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Arboreal review

Fruit tree crop models: an update

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Functional structural plant models of tree crops are useful tools that were introduced more than two decades ago. They can represent the growth and development of a plant through the in silico simulation of the 3D architecture in connection with physiological processes. In tree crops, physiological processes such as photosynthesis, carbon allocation and growth are usually integrated into these models, although other functions such as water and nutrient uptake are often disregarded. The implementation of the 3D architecture involves different techniques such as L-system frameworks, pipe model concepts and Markovian models to simulate branching processes, bud fates and elongation of stems based on the production of metamers. The simulation of root architecture is still a challenge for researchers due to a limited amount of information and experimental issues in dealing with roots, because root development is not based on the production of metamers. This review aims to focus on functional–structural models of fruit tree crops, highlighting their physiological components. The potential and limits of these tools are reviewed to point out the topics that still need more attention.

Keywords: architecture, FSPM, physiology, plant modeling, tree crops.

Introduction

Trees are complex organisms in which environmental factors interact with plant physiology over multiple seasons. This characteristic represents a challenge for scientists working on tree crops: indeed, a large number of experiments are required to assess possible interactions among multiple factors. These experiments on trees are numerous but also long-term, due to the long life of these organisms. Computer models offer a comprehensive method for studying complex problems that can lead to innovative solutions. Indeed, computer modeling, applied to agricultural science, aims to enhance the understanding of how plants react to the environment to evaluate, for example, how yield is linked to agricultural inputs (Vos et al. 2007). The potential application of models is to support practical management decisions and generally to understand how physical and biological realities work. Initially, in the 1970s, crop-specific simulation models were developed for annual crops (i.e., SIMCOT; Duncan 1972) and later the approach was extended to tree crops (i.e., TREEDYN; Bossel and Schafer 1989).

Tree modeling posed new challenges such as the simulation of tree development over multiple years (e.g., secondary growth and spring bud burst needs to be assessed) and the carry-over effect caused by the previous season growth that makes model validation, at tree-scale, difficult through the comparison of simulated growth to real growth. Moreover, modeling indeterminate tree growth (i.e., vegetative growth does not end with the formation of a reproductive organ) was challenging considering that most herbaceous crops that have been modeled are determinate. Tree architecture is more variable and complex than that of herbaceous plants where, within the same species, sink organs, such as inflorescent spikes, are located at the same position each year. This implies that tree crop models need to simulate carbohydrate distribution based on rules within a system that do not depend on empirically derived partitioning rules but on mechanistic rules that consider the complexity of the tree system, integrating architecture and structure. For these reasons, tree modeling took advantage of the previous experience of plant modeling on herbaceous plants but developed new solutions to simulate tree functions to address the challenges posed by the biological diversity of trees as compared with herbaceous crops.

The present review intends to provide a perspective of the evolution of tree crop modeling from the translation of herbaceous process-based models, to tree crop process-based models. Furthermore, we reviewed the substantial advancements borne by the integration of tree architecture and the setup of functional–structural plant models (FSPMs). Finally, we analyzed the different strategies used to model tree functions. The majority of fruit tree species described in the review are deciduous. However, evergreen trees pose further challenges concerning the leaf life span, which is usually longer than one season, and the different roles of leaves that are an important storage of nutrients and carbon in evergreen species in comparison with deciduous.

Based on a comprehensive update of the state of the art of tree crop models, the ultimate aim of the present review is to point out the knowledge gaps that deserve more attention in the development of new tree crop models.

Processed-based models

Process-based models (PBMs) (see Table 1) were the first type of mechanistic-based models developed in plants; before PBMs, there were just empirical models that described a process (e.g., photosynthesis) by mere observation (Landsberg et al. 1975). Process-based models are focused on plant processes, i.e., photosynthesis, respiration, water uptake and loss (transpiration), and their influence on crop growth. Indeed, plant growth is modeled as a process based on environmental conditions, such as light, temperature, nutrients, water and CO_2 concentration (Vos et al. 2007, 2010). The components of the simulated crop are leaves, stems, roots and reproductive or storage organs. Plant development is computed from carbon balance and is expressed as a quantitative variable (e.g., weight, surface area and N content) per unit area of soil surface (Sievänen et al. 2000, Vos et al. 2007, 2010). In PBMs, the allocation of carbohydrates among organ categories is driven by phenological stages by the relationship between plant development and seasonal temperature that is often expressed as thermal time (i.e., degree days) (Marcelis et al. 1998).

The first PBMs were developed on specific herbaceous annual crops such as cotton, potato, wheat and corn (Jones et al. 2016 for a review). In cotton, GOSSYM (Baker et al. 1983, Raja Reddy et al. 2002) was a model integrating a soil model to the previous SIMCOT (Duncan 1972), which described the response of cotton plant to environmental conditions. Later, OZCOT (Hearn 1994) was developed as a decision support model for cotton production. It considers environmental (e.g., temperature), agronomic (e.g., nitrogen) and varietal parameters (e.g., boll size). The POTATOS model (Spitters 1990, Kooman and Spitters 1995) was able to simulate tuber development on daily time steps based on nutrient and water availability. NPOTATO improved POTATOS through accurate models of growth, assimilate production, nitrogen and water balance (for description on potatoes models, see Wolf 2002). SWHEAT (Van Keulen and Seligman 1987) and AFRCWHEAT2 (Porter 1993) were built to simulate the development of spring and winter wheat, respectively, on an average population of plants (Porter 1993). The Crop-Environment Resource Synthesis (CERES) series of models describe crop growth, development and economic yield of wheat (Ritchie and Otter 1985), corn (Jones and Kiniry 1986), barley (Otter-Nacke et al. 1991), rice (Singh et al. 1993) and rapeseed (Gabrielle et al. 1999).

Simple Universal CROp Simulation (SUCROS) (Van Keulen et al. 1982) was a simple and generic growth model that simulated dry matter production of an herbaceous crop from emergence to maturity at daily steps. Successor versions are SUCROS87 (Spitters et al. 1989), integrating a more accurate method for simulating photosynthesis, SUCROS1 (Spitters 1990) for potential production and SUCROS2 (Van Laar et al. 1992) for water-limited production. Process-based models for rice were developed from SUCROS concepts. For a review, see Li et al. (2017).

