

REVIEW: PART OF A SPECIAL ISSUE ON FUNCTIONAL-STRUCTURAL PLANT  
GROWTH MODELLING

**Two decades of functional–structural plant modelling: now addressing  
fundamental questions in systems biology and predictive ecology**

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- **Background** Functional–structural plant models (FSPMs) explore and integrate relationships between a plant's structure and processes that underlie its growth and development. In the last 20 years, scientists interested in functional–structural plant modelling have expanded greatly the range of topics covered and now handle dynamical models of growth and development occurring from the microscopic scale, and involving cell division in plant meristems, to the macroscopic scales of whole plants and plant communities.
- **Scope** The FSPM approach occupies a central position in plant science; it is at the crossroads of fundamental questions in systems biology and predictive ecology. This special issue of *Annals of Botany* features selected papers on critical areas covered by FSPMs and examples of comprehensive models that are used to solve theoretical and applied questions, ranging from developmental biology to plant phenotyping and management of plants for agronomic purposes. Altogether, they offer an opportunity to assess the progress, gaps and bottlenecks along the research path originally foreseen for FSPMs two decades ago. This review also allows discussion of current challenges of FSPMs regarding (1) integration of multidisciplinary knowledge, (2) methods for handling complex models, (3) standards to achieve interoperability and greater genericity and (4) understanding of plant functioning across scales.
- **Conclusions** This approach has demonstrated considerable progress, but has yet to reach its full potential in terms of integration and heuristic knowledge production. The research agenda of functional–structural plant modellers in the coming years should place a greater emphasis on explaining robust emergent patterns, and on the causes of possible deviation from it. Modelling such patterns could indeed fuel both generic integration across scales and transdisciplinary transfer. In particular, it could be beneficial to emergent fields of research such as model-assisted phenotyping and predictive ecology in managed ecosystems.

**Key words:** Functional–structural plant model, modular structure, architecture, plant modelling, individual-based model, systems biology, plant plasticity, predictive ecology, review.

## INTRODUCTION

The idea of a plant as a population of parts is an important concept for integrating and understanding both plant biology and plant community ecology. From an organismal perspective, plants are modular organisms whose growth and development occur throughout their whole life cycle (White, 1979). The elementary modules are organs or groups of organs (e.g. phytomers) that are repeatedly produced by the apical meristems of shoots and roots (Doussan *et al.*, 2003; Barthélémy and Caraglio, 2007). In higher plants, this results in a branched structure that is typically anchored to the germination site and develops specialized structures above and below ground to forage both 'sides' of its environment for light, water and nutrients. Though a plant as a whole can be seen as an autotrophic organism, none of its parts truly is; rather, it can be described as an expanding collection of semi-autonomous organs that each adjust to local conditions while being connected to exchange

complementary resources and coordinating their development through internal signalling and the actions of shared genetic information. From a population and community perspective, the modular structure of plants also plays a prominent role in explaining the fitness of individuals under selection (McGraw and Wulff, 1983; Tuomi and Vuorisalo, 1989; Salguero-Gómez *et al.*, 2018). Contrary to unitary organisms, the counting of individuals contributes remarkably little information to the study of plant populations (Harper 1977, 1980). Even considering age or stage classes cannot account for the broad variability of inter-individual contributions to sexual reproduction and population dynamics. Plant size, more precisely the number and size of reproductive parts, is best suited to describing this variability (Samson and Werk, 1986; Weiner, 2004). Plant architecture, which accounts for the interconnections and spatial distribution of plant organs, thus represents altogether (1) the support for organismal integration, (2) the product of decentralized

ontogenetic processes and (3) the effect of life history on plant fitness (DeJong *et al.*, 2011; Hallé *et al.*, 2012).

