure 2) [15,16]. A recently developed FSP model of auxin transport provides an explanation for bud break under the control of growing (apical or axillary) meristems [17]. Based on the assumption that buds break only when they can export locally synthesised auxin into the auxin flow of the mother shoot, the model suggests that buds are kept dormant by the positive feedback between polarisation of auxin transport and auxin flux from stem segment to stem segment (and also from cell to cell) in the main shoot. Subsequently, the model reproduces various bud break patterns as observed in wild-type and mutant plants faithfully. Other FSP models have focused on branching control in relation to light interception and associated assimilate sink:source dynamics [18] (Figure 1a) and light signalling through R:FR [19,20] (Figure 1b). Simulations have shown that local R:FR within a canopy of plants is very variable and depends on canopy development, sky conditions, and the orientation and ‘field-of-view’ of R:FR-sensing organs [19]. Branching patterns can be simulated at varying levels of accuracy, based on R:FR locally perceived [20] and on assimilate allocation [18].

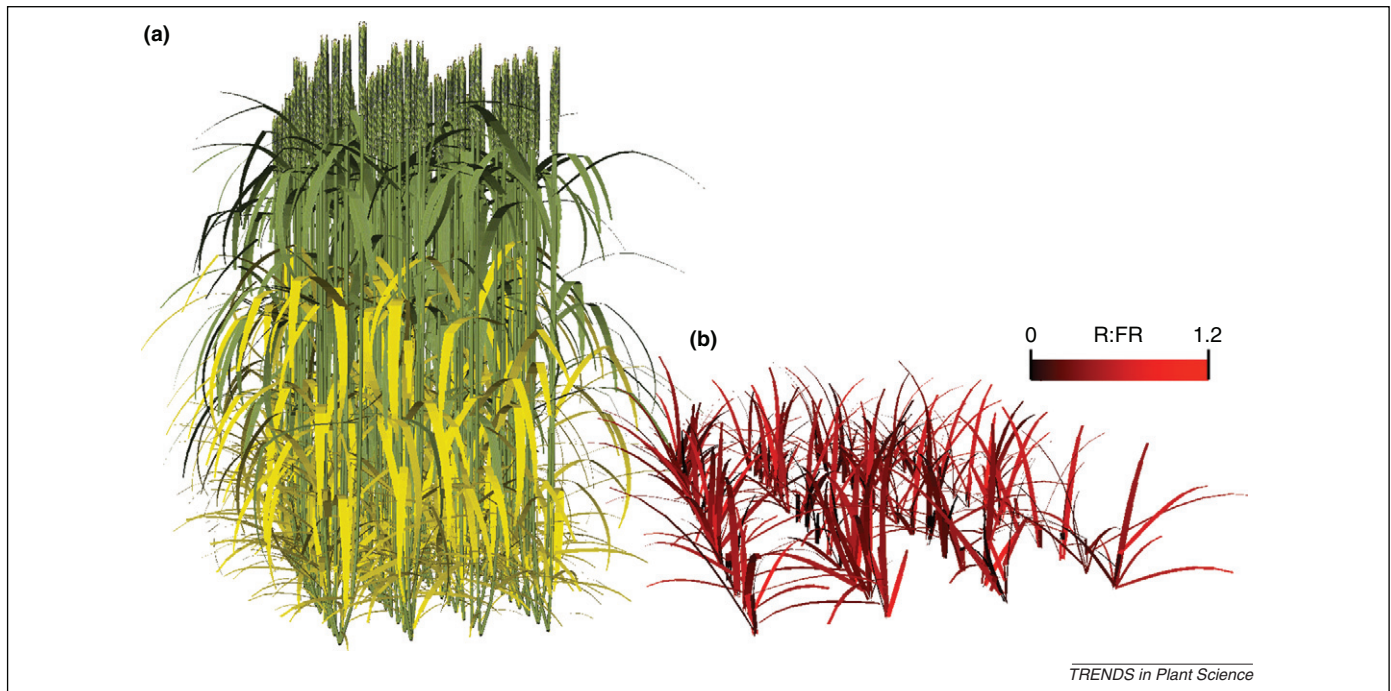


Figure 1. Functional–structural plant (FSP) models of wheat tillering. Small canopy of 60 simulated wheat plants in (a) mature and (b) early stages of development. Each plant is composed of stems, leaves and ears, all with their own position and orientation. The state of the plants is the result of light interception and photosynthesis at the organ level, transport of assimilates through the plant structure and associated growth. In (a), yellow leaves have senesced, whereas green leaves are still photosynthetically active. In (b), the colour of leaves and internodes represents the R:FR as perceived locally, ranging from black (R:FR = 0) to bright red (R:FR = 1.2). Pictures created using a reimplementation of FSP models presented in [18] (a) and [19] (b).