Kiwifruit was one of the first fruit crops that was modeled (Buwalda et al. 1990). In this model, vine photosynthesis was simulated in relation to canopy shape and plant development. In addition, the influence of environment and crop management on carbon partitioning was considered. Net photosynthesis was computed hourly, considering the total leaf area density, using the incident solar radiation, and attenuation of light through the canopy. The more recent MaluSim (Lordan et al. 2019) model is derived from extending and improving pre-existent models. MaluSim integrates physiological and environmental data to simulate natural apple fruit abscission to help growers with thinning practices. The model is based on a dry matter production model and a carbon partitioning sub-model (Lakso et al. 2001) with the addition of fruit growth and abscission sub-models (Lordan et al. 2019). The same sub-models used for MaluSim were adapted for *Vitis vinifera* to create VitiSim, which models daily carbon balance and dry matter accumulation in grapevine canopies through different sub-models for photosynthesis, respiration and leaf area development (Lakso and Poni 2005). VitiSim was later improved including the effect of water stress and irrigation on dry mass production (Mirás-Avalos et al. 2018). PEACH (Grossman and DeJong 1994*a*) was a functional model that simulated the carbon supply and demand for peach trees. The model treated the plant as a collection of semi-autonomous, interacting organs that compete for resources (White 1984, Harper et al. 1986). Similar organs were modeled into composite compartments and carbon was allocated to them depending on their collective sink strength (Grossman and DeJong 1994*a*, 1994*b*, DeJong 1999).

Table 1. Process-based models in fruit tree crops.

Model name	Species	Processes simulated	Reference
-	*Actinidia deliciosa*	Carbon acquisition and utilization: maintenance of perennial biomass; growth of deciduous tissues; hydrolysis and restoration of carbon reserves Management operations: pruning; thinning	Buwalda et al. 1990
PEACH	*Prunus persica*	Carbon supply and demand: photosynthesis; maintenance and growth respiration; carbohydrate portioning	Grossman and DeJong 1994*a*
ALMOND	*Prunus dulcis*	Carbon supply and demand: photosynthesis; maintenance and growth respiration; carbohydrate portioning	Esparza et al. 1999
VitiSim	*Vitis vinifera*	Carbon balance: daily photosynthesis rate; carbon portioning; respiration of organs (roots considered) Water stress effect: simulation scenarios	Mirás-Avalos et al. 2018
OliveCan	*Olea europaea*	Water balance: root water uptake; turn off; soil evaporation; drainage; precipitation Carbon balance: photosynthesis; maintenance and growth respiration; partitioning of assimilates Management operations: tillage; irrigation; harvest; pruning	López-Bernal et al. 2018
MaluSim	*Malus × domestica*	Carbohydrate supply and demand balance: fixed carbon, respiratory costs, dry matter, carbon exchange among the plant Effect of environmental changes and cultural practices (i.e., thinning) on dry matter	Lordan et al. 2019

PEACH was modified to simulate almond tree development and this resulted in the ALMOND model (Esparza et al. 1999). The largest modification concerned the computation of canopy light interception by changing the surface response curve related to light.

OliveCan (López-Bernal et al. 2018) is a model that simulates the impact of environmental conditions and management practices on water relations, growth, development and productivity of *Olea europaea.* It has three sub-models for water balance (Gómez et al. 2001, Testi et al. 2006), growth (Jones et al. 1983, Morales et al. 2016) and management operations (i.e., tillage, irrigation, harvest and pruning).

QualiTree (Lescourret et al. 2011) is a generic fruit tree model, originally parametrized for peach, that simulates how horticultural practices (i.e., thinning, pruning and irrigation) influence fruit quality and growth. It integrates pre-existent models for: carbon (Lescourret et al. 1998); water (Lescourret et al. 2001); sugar (Génard et al. 2003) and fruit quality (Léchaudel et al. 2005). It was later upgraded with a simple light interception sub-model and it was tested on peach in different scenarios including simulation of pest damages (Mirás-Avalos et al. 2011). Because the architecture is considered as an input in the model, QualiTree can be thought of as an intermediate model between PBMs and FSPMs.

Functional–structural plant models (FSPM)

Functional-structural plant models, also named virtual plant models (Room et al. 1996, Hanan 1997), can describe the development, over time, of the 3D architecture of plants as influenced by physiological processes, which are affected by environmental factors. The main limitation of PBMs is related to limited or no consideration of canopy architecture, while, in trees, architecture largely affects the micro-climate to which each organ is exposed and, consequently, functions such as light interception, photosynthesis, respiration, carbon allocation, water and nutrient uptake (Sievänen et al. 2000).

Although there is a close link between herbaceous and tree modeling, the substantial biological differences between annual herbaceous plants and trees pose challenges that are still critical in tree crop modeling. Indeed, tree models have to represent indeterminate instead of determinate growth typical of many annual plants. This implies that the carbon sub-models have to account for winter reserve storage and spring reserve remobilization. Moreover, the architectural sub-models need to consider new branching that grew from buds that were formed during the previous season and that remained dormant during the winter. Simulations grow more complex if the models simulate horticultural practices such as pruning. This requires, firstly, the calculation of carbon losses due to the biomass removed and, secondly, the regrowth responses of the tree after pruning. Moreover, the carbon balance in perennial plants is difficult to simulate because it is not driven by empirically derived rules but by a complex source–sink system that requires the development of specific organ sub-models. Thus, the available carbon pool needs to be computed at the organ scale and not at the whole-plant scale. For example, in L-PEACH (Allen et al. 2005) and L-ALMOND (DeJong et al. 2015) FSPMs, carbohydrate distribution is computed for individual organs, while the PEACH (Grossman and DeJong 1994*a*) and ALMOND (Esparza et al.

1999) PBMs handled carbohydrate availability as one common source. This consideration is important when modeling tree crops, compared with annual crops. This is because trees are large and carbohydrate distribution between each sources and sinks needs to be context-specific because carbohydrates are not equally available to all sources and sinks (Allen et al. 2007, DeJong et al. 2015).

Furthermore, the validation of models of perennial plants is more difficult than for annual plant models: many determinate annual plants all grow in the same way, while this is not true for trees that are indeterminate, large and often manipulated by pruning. For these reasons, it is rare to find two identically growing trees. Thus, in tree plants, the validation through quantitative comparisons of simulated plants with actual plants, as it is done for annual crop models, is of limited value. Model validation at the tree-scale, thus, tends to be more qualitative than quantitative when evaluating modeled tree behavior. Indeed, some attempts have been done using the 3D digitized techniques to validate the model at a tree-scale (i.e., in MappleT model; Costes et al. 2008). However, to overcome the difficulties of tree-scale, many tree crop models are validated at the organ-scale, for example, checking if those data of simulated organ growth, in a given year, are consistent with field data (i.e., in L-PEACH (Da Silva et al. 2011), in V-Mango (Boudon et al. 2020) or in MuSCA (Reyes et al. 2020)).