Plant scientists have been engaged in building conceptual models of plant growth and development for centuries (DeJong *et al.*, 2011). But quantitative models that consider the interplay between plant modular structure, the abiotic environment and internal functioning and signalling are relatively recent (Prusinkiewicz, 2004; Godin and Sinoquet, 2005; Fourcaud *et al.*, 2008). Such functional–structural plant models (FSPMs) were initiated after the concepts of plant architecture became widely acknowledged in botany (Hallé and Oldeman, 1970; Hallé, 1986; Fitter, 1987; Hutchings and de Kroon, 1994; Sussex and Kerk, 2001) and in parallel with development of the computational power offered by personal computers. An initial and critical period of research was necessary to establish the first methods (e.g. Sinoquet and Andrieu, 1993; Guédon *et al.*, 2001) and standards (e.g. Godin *et al.*, 1999) to describe and analyse a diversity of plant architectures. The general principles for modelling branching structures (Bell, 1986; Prusinkiewicz and Lindenmayer, 1990; Jaeger and De Reffye, 1992) and coupling 3D models with models of their abiotic environment (Room *et al.*, 1994; Takenaka, 1994; Chelle and Andrieu, 1998; Sievänen *et al.*, 2000) were also the subject of early research. The first ‘virtual’ plants that interacted dynamically and quantitatively with their environment provided simulations in the late 1990s (De Reffye *et al.*, 1997; Perttunen *et al.*, 1998; Fournier and Andrieu, 1999). Since then, FSPMs have attracted a significant audience. A dedicated journal was

launched last year by Oxford University Press (Long, 2019). Recent reviews have illustrated the relevance of this modelling approach at various scales in the fields of developmental biology (Cieslak *et al.*, 2016; Galvan-Ampudia *et al.*, 2016; Schneider *et al.*, 2019), integrative or systems biology (Zhu *et al.*, 2016; Chang *et al.*, 2019; Millar *et al.*, 2019) and applied plant sciences such as forestry and agronomy (Evers, 2016; Renton and Chauhan, 2017; Evers *et al.*, 2019; Gaudio *et al.*, 2019; Postma and Black, 2020). Two decades after the first models were launched, this special issue is introducing a series of original articles that present the cutting-edge science in the field of plant modelling. This symbolic date offers an opportunity to assess the progress, gaps and bottlenecks along the research path originally foreseen for FSPMs. It also enables updating of the research agenda for the coming years and the repositioning of recent questions that have arisen because of the remarkable shift ignited by ‘omic’ approaches in biology, the increasing awareness of the impacts of global change on plant communities and the development of computing technologies.

From the start (Sievänen *et al.*, 2000; Godin and Sinoquet, 2005), three general objectives were identified for the development of FSPMs (Fig. 1):

- To understand the functioning of plants at and across different scales, ranging from meristems to plant communities;
- To integrate knowledge from different disciplines, including plant biology, biophysics, ecology and computer science,