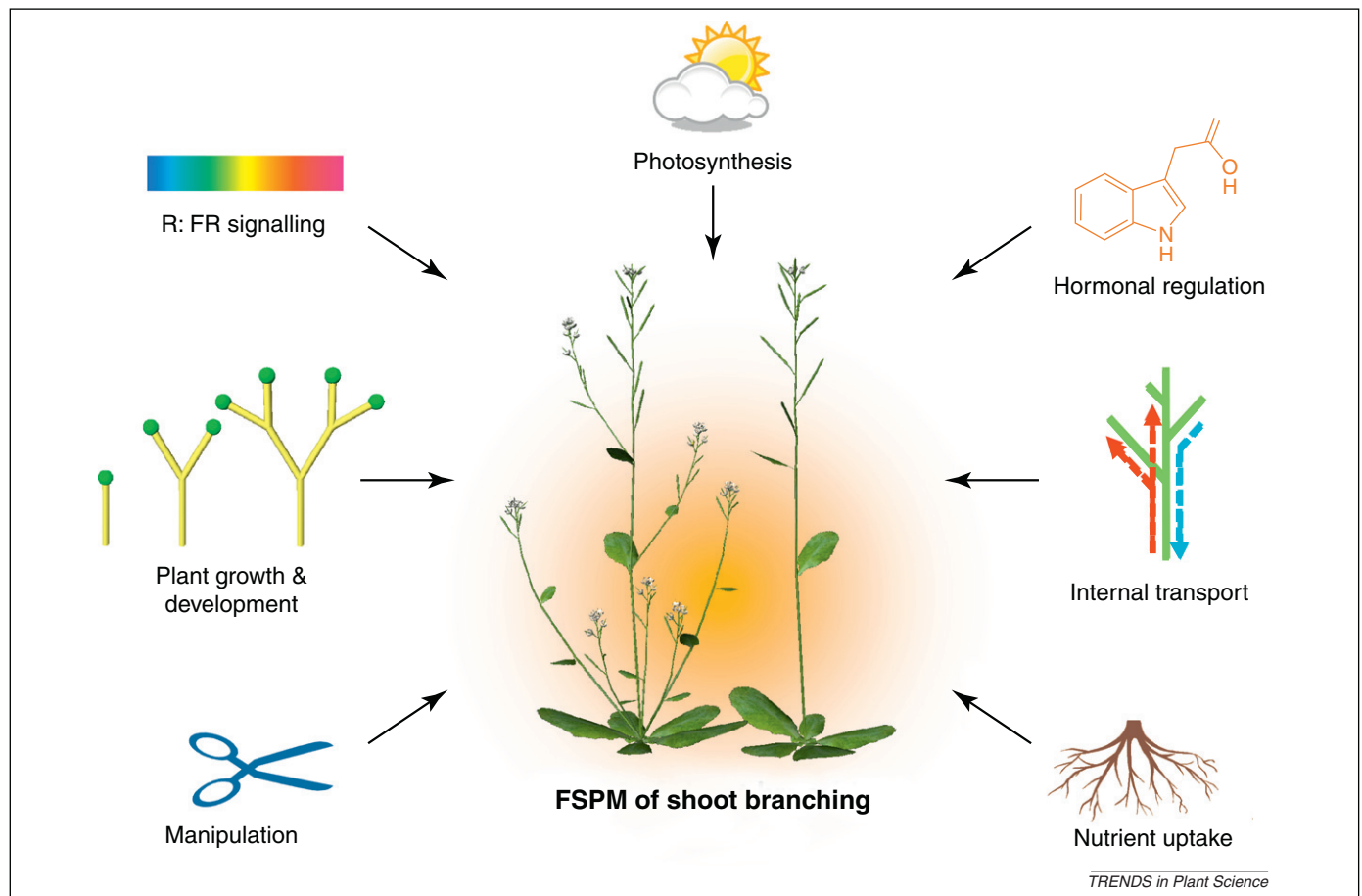


Figure 2. Components of a functional–structural plant (FSP) model of shoot branching. Representation of several key internal and environmental factors related to shoot branching. Each of these factors can be a component of an FSP model of shoot branching, represented here by two simulated *Arabidopsis* plants with contrasting branching phenotypes.

Although these FSPM examples provide valuable information on some of the aspects in branching control, they cannot be used to simulate branching of whole plants in a specific environment. For that purpose, the bud break model based on auxin transport [17] lacks environmental input and realistic plant structure, and the branching model based on light signalling [20] lacks an internal mechanistic basis that links light signalling and branch growth [11]. Additionally, related efforts to simulate branching control [21] provide valuable new mechanistic insights, but ignore environmental input and plant structure. Understanding the branching behaviour of a plant in relation to its environment requires integration of all factors controlling branching at different levels of organisation in one FSP model. Such a model should contain aspects of branching control at the levels of the cell, organ, the whole plant and plant community and, therefore, would display emerging feedbacks between those levels (e.g. surrounding plants determining R:FR perceived by a specific organ, or auxin flow within the plant structure determining auxin export of a specific bud). Special experiments, in which variables such as hormone activity in relation to R:FR and bud break frequency is measured, can provide valuable information on branching control, and should be used to calibrate and validate such a model.

From FSPM to understanding and manipulating plant structure

Shoot branching is the result of several physiological drivers, which themselves are under the control of environmental inputs [11]. Long-range hormonal signalling, transport of nutrients and assimilates from source to sink organs, and local light signalling all shape plant structure and, in turn, highly depend on plant structure (Figure 2). Plant structure is an integral part of FSPM; therefore, this approach has great potential for branching research. FSPM is an ideal tool in a plant systems biology approach [15,16], because it provides opportunities to integrate knowledge from cellular up to whole-plant aspects of branching control, and enables the study of branching in the context of the whole plant and its environment. Neither does it not stop there: other aspects of shade avoidance and plasticity in plant development in general can also be addressed using a similar modelling approach; for example, stem extension and leaf angle adjustments, foraging behaviour [22–24] and linking the circadian rhythm of the plant to diurnal changes in light distribution [25]. Such modelling approaches can play a pivotal role in developing tools to predict branching, growth and yield for agricultural and horticultural purposes.

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