Modeling the structure and function

Combining structural information with physiological functions, FSPMs are good tools for describing the realistic growth and development of tree crops (for reviews, see Sievänen et al. 2000, Vos et al. 2007) and can address many of the challenges posed by tree modeling.

Depending on the process and the species, different modeling strategies have been used in different models. In this section, the main approaches used in tree crop modeling per each structural part and function are reviewed.

Structure

It is now widely accepted that plant architecture is the result of a series of repetitions of elementary units (White 1984, Room et al. 1994), at different levels (i.e., metamer/phytomer, growth units, axes and branching system; see Table 2), through apical growth and branching processes (Cohen 1967, Honda 1971, Barthélémy 1991, Barlow 1994). The elementary units most frequently used are the metamer (e.g., in the model L- KIWI; Cieslak et al. 2007), growth unit (e.g., in the model LIGNUM (Perttunen et al. 1996) and INCA (Le Dizès et al. 1997)), or both (e.g., in the generic GREENLAB (Hu et al. 2003, De Reffye et al. 2021)).

Models that describe canopy architecture are called architectural or geometrical models (Halle et al. 1978). Plant architecture description is based at least on one of three types of information: composition, geometry and topology (Godin and Caraglio 1998, Godin 2000, Vos et al. 2007). Plant composition defines the different types of elements that compose the plant; geometry describes the shape and the spatial position of such components; topology characterizes the connections between those elements (Godin 2000, Vos et al. 2007).

The topological connection of tree components can be interpreted using a tree-graph (Godin and Caraglio 1998). Through edges and vertices, it is possible to represent the connections between a plant's organs. In L-systems (Prusinkiewicz and Lindenmayer 1990), a similar approach was called an 'axial tree'.

From the simplest to the most detailed, the ways through which it is possible to describe plant architecture are global, modular and multiscale representations (for a detailed review, see Godin 2000). In global representations, the plant is not described as decomposed into modules but is considered as a whole. The architecture is represented by geometric figures such as ellipses and cylinders used to describe the canopy and trunk, respectively. In modular representations, the plant is treated as a modular organism. In the modular approach, the plant is described, according to the model aim, by choosing one of the many repeated modules that compose the plant (e.g., metamers/internode, growth units and axes) (Harper et al. 1986). Multiscale representations are the most detailed, describing the plant at different levels (i.e., metamer scale, growth unit scale and main branching scale). Multiscale representations were created in the 1980s based on fractals (i.e., an object that can be described at every scale) (Mandelbrot 1982). Because multiscale representations describe plant growth at different time and space scales, it is the one that best corresponds to the complexity of plant architecture. The multiscale-topological representation describes the plant through the multiscale tree graph (MTG) (Godin and Caraglio 1998), which is the result of several tree-graphs, each one at a different scale.

Topological representations can be described using specific formalisms such as L-systems (Lindenmayer 1968, Prusinkiewicz and Lindenmayer 1990). In the late 1960s, Lindenmayer (1968) introduced a formalism to model the development of multicellular organisms (i.e., algae). This formalism was later named as the Lindenmayer-system or L-system. Plants are represented through a set of modules that evolve following some basic and repetitive rules that are applied simultaneously (Lindenmayer 1968, Prusinkiewicz et al. 1997). In L-systems, a module is defined as a repeated plant unit that is involved in its development (e.g., metamer, apex and branch). The core of the L-system is the rewriting system; according to it, the ancestor module is substituted with a descendant module using a definite set of rewriting rules. The system works with

Table 2. Term definitions (for review see Costes et al. 2006).

Organ	Definition	Original reference
Metamer/phytomer	Fundamental structure of plants. It consists of a node with axillary leaf/leaves and axillary bud/buds, and an internode	White 1979
Growth unit	A part of an axis that is formed in a period of non stop elongation Annual growth, in temperate climates, is composed by all the growth unts produced during a growing season	Hallé et al. 1978
Axis	A sequence of units of growth in the same general direction from one (monopodial) or more (sympodial) meristems	Room et al. 1994
Branching system	It is the organization of the branches within the same plant	Edelin 1991

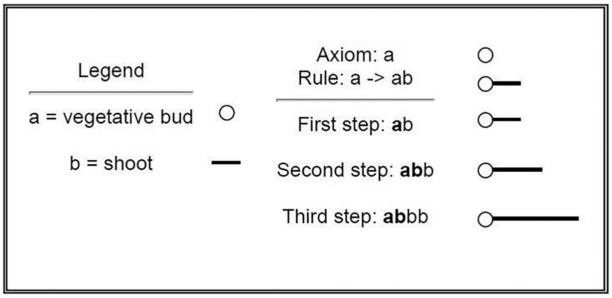

Figure 1. Example of L-system rewriting rules. The legend is on the left, while the effect of the application of the rewriting rule is on the right.

an initial string, called the axiom, that transforms itself following the rewriting rules (e.g., the axiom is a, and the rule is a → ab; the L-system will transform each ‘a’ of the axiom into ‘ab’ for each step of the process; Figure 1) (Prusinkiewicz et al. 1997). Within L-systems, it is possible to use other models to increase the realism of the simulated plant. The pipe model (Shinozaki et al. 1964*a*, 1964*b*) is used to model the thickness of the simulated stems and roots (Jirasek et al. 2000, Allen et al. 2005, Cieslak et al. 2011*b*) or xylem and phloem conduits (Hölttä et al. 2006). According to the ‘pipe model theory’, a tree is composed of pipes that connect each canopy element to the roots (for a review, see Lehnebach et al. 2018). The thickness and cross-sectional area of the pipes are constant and each pipe bears a fixed amount of leaves. According to this theory, the total cross-sectional area of stems and branches, at a certain height, is proportional to the total amount of leaves existing above that height. Pipes serve both as vascular paths and mechanical supports and their length runs from each group of leaves to the ground without breaking (Shinozaki et al. 1964*a*, 1964*b*). Such a model has been used, for example, in the LIGNUM model (Perttunen et al. 1996).