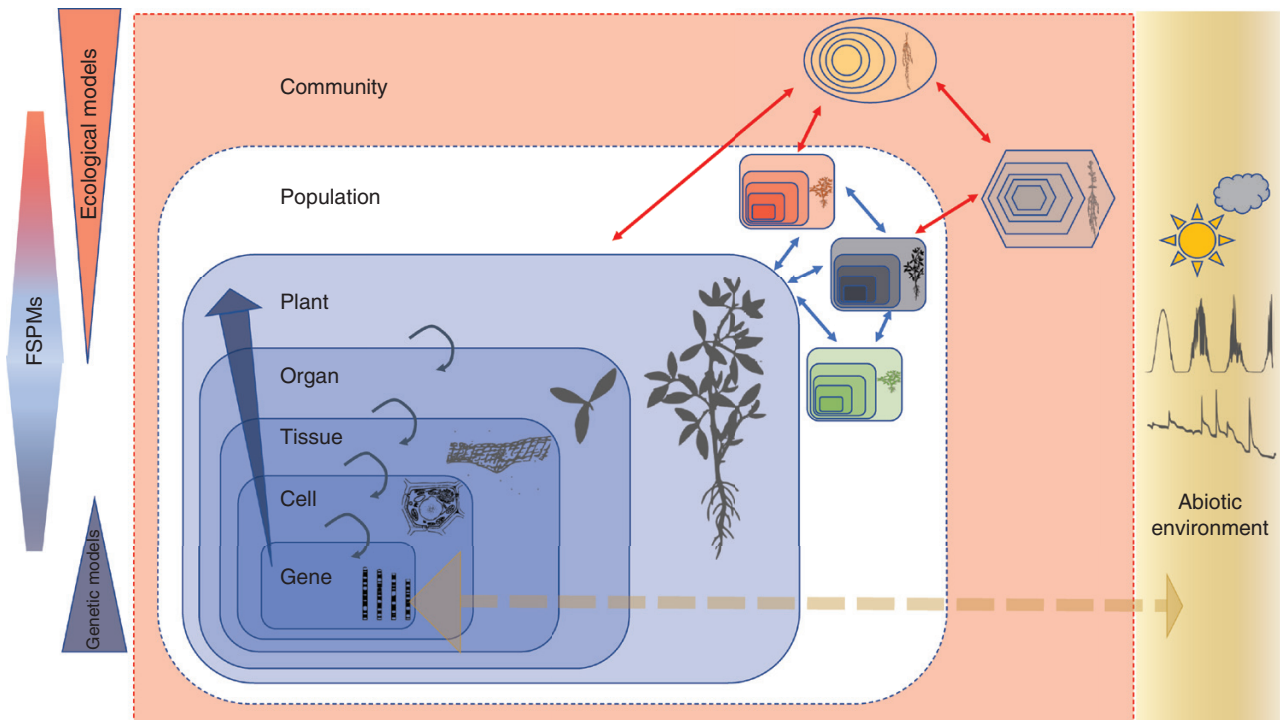


FIG. 1. FSPMs cover a range of scale integration from gene to community level, with the focus of attention being the explanation of how plant phenotypes (centre of the figure) are built from interactions with their inner (including genetic determinants and self-regulation loops expressed at various levels) and outer (including abiotic factors and biotic interactions in plant populations and communities) environments. Interactions up to the plant scale involve sub-parts that all share the same genetic material (same shape and colour gradient in the figure) and proceed from systems biology. Interactions at higher scales integrate the interplay between entities that are genetically distinct (either from the same or different species), and contribute to predictive ecology by linking organismal traits with population and community functioning. FSPMs thus complete both classical genetic and molecular network models that are usually applied up to the cellular level, and population ecology models that are lacking a robust physiological response to environmental drivers.

and enable hypothesis testing relative to plant structure and function in these different fields of research;

To develop predictive models in applied domains wherever plant architecture plays a critical role, including plant modelling in spatially heterogeneous environments (understorey, greenhouses, etc.), competition in plant communities, selective canopy perturbation (herbivory, pruning, etc.) and the definition of ideotypes for breeders.

Achieving these objectives has also required interdisciplinary efforts regarding the development of specific tools and methods to tackle the lack of a modelling framework and the shared paradigms that existed then, and which is still partly ongoing today (Henke *et al.*, 2016; Marshall-Colon *et al.*, 2017). The articles in this special issue illustrate the progress that has been made towards these different research goals, covering both the heuristic aspects permitted by plant modelling and application-driven models.

### ACHIEVEMENTS

Among the advances enabled by FSPMs, integrating plant functioning in complex architectures and providing insights into the ontogenic gradients that emerge during shoot, root and whole plant development (Mathieu *et al.*, 2012; Eloy *et al.*, 2017; Peyhardi *et al.*, 2017) have represented major progress. Complex architecture is not directly coded in any plant's genome, but results from a hierarchy of developmental processes (from the molecular to the macroscopic organizational level) that interact with the plant's life history. The causal effects of genetic determinism, size-related drift in the ontogeny and external environment on plant form can only be deciphered by means of modelling.

One example of a model that simulates the development of complex architecture in space and time is presented by Boudon *et al.* (2020) in mango trees. This tropical evergreen fruit tree displays irregular patterns of vegetative and reproductive cycles, with an asynchronous development of inflorescences and fruits within and between trees. Their model demonstrates the usefulness of a multi-scale approach to analysing the effects of endogenous structural, temporal (ancestor fate and history) and trophic factors on plant form while simulating the population dynamics of new shoots and fruits.

Different mechanistic models have been proposed to explain the size variation of organs and the regulation of plant development during ontogeny. They are usually based on either a hypothesis of C-driven trophic regulations (e.g. Luquet *et al.*, 2006; Kang *et al.*, 2011) or the integration of non-trophic signalling (which may be internal to the plant, external or an integration of both; e.g. Fournier *et al.*, 2005; Verdenal *et al.*, 2008; Evers *et al.*, 2011) to modulate growth and development. The two articles by Letort *et al.* (2020) and Vidal and Andrieu (2020) illustrate these two modelling approaches. The latest developments of the GreenLab model, one of the pioneering FSPMs published two decades ago (De Reffye *et al.*, 1997; Yan *et al.*, 2004), are presented by Letort *et al.* (2020). Their study highlights the interest

of associating stochastic developmental rules with a state variable that represents the internal trophic pressure on C, to explain the variability of morphogenesis observed in young *Coffea* trees. By contrast, the dynamic scheduling of organ initiation and extension is triggered by non-trophic events in the grass model proposed by Vidal and Andrieu (2020). They further developed the concept of 'coordination rules', which designate the temporal relationships and apparent triggering of successive developmental events during ontogeny (Fournier and Andrieu, 1999). Their study has established that common coordination rules can be applied to predict the patterning of shoot architecture in maize for genotypes that display contrasting phenotypes.