Aerial part

The first architectural analysis was made in the 1970s on tropical trees (Hallé and Oldeman 1970, Halle et al. 1978). They proposed 23 models of tree architecture, usable for all higher plants, at the whole-tree scale. For modeling the architecture of fruit tree species, it is crucial to study shoot types (i.e., long or short shoots, shoots with preformed or neoformed organs and diameter), organ development and form (i.e., phyllotaxy, shape, orientation and size), branching process (i.e., monopodial and sympodial) and tree form (i.e., cone and globular) (Costes et al. 2006). To analyze the branching pattern, 1-year-old shoots are analyzed, in winter, by recording bud-type observations, node by node (from the base to the tip; Caraglio and Barthélémy 1997, Costes and Guédon 2002). Each node’s observation represents the fate of a bud of that specific node rank (Negrón et al. 2013, Costes et al. 2014, Prats-Llinàs et al. 2019). Based on these data, an exploratory analysis of the shoot will denote different homogeneous zones that compose the 1-year shoot (e.g., distal zone has more flower buds and is preceded by a zone with more sylleptic shoots). The transition probability between two zones (i.e., the probability that one zone will follow another zone) is statistically assessed through the use of Markovian models (Taylor and Karlin 1998). Markov models and hidden semi-Markov models are used in plant modeling. These models have been used for several fruit species: apple, (MappleT (Costes et al. 2008) peach (L-PEACH (Allen et al. 2005, DeJong et al. 2011)), almond (L-ALMOND (Negrón et al. 2013, DeJong et al. 2015)), grapevines (GrapevineXL; Zhu et al. 2018) and kiwifruit vines (L-KIWI; Cieslak et al. 2009, 2011*a*; Figure 2).

Plant topology can be assessed through the use of 3D digital measurements (i.e., magnetic or sonic digitizers) (Sinoquet et al. 1997, Sonohat et al. 2006, Belhassine et al. 2020), allometric relationships (Casella and Sinoquet 2003, Yang et al. 2021) or the use of photographs (Kaminuma et al. 2004).

Roots

Roots are an important organ playing fundamental roles in many physiological processes such as carbon storage and water/nutrient uptake. Root apparatus modeling is fundamental to effectively represent whole-plant functioning (Pages et al. 2000, Ndour et al. 2017). However, mapping root architecture is more difficult than mapping the canopy since the root system is underground, and invasive and destructive methods are needed to study it (Danjon and Reubens 2008). Additionally,

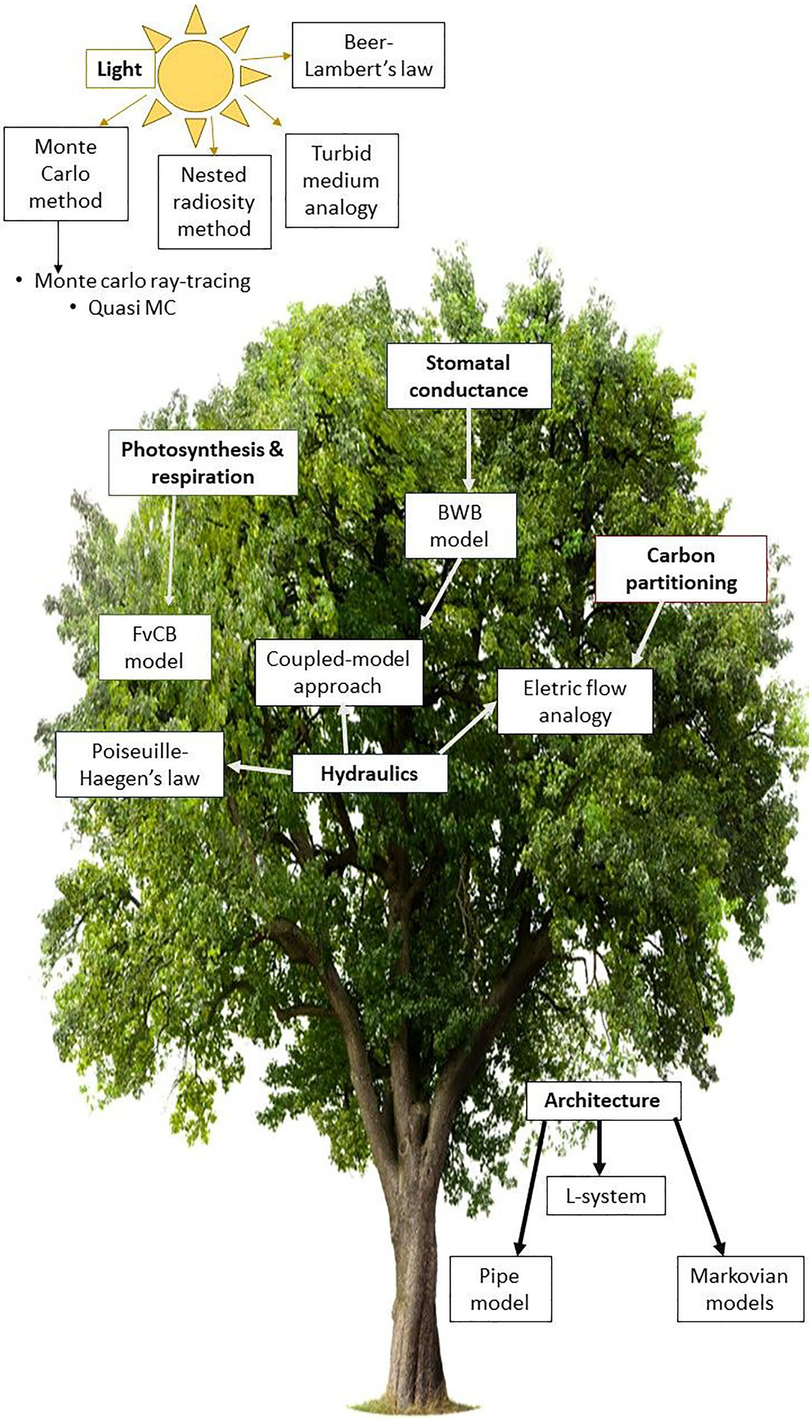

Figure 2. Conceptual maps describing FSPMs' structure and functions.

roots do not grow as a set of repeating units (i.e., metamers) like shoots; indeed, their architecture cannot be modeled in the same ways. Recently, a review about root phenotyping to overcome some of these issues was published (Takahashi and Pradal 2021), but tree roots are still poorly investigated.

Indeed, roots are poorly represented in tree FSPMs and they are often considered collectively as a single module as in LIGNUM (Perttunen et al. 1996), MappleT (Costes et al. 2008), L-PEACH (Lopez et al. 2010) and MuSCA (Reyes et al. 2020). In herbaceous crop models, root architecture is more often considered, such as in barley (Drew et al. 1973), clover (Fitter 1987), wheat (Diggle 1988) and maize models (Pages et al. 1989). To overcome the issue of modeling, the root architecture, in the late 1980s, some architectural models specific for the root systems were created. ROOTMAP simulates the root system of wheat (Diggle 1988). The fibrous roots are described in terms of growing time, number of axes, growth rate, growth direction and branching characteristics of roots. The root system is the result of the growth and branching processes of individual roots. ROOTMAP differs from previous similar models (Lungley 1973) because it computes the growth of all root tips in each time step, before proceeding with the next step. This allows the use of sub-models that can compute water and nutrient uptake of growing roots (Diggle 1988). The parameters are elongation rate, branching density and duration of apical non-branching (Hackett and Rose 1972, Rose 1983, Porter et al. 1986). The output of ROOTMAP is the projection of the simulated root system into a vertical and horizontal plane (Diggle 1988). Twenty years later, RootTyp (Pagès et al. 2004), a generic model for root systems, was developed. It describes some processes such as root emission, axial and radial growth, sequential branching, reiteration, transition, decay and abscission of roots. Each root tip extends axially (i.e., axial growth) and develops laterals (i.e., branching). The time step is a day and at each time step, the positions of apices and the branching points are represented (Pagès et al. 2004). Other models that deal with root architecture are CRootBox (Schnepf et al. 2018) and DigR (Barczi et al. 2018). They are generic root models, suitable both for annual and perennial plants. They can describe growth, development, branching and directions of the architecture of different roots.

In perennial woody plants, root system model development is further complicated by the root mortality of both fine roots and structural roots. Moreover, it is necessary to consider also the over-winter nutrient storage capacity of roots (Danjon and Reubens 2008). Some empirical experiments regarding the effect of nutrients can be settled using a drainage lysimeter model as was done in almond by Sperling et al. (2019). Despite the limited amount of information regarding roots, several attempts at modeling the root system have been carried out in tree crops. Vercambre et al. (2003) described the roots of *Prunus persica* and included two levels of information in their model: the typology of root axes, based on morphological and developmental characteristics, and a set of elementary processes such as axial and radial growth, ramification, reiteration and decay (Vercambre et al. 2003). In INCA (Le Dizès et al. 1997) and SIMWAL (Balandier et al. 2000), the root system was simplified into three elements: tap roots, coarse roots and fine roots. In SIMWAL, roots are depicted as cylinders and are treated as branches: their growth is computed through carbon allocation and growth sub-models. Fine roots are modeled separately because their development is related to soil characteristics (Cooper 1973). In L-KIWI (Cieslak et al. 2011*a*, 2011*b*), root growth is modeled considering only fibrous roots. The potential growth rate is assumed to be the relative elongation rate of the fibrous root in late summer, the period of maximum growth.

Functions

Functional-structural plant models aims to model the growth and development of the plant. To reach this goal, an architectural model is implemented with one or more functional sub-models to describe: light interception, photosynthesis, respiration, carbon partitioning, root up-take and hydraulics (Figure 2).

Light interception

Reflection, absorption and transmission of light are the three main steps a light ray goes through when it reaches the leaf surface. Different strategies can be used to model light interception. Some of the most used tools are based on the Monte Carlo method (Chelle and Andrieu 2007). From this method, Monte Carlo ray-tracing methods were formalized (Cieslak et al. 2008). It computes the path and interactions with surfaces, of multiple photons, until they leave the canopy, or are absorbed by surfaces (Disney et al. 2000). From the Monte Carlo ray-tracing method, a slightly different approach called QuasiMC was developed (Cieslak et al. 2008). QuasiMC was used in the L-KIWI (Cieslak et al. 2011*a*, 2011*b*) and on the first version of L-PEACH (Allen et al. 2005). Later, in the peach light model, the QuasiMS was substituted with a layer turbid medium approach (Monsi and Saeki 1953) to speed up calculations but, according to authors, it needed further improvements because this approach does not consider the shade effect of adjacent trees (Da Silva et al. 2011).

The nested radiosity model (Chelle and Andrieu 1998) merges the radiosity method (Sparrow 1963) with the turbid medium approach (Monsi and Saeki 1953) and allows modeling of the distribution of natural light. It considers each organ as a set of polygons and, for each organ, the contribution of three light sources is computed: direct light coming from the source, light coming to close organs and light coming from far organs (Chelle and Andrieu 1998). This light model can communicate with the L-system through CARIBU software (Chelle et al. 2004) (e.g., used in the model developed for *V. vinifera*; Prieto et al. 2020). Both the radiosity model and CARIBU are good models for simulating light interception. However, they are hardly used in tree crops due to their computational time.

Other widely used models to describe light interception are the one based on turbid medium analogy (i.e., in RATP; Sinoquet et al. 2001) and the attenuation based on Beer–Lambert's law (i.e., in the QualiTree model; Lescourret et al. 2011).

RATP is a model that simulates the spatial distribution of radiation absorption, transpiration and photosynthesis inside the canopy. The plant is described as an array of 3D cells that can be empty or contain plant components. The incident radiation is computed considering direct and diffuse radiation that passes through the array. The Beer–Lambert's law attenuation model is often used to account for attenuation of light beam inside the canopy. In QualiTree (Lescourret et al. 2011, Mirás-Avalos et al. 2011), for example, the light interception model computes the photosynthetic active radiation (PAR) considering the canopy as composed of geometric figures (e.g., originally ellipsoids later changed into cubes) and the light beam inside the canopy is attenuated according to the Beer–Lambert's law.

Photosynthesis and respiration

Photosynthesis and respiration are the two main processes through which the plant gains and loses carbon, respectively. They can be modeled through a biochemical approach such as the one proposed by Farquhar et al. (1980) or using the light-response curve. Farquhar et al. formalism describes a biochemical model of photosynthesis of C3 plants and it is called the Farquhar-von Caemmerer-Berry (FvCB) model (Farquhar et al. 1980, 2001). The biochemical approach of this model allowed users to describe processes that are difficult to define with empirical approaches. The disadvantage of FvCB is that it requires extensive calibration of several parameters, which makes it difficult to use for agricultural or horticultural purposes (Wullschleger 1993, Kim and Lieth 2003). To overcome these problems, a coupled-model approach was proposed. It is a photosynthesis–stomatal conductance–transpiration model (Collatz et al. 1991, Harley et al. 1992) that combines the pros of FvCB (Farquhar et al. 1980) with a model of stomatal conductance, called the BWB model (Ball et al. 1987, Leuning et al. 1995), and an energy budget equation. Briefly, the coupled approach proposed by Collatz et al. (1991) simulated leaf photosynthesis of a C3 plant (soybean in their experiments) considering environmental and leaf parameters as well as stomatal conductance (g_s). Functional-structural plant models that use the Farquhar et al. formalism are INCA (Le Dizès et al. 1997), SIMWAL (Balandier et al. 2000), RATP (Sinoquet et al. 2001), L-PEACH (Da Silva et al. 2011), GrapevineXL (Zhu et al. 2018) and MUSCA (Reyes et al. 2020).