Beyond morphogenesis and the acquisition of plant form, functional-structural plant modelling has also been used for the integration of plant physiology across spatial and temporal scales. Where the integration of knowledge has received the greatest concern is undoubtedly the assimilation of C through photosynthesis (e.g. Evers *et al.*, 2010; Zhu *et al.*, 2013) and solving the issue of dynamic photo-assimilate distribution among plant parts (e.g. Grafahrend-Belau *et al.*, 2013; Sonnewald and Fernie, 2018; Lacoite and Minchin, 2019), two processes that have been modelled from the molecular to the population scale. In this issue, a historical viewpoint is proposed by Stirbet *et al.* (2020) on the role of modelling in the understanding of photosynthesis. Song *et al.* (2020) present a detailed model that integrates photosynthesis from the leaf to the whole canopy, based on a 3D architecture model of soybean. They illustrate the potential of such an approach to analyse the response of crops to elevated CO<sub>2</sub> levels and dissect the relative contributions of structural and functional traits. Regarding photo-assimilate distribution, two generic multi-scale models are introduced by Reyes *et al.* (2020) and Auzmendi and Hanan (2020). The two models, namely MuSCA and AUCAM, will enable further improvements to the computation time of FSPMs and should facilitate the inter-comparison of C partitioning models and the refining of tests on the physiological processes at work.

As for applications, the advances achieved by FSPMs in terms of the integration of plant architecture and plant primary production now mean this is a mature tool to quantify the effects of architectural traits and canopy management on light interception and potential C assimilation. Zhang *et al.* (2020a) illustrated this by quantifying the effects of shoot-bending on cut rose production under greenhouse conditions, thus integrating heterogeneous canopy effects and light conditions (natural and artificial light). Prieto *et al.* (2020) used a similar approach in grapevine to compare the gains in photosynthesis enabled by different training systems, including situations with free shoots displaying a complex architecture. In horticultural science, the handling of production with FSPMs has found applications in various crops and ornamental species (Sarlikioti *et al.*, 2011; Kang *et al.*, 2012; Chen *et al.*, 2014). Vermeiren *et al.* (2020) present a study on the value of refining leaf shape representations in a tomato model. Their study suggests that the cost-benefit ratio of realistic 3D shape representations tends to favour their inclusion in FSPMs.



## CHALLENGES

### *Integration*

Despite being firmly established in plant science and having achieved significant progress, the full promise of FSPMs is still far from being delivered, even after two decades. One striking observation is that until now the vast majority of studies have focused on particular biological questions, using models applied specifically to a single species or integrating a limited array of physiological processes. The ability to effectively derive knowledge from the integration of complex structures and functions is thus likely still in its infancy. To illustrate this lack of integration, the fundamental issue of whole-plant integration, which considers together root and shoot foraging for light and soil resources, has received very limited attention (Drouet and Pagès, 2007; Louarn and Faverjon, 2018). Most current ‘virtual’ plants are at best ‘virtual’ half-plants. They focus either on shoot or root functioning, but do not examine the interplays between the two ‘sides’ of a plant that become critical when adapting to stressful conditions (Dunbabin *et al.*, 2013; Hill *et al.*, 2013; Ndour *et al.*, 2017; De Bauw *et al.*, 2020). In this issue, Braghieri *et al.* (2020) introduce a mechanistic model that combines soil, roots and shoots in terms of the acquisition of water and carbon by plants. They illustrate the heuristic potential of such an approach to explaining plant plasticity in response to drought and identifying successful trait combinations for water acquisition in plant communities. Attempts at modelling also do exist regarding the coupling of shoots and roots with respect to mineral acquisition. However, the models were developed for only one form of mineral uptake (Drouet and Pagès, 2007; Barillot *et al.*, 2016) and they do not currently take account of interactions with drought.