Another method to model photosynthesis process is through the photosynthesis-light response curve. Models that use this kind of strategy are LIGNUM (Perttunen et al. 1996), L-KIWI (Greer et al. 2004) and QualiTree (Lescourret et al. 2011). This method can be implemented including other functions that affect photosynthesis. For example, in QualiTree, the daily photosynthesis is computed considering leaf reserves as detailed by Quilot et al. (2004) and leaf water potential as outlined by Ben Mimoun et al. (1999).

Carbon partitioning

In leaves, net photosynthesis is the balance given by gross photosynthesis and respiration (first maintenance respiration and then growth respiration). Source organs (i.e., mature leaves) accumulate photosynthates that are then distributed to sink organs (i.e., young leaves, fruits, shoots and roots). In tree plant models, carbon distribution is often not driven by an allocation factor as in herbaceous crop models (Le Roux et al. 2001, Fourcaud et al. 2008), but depends on the source capacity and the sink strength of each organ (Wilson 1967). This implies an approach that considers the description of the growth of all of the major organ types of a tree, through the development of different sub-models.

The carbon balance, in QualiTree, is evaluated by computing the pool of useful carbon per each organ adding to photosynthesis the carbohydrate reserves. Carbohydrates are then allocated to each organ to satisfy first the maintenance respiration and growth of leafy shoots. Then, the residual carbon supply is allocated to the organs that have not yet satisfied maintenance respiration. The remaining carbon supply is shared among all the organs of the tree to satisfy the growth requirements. Finally, organ growth and reserve storage are simulated.

In LIGNUM (Perttunen et al. 1996), the production and allocation of carbon follow the principle of functional balance (Nikinmaa 1992) that together with the pipe model hypothesis (Shinozaki et al. 1964*a*) describes the relationship between biomass and tree cross-sectional area. According to these theories, net photosynthesis is calculated for the growth of new tree segments and leaves and then allocated to the different segments of the tree.

In INCA (Le Dizès et al. 1997), L-PEACH (Allen et al. 2005), L-KIWI (Cieslak et al. 2011*a*, 2011*b*) and L-ALMOND (DeJong et al. 2015), carbohydrate distribution is driven by potential source carbohydrate pools (photosynthesis and reserve), potential sink demands (growth, respiration and storage), potential growth, carbohydrate availability from sources, location of sources relative to the sinks within the tree architecture and the transport resistance between each source and sink (DeJong and Moing 2008, DeJong 2019). To simulate the movement of substances in the plant from source to sink, as well as simulating the movement of water, the original method, used in L-PEACH (Allen et al. 2005), was the analogy between the fluid flow in plant vessels and the current flow in an electric circuit. This approach was called the carbon transport resistance allocation model (C-TRAM) (Prusinkiewicz et al. 2007). In this model, each metamer was simulated as a conducting element, including an internode, and a distal sink or source element representing a leaf, bud, flower or fruit. In L-KIWI, authors extended the L-PEACH method to include the possibility to simulate several source/sink organs per metamer (Cieslak et al. 2011*a*, 2011*b*). They used the multiscale approach using one set of L-system rules to represent plant development at the organ scale and another set of rules to simulate carbon dynamics at the sink/source scale. C-TRAM involves elaborate computations and parametrization that can make it a complex model to use. A direct L-system approach was developed in L-Studio (Prusinkiewicz et al. 2000). It was based on the Münch hypothesis (Münch 1927) and Michaelis–Menten sources and sinks (Thornley and Johnson 1990) and resulted in a simplified model of carbohydrate transport in growing plants (Seleznyova and Hanan 2017, 2018).

In SIMWAL (Balandier et al. 2000), carbon allocation is based on a proportional model originally developed by Wilson (1967). The photosynthates allocated to each sink were proportional to its demand without exceeding it. However, this formalism does not allow for the variation of fluxes according to the source–sink ratio. To fix that, the original formalism was modified by splitting the sink strength into two components (i.e., affinity and maximum import rate; Escobar-Gutiérrez et al. 1998) and considering the effect of source–sink distances (Balandier et al. 2000). SIMWAL considers both leaves and roots as source organs, respectively, due to photosynthesis and remobilization of resources in winter and spring. In winter, the model assumes that each organ relies on its reserves for maintenance respiration, while in spring, the reserves are used for respiration and growth until photosynthesis reaches or exceeds carbon demand (Balandier et al. 2000).

From an application point of view, of particular importance are the model implementations that allow simulating horticultural practices such as pruning effects on the carbon submodels. Pruning is a fundamental technique that is used to equilibrate the reproductive and the vegetative parts of the plant and is one of the main tools for growers to drive tree behavior in commercial orchards. Thus, modeling regrowth responses after pruning is an interesting upgrade of FSPMs to make successive year simulations more realistic. Examples of models that already have this upgrade are L-PEACH (Allen et al. 2007), L-KIWI (Cieslak et al. 2011*a*, 2011*b*) and SIMWAL (Balandier et al. 2000), while in other models, it is still to be implemented (for instance, V-MANGO; Boudon et al. 2020).

Root uptake

Carbon and nitrogen distribution in the plant has been studied for many years especially in annual crops (Hirose and Werger 1987, Boonman et al. 2007). In wheat, the simulation of nitrogen distribution and accumulation of nitrogen into the leaf lamina and grain are modeled into a PBM (Bertheloot et al. 2008). In maize, the model called GRAAL-CN (Drouet and Pagès 2007*a*) roots is considered with the same amount of detail as the shoot system, and the main processes regarding carbon and nitrogen management are simulated for each organ. These processes are functions of external (i.e., temperature, light and nitrogen supplies) and internal (i.e., carbon and nitrogen availability in the plant) variables (Drouet and Pagès 2007*b*). Carbon acquisition depends on light intensity, while nitrogen uptake depends on its concentration in the soil. In tree crops, nutrient modeling has been integrated into a few existing FSPMs and PBMs such as in grapevines (Wermelinger et al. 1991, Prieto et al. 2012, Zhu et al. 2018) and peach (Rufat and DeJong 2001), but this aspect still deserves more investigations.