Integration across scales also remains very patchy. Although first advocated as a tool to link genotype and phenotype (Godin and Sinoquet, 2005), few FSPMs have tried to tackle this issue up to the plant scale (Baldazzi *et al.*, 2016; Migault *et al.*, 2017; Picheny *et al.*, 2017). The effective integration of genetic control has mostly been considered regarding the functioning of meristems and plant tissues (e.g. Lucas *et al.*, 2008; Galvan-Ampudia *et al.*, 2016). Paradoxically, the issue of phenotypic prediction from genetic data is now more widely addressed using simpler crop models that define plant phenotypes from a few integrated traits but consider a broad range of environmental responses (Chenu *et al.*, 2017). In the search for breeding targets, the possibility offered by FSPMs to break down the plant phenotype into elementary phenotypic traits and to account for interactions between these traits at different scales mean that they continue to be an appropriate approach to addressing genotype by environment interactions. In these efforts to predict the emergence of complex phenotypes, much more attention should be paid to multi-scale models in the years to come, as we improve our abilities to integrate different sources of knowledge.

### *Biological understanding*

In these conditions, the validity domain of FSPMs is currently restricted. The integration of plant physiology is still too limited

to embrace the challenge of breaking down plant responses to multiple stressors under most ‘real-life’ conditions. The main advances reported have concerned the integration of multiple light responses when modelling competition above ground (e.g. Gautier *et al.*, 2000; Kahlen and Chen, 2015). Light is indeed both a trophic resource that supplies excitation energy to the photosynthetic process and a physical signal that informs plants of competitors in their neighbourhood in order to trigger adaptive responses (Ballaré and Casal, 2000). In this issue, Zhang *et al.* (2020b) present a model that considers the trophic and signalling effects of light on photosynthesis in rose plants. Their approach enables the integration of trait responses at the organ level and can disentangle the interactive effects generated on C assimilation at the whole plant level. Further physiological integration is also tested in the study by Coussemont *et al.* (2020). These authors present a soybean model that incorporates both C metabolism and plant–water relationships, so that plant growth is driven by turgor pressure. This state variable allows the synthesis of both source and sink-related controls on organ growth over short time scales. Although preliminary, this work could serve to build future mechanistic models that aggregate trophic and non-trophic effects on sink activity in plant models (Pantin *et al.*, 2012; Fatichi *et al.*, 2019; Gauthier *et al.*, 2020).

Such advances in mechanistic plant modelling are urgently needed to challenge and fill the gaps in the understanding of plant functioning. For instance, this is necessary to enable projections of climate change impacts on crop production, where the refining of existing models remains a burning question (Tao *et al.*, 2018, 2020). Beyond crops, the general question of adaptive responses in plants, and of the major traits involved, is also central to predictive ecology (Mouquet *et al.*, 2015). FSPMs have an important role to play in classifying the plastic responses of plants and in analysing the roles of ontogeny and ‘true’ plasticity (i.e. inducing a change to the ontogenetic trajectory) in their adaptive value (Wright and McConnaughay, 2002; Miner *et al.*, 2005). Solving such theoretical questions has to date received limited attention from functional–structural plant modellers (e.g. Renton and Poot, 2014; Pagès, 2016; Lehnebach *et al.*, 2018). This is probably due in part to the diversity of models, driven by a diversity of applied questions, which makes the use of FSPMs naturally lean towards grasping the diversity of observed situations. But identifying and explaining regularities across the plant kingdom, solving paradigmatic questions in plant science (the emergence of allometry, self-similarity, stoichiometry or homeostasis, etc.), should also be important objectives for FSPMs in the future.

### *Complexity*

Because FSPMs deal with numerous entities, spatial scales, heterogeneities and parameters, they are usually seen to be more complex and less tractable than common crop models or analytical models in ecology. In the same way as other types of complex models (Grimm and Railsback, 2005), it cannot be denied that this complexity comes at a cost. It has consequences in terms of model development and maintenance, which are generally more time-consuming. It also affects all aspects related to communication regarding the model, whether this concerns publication (limited description of the details) or the training of