Hydraulics

In trees, water moves in the xylem from the soil, through roots, to the crown, and then it evaporates from the leaves. Thereby, to model water flow through the plant, it is essential to simulate the xylem circuit, water uptake from the soil and leaf transpiration along with the soil-plant-atmosphere continuum (SPAC) (Slatyer and Markus 1968, Thornley and Johnson 1990). In the last century, many authors tried to simplify all these interactions (for a review, see Jones and Tardieu 1998) or ignored them, assuming optimal plant water status (INCA (Le Dizès et al. 1997) and SIMWAL (Balandier et al. 2000)).

Modeling water flow using the electric current flow analogy was an idea developed in the early 1920s (Gradmann 1928). This idea was not considered for decades until Van den Honert used it to describe hydraulic resistance and water potential differences that drive water flow from the roots to the leaves (Van den Honert 1948). To model the xylem circuit, many studies have applied Poiseuille-Haegen's equation to xylem vessels assuming the xylem functions as a set of pipes (Ewers and Fisher 1989, Tyree and Ewers 1991, Tombesi et al. 2010). Haegen and Poiseuille independently, in the nineteenth century, wrote an equation for fluid flow through a 'bundle of cylindrical pipes' (Tyree and Ewers 1991). In this way, they demonstrated that hydraulic capacity (Q, kg s^{-1}) depends on the diameter of vessels. Because xylem is not perfectly circular, the equation was later modified considering pipes with elliptical or rectangular shapes. Even though this modification was applied, real conductivity can vary between 20% and 100% of the theoretical one according to the species and current environmental conditions (Calkin et al. 1986, Ewers et al. 1990). The pipe model theory (see 'Structure' paragraph) can be used also to model the xylem circuit. In this interpretation, stem and branches are considered as the assemblage of pipe units, each supporting one leaf. A limitation of this approach was the lack of accounting for the variation of stem cross-section and vessel diameter within the crown (Tyree and Ewers 1991). These data are needed to compute the changes in water potential (Ψ) and consequently the diurnal and seasonal changes in water content of leaf and stem segments. Besides that, to understand water flow in trees, it is necessary to build a hydraulic map of a representative tree of each species. A map can be created by cutting the tree or large branches into segments so that it is easier to understand the stem and leaf distribution. Data that should be recorded per each segment are the basal diameter of the segment, length of the segment, surface area of all leaves attached to the segment and information on how conductivity can be reduced by cavitation. Each leaf in the map has the same evaporative flux density (E, kg s^{-1} m^{-2}) (Tyree 1988, Tyree et al. 1991, Tyree and Ewers 1991).

L-PEACH uses both the coupled approach (Collatz et al. 1991, Kim and Lieth 2003) and the electric circuit analogy to simulate the water flow into the xylem circuit (Da Silva et al. 2011). This allowed the calculation of the transpiration rate as a function of leaf properties and environmental variables such as intercepted radiation, air temperature, air relative humidity, wind speed and leaf water potential. The xylem circuit was composed of stems, leaves and roots. Stem conductance was simulated using Hagen-Poiseuille's law (Tyree and Ewers 1991, Tombesi et al. 2010). Leaf transpiration was simulated as a function of environment, local carbohydrate availability and water potential. The root conductance was simplified by setting the maximum value for root conductance equal to the conductance value of the first stem segment contiguous to the root (Da Silva et al. 2011). The water sub-model interacted with the carbon sub-model allowing simulation of the effects of water stress on photosynthesis and carbon partitioning. Moreover, it was also used to simulate the effect of rootstocks that had differing hydraulic conductances on the growth of the peach trees (Da Silva et al. 2015).

Other models that incorporated water are L-KIWI (Cieslak et al. 2009), which uses an aspect-oriented approach that considers leaf transpiration fluxes, leaf water potential and soil water potential; GrapevineXL (Zhu et al. 2018) that couples the Farquhar et al. (1980) equations for photosynthesis and the Tardieu-Devies model (Tardieu et al. 2015), which calculates the water transport from soil to leaf with an electric resistance analogy. In Hydroshoot, the hydraulic module calculates plant water potentials as a function of soil water potential and plant water flow (Albasha et al. 2019). V-Mango includes water relations modeling into the fruit growth module (i.e., fruit water potentials, fruit transpiration and water flows) (Boudon et al. 2020) and MUSCA (Reyes et al. 2020) through the RATP model (Sinoquet et al. 2001).

Examples of FSPMs set up for herbaceous crops are COTONS (Jallas et al. 1998) and L-OZCOT (Hanan and Hearn 2003) or ADEL maize (Fournier and Andrieu 1999). The evolution of PBMs to FSPMs was much faster in perennial species due to the importance played by the architecture in influencing carbon partitioning and long-term light interception (Table 3). One of the most important phenomena influenced by architecture is alternate bearing that affects many fruit crops. Through crop management practices such as pruning, it is possible to modify the plant architecture to balance the vegetative and reproductive parts of the tree and minimize alternate bearing. To accurately model this process, the simulation of single-organ status (e.g., vegetative growth, bearing and eventual death) is necessary. Indeed, in PBMs, alternate bearing can only be modeled in a simplified way. In Filbert's PBM (Bregaglio et al. 2020), for example, the allocation of photosynthate to fruits was reduced by empirical coefficients based on the negative correlation between previous year crop and current year crop. Modeling of this type of phenomenon can be improved through architectural information merged with rules that regulate carbon availability in every organ.

One of the first FSPMs created for trees was calibrated to simulate forest species such as Scots pine (Perttunen et al. 1996) and *Acer saccharum* Marsh (Perttunen et al. 2001). In the same period, in tree crops, INCA was set up to simulate the growth and development of a young walnut tree over three or four years (Le Dizès et al. 1997). *Juglans* spp. were also modeled in SIMWAL (SIMulate WALnut) (Balandier et al. 2000). SIMWAL describes the growth of the tree driven by environmental conditions. Later, FSPMs were also built for peach trees: L-PEACH (Allen et al. 2005) is a model derived by adding the architecture of a peach tree to the existing PEACH model (Grossman and DeJong 1994*a*). L-PEACH was later reparametrized and adapted to almonds to create the L-ALMOND (DeJong et al. 2015, Lopez et al. 2018). The most important functional change in the conversion from peach to almond was the simulation of shoot mortality: since peach trees are heavily pruned each year, L-PEACH did not include this process. Because shoot mortality is a shade-dependent process (Lampinen et al. 2011), a shadow propagation method that computes the exposure of each shoot to light was added to L-PEACH (DeJong et al. 2015).

In apple trees, the MappleT architectural model was implemented by adding the QualiTree model for carbon allocation (Lescourret et al. 2011). The authors modified the architecture of QualiTree to consider the shoot polymorphism that exists in apple trees. The resulting FSPM allowed MappleT to realistically simulate shoot and fruit growth and their within-tree variability during a growth cycle (Pallas et al. 2016). Using L-PEACH as a starting point, L-KIWI, an FSPM for kiwifruit vines, was developed (Cieslak et al. 2009). The pre-existent architectural model of kiwifruit (Cieslak et al. 2007) was implemented with a light model and was integrated with a carbon balance model. Based on L-KIWI but with changes in the architecture and parameters, a mechanistic FSPM for apple was developed and is currently under changes to include orchard management (Seleznyova et al. 2019).

Functional-structural plant models can also be not specific on one species but rather be generic (Henke et al. 2016): this is the casa of GreenLab and MuSCa. GreenLab (Hu et al. 2003) is an FSPM that can be used to describe the architecture and processes of both herbaceous and tree plants (for a review, see De Reffye et al. 2021). Focusing on trees, Musca is a generic model (Reyes et al. 2020) built to simulate carbon allocation and growth of organs during one vegetative season by choosing different topological scales of the plant. The first application of this model was done in apple trees using MappleT's MTGs. MuSCa showed that reducing the topological resolution will reduce the computation time of the model; the best compromising scale, in apple, that allows good architectural resolution and acceptable time of computation was the growth unit (Reyes et al. 2020). In the same year, V-Mango was set up to simulate the growth and fruit production of the mango tree at a daily time scale (Boudon et al. 2020). GrapevineXL is an FSPM for grapevines that was developed to simulate the

Table 3. List of FSPM for fruit tree crops.

Model name	Species	Simulation	Reference
LIGNUM	Generic forest free	Architecture: pipe model Functions: photosynthesis; respiration; senescence; growth	Perttunen et al. 1996
INCA	*Juglans regia*	Architecture: 3D representation Functions: solar radiation interception; photosynthesis; respiration; growth and portioning of photosynthate	Le Dizès et al. 1997
SIMWAL	*Juglans* sp.	Architecture: 3D representation Functions: photosynthesis; radiation interception; respiration; allocation of photosynthate; reserve storage and mobilization Management operations: Pruning	Balandier et al. 2000
L-PEACH	*Prunus persica*	Architecture: L-system and Markov chains Functions: photosynthesis; carbon storage; carbon partitioning; maintenance respiration and growth Management operations: pruning; budding; fruit thinning; harvesting	Allen et al. 2005, 2007
L-KIWI	*Actinidia deliciosa*	Architecture: L-system and Markov chains Functions: carbon transport; carbon allocation; leaf irradiance absorption Management operations: pruning; training	Cieslak et al. 2009, Cieslak et al. 2011*a*, 2011*b*
L-ALMOND	*Prunus dulcis*	Architecture: L-system and Markov chains Functions: photosynthesis; carbon storage; carbon partitioning; maintenance respiration and growth	DeJong et al. 2015
MappleT	*Malus x domestica*	Architecture: L-system and Markov chains Functions: assimilates demand; light interception model; carbohydrate reserve mobilization; carbohydrate allocation; fruit quality; growth and maintenance respiration	Pallas et al. 2016
GrapevineXL	*Vitis vinifera*	Architecture: 3D reconstruction Functions: photosynthesis, stomatal functions, water transport from soil to leaves	Zhu et al. 2018
MuSCa	Generic	Architecture: L-system and Markov chains Functions: carbon allocation	Reyes et al. 2020
V-Mango	*Mangifera indica*	Architecture: L-system; Functions: thermal time for growth and development; pipe model for girth growth; fruit growth; water-related processes at fruit branch scale; accumulation of organic compounds and minerals in fruits	Boudon et al. 2020
/	*Vitis vinifera*	Architecture: 3D representation Functions: light interception; photosynthesis; and stomatal conductance model	Prieto et al. 2020

stomatal functions and water transport within the plant (Zhu et al. 2018). GrapevineXL describes well the diurnal pattern related to water flow in *V. vinifera* growing in drying soils. It needs further improvement to better consider the hydraulic conductance of roots and leaves. Recently, another FSPM for grapevine was set up (Prieto et al. 2020). It was based on the TOPVINE architectural model (Louarn et al. 2008*a*, 2008*b*) and evaluates how canopy architecture influences canopy gas exchange.

Conclusions

Computer tree modeling largely evolved in the last decades by developing the PBMs initially created for herbaceous crops. The introduction of architectural modeling, which was concurrent in herbaceous and tree crops, greatly improved the reliability of models in simulating plant functions by introducing spatial scales and integrating the simulation of the effect of canopy colonization of space and its impact on light interception and carbon distribution among source–sink organs. The introduction of FSPM led to the development of models that can provide useful insights into plant–environment interactions and crop management.

Future research

Major progress has been made since the development of LIGNUM, one of the first FSPMs for trees (Perttunen et al. 1996). However, to improve the realism of the simulation, further implementations are needed. In particular, few tree models integrate nutrient distribution within the tree canopy or root architectural growth. The integration of canopy and root growth, architecture and functions into one FSPM is still missing. Currently, tree reserves, winter dormancy and bud break processes are empirically modeled, and further physiological information is needed to improve the modeling of these functions. Light environment and microclimate in tree canopies vary greatly over the day and major horticultural practices such as pruning are aimed at driving plant activity by setting the optimal microclimate for vegetative/reproductive activity (DeJong 2019). Simulation of these processes implies hourly time-step sub-models, but, up to now, only a few models can do this. This last point highlights computing power as one of the main limitations for computer tree modeling. In computer simulation of trees, the number of growing units and organs exponentially increases over time and this limits the capability of performing long-term simulations (i.e., several years) of mature trees.

Important conclusions

Functional-structural plant models are powerful tools that in tree crops are still relegated to the use by developers and their use by the commercial sector is limited. The understanding of plant growth, development and productive processes that are derived from the development of these models can be used to solve concrete horticultural problems but their direct use as practical decision-support tools is still limited (DeJong 2019). The continued improvement of FSPMs and the knowledge resulting from them will benefit scientific research, commercial sector applications and grower education.

Finally, the likely increase of tree modeling capabilities and capacity for predicting changing environmental impacts on tree growth and productivity and the application of models for developing alternative crop management strategies will make FSPMs a fundamental tool to address future challenges imposed on the horticultural sector.

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