users and transparent dissemination to a broader audience. The deployment of dedicated modelling platforms has considerably alleviated these costs and improved model reusability and accessibility in the past few years (Knemeyer *et al.*, 2007; Barczy *et al.*, 2008; Pradal *et al.*, 2008; Marshall-Colon *et al.*, 2017). However, these platforms remain mostly accessible only to experts in the field. They are based on different strategies of integration (programming languages; soft versus hard coupling of structure and function; open science versus community-driven exchanges) and still lack interoperability for most aspects of plant modelling. Computational requirements are less of an issue than they used to be (Sievänen *et al.*, 2000) but still hamper the range of methods that can effectively be applied for the calibration and sensitivity analysis of FSPMs. Further research is needed that considers the peculiarities of complex models and the issue of limited data availability (Evans *et al.*, 2014; Evers *et al.*, 2018). Wang *et al.* (2020) address the question of FSPM calibration when data are scarce. They have developed an approach reliant on pattern-oriented modelling to sort parameter sets during the parameterization process and reduce the uncertainty of model outputs. More generally, solving the theoretical, methodological, engineering and communicability problems related to complex multi-scale models will be critical to fuel the future development of FSPMs (Bucksch *et al.*, 2017).

### Standards

A part of the solution to the diversity–genericity dilemma raised above is the definition of standards that could be used by modellers to exchange ideas, formalisms and data, independent of platforms and of the types of plants on which they are working; the establishment of such a definition would be a sign that this research field is maturing. Considerable progress has been achieved in this area with respect to data structures (e.g. for roots, Lobet *et al.*, 2015), modelling formalisms (e.g. Boudon *et al.*, 2012; Postma *et al.*, 2017), exchangeable modules (Albasha *et al.*, 2019) and gateways between FSPM platforms (Long *et al.*, 2018). However, the state of the art in terms of model interoperability is still markedly heterogeneous and probably a factor that is more dispersive than unifying at present. To become more widespread, and contribute to building scientific knowledge beyond a community of specialists, such standards must be widely shared and acknowledged. The formal comparison of models also needs to be made easier. One trend already at work consists in developing generic plant models that can cope with a broad range of species (Pagès *et al.*, 2014; Henke *et al.*, 2016; Kang *et al.*, 2018; Faverjon *et al.*, 2019; Braghieri *et al.*, 2020). This should obviously be encouraged as it will facilitate future comparisons and integration. Another step towards this convergence objective should be the identification of standards to describe and test multi-scale models. This is clearly an issue, as different disciplinary and scale-dependent ‘good practices’ already coexist (e.g. Grimm *et al.*, 2006; Bellocchi *et al.*, 2011; Marshall-Colon *et al.*, 2017). But the FSPM community could learn from the success of such standards in other modelling fields. Finally, the sharing of data sets and minimal target patterns at each scale between modelling groups could be as important as sharing technical knowledge of the models (e.g. Rosenzweig *et al.*, 2013, for

the AgMIP initiative in crop models; Poorter *et al.*, 2013, for proposing testable dose–response curves in mechanistic plant models). Complex models seek to embrace and reflect some of the complexity of the real world, but also require the collection of appropriate data at various scales. A lot might be gained if high-quality datasets could be published and widely shared, for reuse (Molloy, 2011).

### NEW HORIZONS AND OPPORTUNITIES

Some of the changes in the research landscape that have occurred during the past decade represent real opportunities for the future development of FSPMs. These include the rise of plant phenomics, i.e. the methods and facilities to generate high-throughput and valuable phenotypic information (Furbank, 2009; Tardieu *et al.*, 2017), which constitutes a major evolution. It changes both the availability of data on plant structure and function and how existing models can be used to link genetic and phenotypic data (Chang *et al.*, 2019; Chen *et al.*, 2019; Van Eeuwijk *et al.*, 2019). Non-invasive, imaging- and model-based methods have become more common and widely used to characterize plant phenotypes. One example is presented in the paper by Zhu *et al.* (2020), where 3D plant architecture in the field is derived from multi-view photography. Their study applies this method for the first time to strip-intercropping systems to assess light partitioning over the entire growth season. Che *et al.* (2020) apply a similar approach for high-throughput phenotyping of maize genotypes in the field. In addition to directly assisting in the measurement and analysis of integrated traits, FSPMs could also be involved in developing the deep learning methods used for automatic image analysis. Complementary to real plant images, the realistic representation of plant architecture that FSPMs can generate could serve as a novel way to provide cost-effective datasets of rendered images for a broad array of phenotypes (Liu *et al.*, 2017; Ubbens *et al.*, 2018).

Another important trend that is of increasing interest to functional–structural plant modellers is a concern for including detailed physiological traits and plastic responses in ecological models. Complex questions on how populations and communities respond to environmental drivers have attracted considerable attention in the context of global change (Harte and Shaw, 1995). Regarding plants, individual-based models have proved able to account for complex patterns of interactions, particularly because individuals are the nexus of trait-based integration and can express considerable plasticity in response to their neighbours (Zakharova *et al.*, 2019). On this topic, Zhang and DeAngelis (2020) present a comprehensive review of agent-based models (or individual-based models, IBMs) in plant biology and ecology. They clearly highlight the strengths of this approach with respect to both theoretical ecology and for solving applied questions of conservation ecology and managed ecosystems. FSPMs represent a limit-case for IBM models. Up to the plant scale, they enable analysis of a whole plant as a population of parts, usually focusing on questions of organismal integration and plasticity. But applied at the population scale they can be used to simulate populations of actual interacting individuals (i.e. physiologically distinct; potentially different genotypes) and offer a tool to consider the two regulation levels (i.e. plants and modular units) foreseen by

Harper (1977) in his seminal book on plant population biology. They provide an opportunity to refine the representation of environmental variables and plastic plant responses, which is a critical issue for many plant IBMs (Breckling *et al.*, 2006; Berger *et al.*, 2008). Within the framework of managed ecosystems, making better use of plant diversity is central to the agricultural practices promoted in agro-ecology (Gaba *et al.*, 2015). Under such systems, FSPMs could serve to improve our understanding of plant interactions in mixtures, to optimize mixed crop set-ups and to find optimal trait combinations for mixed species (Evers *et al.*, 2019; Gaudio *et al.*, 2019). In line with these objectives, Louarn *et al.* (2020) investigate the design of mixture ideotypes (or ‘ideomixes’; Litrico and Violle, 2015) using a generic FSPM. They have demonstrated the feasibility of using such models to detect plant traits that are particularly involved in plant–plant interactions and which could serve as new breeding targets for adapting cultivars to intercropping systems. They also suggest the heuristic potential of this tool to investigate favourable combinations of traits as a function of the environment (i.e. nitrogen management). The interest of FSPMs in ecology goes beyond the dynamics of plant communities, and also addresses the questions of plant interactions with organisms at different trophic levels in ecosystems, including host–pathogen systems (Calonnec *et al.*, 2013; Robert *et al.*, 2018), plant–insect relationships (Wang *et al.*, 2016) and plant community responses to herbivory (Combes *et al.*, 2011; Ney *et al.*, 2013). Although less developed, such models could contribute in future to deepening our understanding of integrated plant responses to combined biotic and abiotic stresses.

## OUTLOOK

The development of FSPMs has matured considerably during the past 20 years and has already delivered significant results at different levels of organization and in diverse fields of plant science. After a mainly exploratory phase, the approach has yet to reach its full potential in terms of integration and heuristic knowledge production, but its coverage of the full continuum – from elementary traits to complex plant phenotype and then population functioning – renders it a unique tool for modern biology (Fig. 1). This places it in a central position at the crossroads of fundamental questions in plant biology and predictive ecology. On the one hand, FSPMs extend systems biology beyond the cellular level and should make it possible to examine causality in the control of plant phenotypes by (1) their genotype, (2) the downward controls of higher plant scales on cell signalling and gene expression, and (3) their local environment (Noble, 2013). On the other hand, FSPMs enable the linking of plant community structure and demographic processes with individuals’ fitness and their underlying physiological and morphological traits. By acknowledging a discontinuity at the boundary of individuals, between sub-parts that are genetically identical at lower scales and interacting entities that are genetically distinct at higher scales, FSPMs could contribute to unravelling the role of intra- and interspecific levels of diversity on the functioning of communities (Zakharova *et al.*, 2019). Given this broad range of applications, the future of FSPMs is unlikely to bridge all scales in a single model, but should rather provide an

array of modelling approaches to explain robust emergent patterns at various scales (e.g. homeostasis, developmental patterning, allometry, population self-thinning) and underpin deviations from such regularities (Passioura, 1979). This knowledge can provide solid ground for diverse applications at higher organization scales using FSPMs either directly or through hybridization with simpler models. This position is altogether stimulating, challenging and dispersive. As a relatively young, multidisciplinary community, the FSPM community still has to figure out how to avoid the trap of being too complex in its approaches while providing limited generality. This may be overcome by improving standards for model integration and by confirming robust predictions of multi-scale patterns in the years to come.

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