Carbon-based models of individual tree growth: A critical appraisal

Xavier Le Roux[a,*], André Lacointe[a], Abraham Escobar-Gutiérrez[b,c]
and Séverine Le Dizès[a]

[a] U.M.R. PIAF (INRA-Université Blaise Pascal), Site de Crouel, 234 av. du Brezet,
63039 Clermont-Ferrand Cedex 02, France
[b] Forestry Commission, Northern Research Station, Roslin, Edinburgh, Midlothian EH25 9SY, UK
[c] Present address: Horticulture Research International, Wellesbourne, Warwick CV35 9EF, UK

Abstract – Twenty-seven individual tree growth models are reviewed. The models take into account the same main physiological processes involved in carbon metabolism (photosynthate production, respiration, reserve dynamics, allocation of assimilates and growth) and share common rationales that are discussed. It is shown that the spatial resolution and representation of tree architecture used mainly depend on model objectives. Beyond common rationales, the models reviewed exhibit very different treatments of each process involved in carbon metabolism. The treatments of all these processes are presented and discussed in terms of formulation simplicity, ability to account for response to environment, and explanatory or predictive capacities. Representation of photosynthetic carbon gain ranges from merely empirical relationships that provide annual photosynthate production, to mechanistic models of instantaneous leaf photosynthesis that explicitly account for the effects of the major environmental variables. Respiration is often described empirically as the sum of two functional components (maintenance and growth). Maintenance demand is described by using temperature-dependent coefficients, while growth efficiency is described by using temperature-independent conversion coefficients. Carbohydrate reserve pools are generally represented as black boxes and their dynamics is rarely addressed. Storage and reserve mobilisation are often treated as passive phenomena, and reserve pools are assumed to behave like buffers that absorb the residual, excessive carbohydrate on a daily or seasonal basis. Various approaches to modelling carbon allocation have been applied, such as the use of empirical partitioning coefficients, balanced growth considerations and optimality principles, resistance mass-flow models, or the source-sink approach. The outputs of carbon-based models of individual tree growth are reviewed, and their implications for forestry and ecology are discussed. Three critical issues for these models to date are identified: (i) the representation of carbon allocation and of the effects of architecture on tree growth is Achilles' heel of most of tree growth models; (ii) reserve dynamics is always poorly accounted for; (iii) the representation of below ground processes and tree nutrient economy is lacking in most of the models reviewed. Addressing these critical issues could greatly enhance the reliability and predictive capacity of individual tree growth models in the near future.

carbon allocation / photosynthesis / reserve dynamics / respiration / tree carbon balance

* Correspondence and reprints
Tel. 33 4 72 43 13 79; Fax. 33 4 72 43 12 23; e-mail: leroux@biomserv.univ-lyon1.fr
Present address: Laboratoire d'écologie microbienne des sols, UMR 5557 CNRS-Université Lyon I, bât 741, 43 bd du 11 novembre 1918, 69622 Villeurbanne, France.

Résumé – **Les modèles de croissance d'individus arbres basés sur le fonctionnement carboné : une évaluation critique**. Vingt-sept modèles simulant la croissance d'arbres à l'échelle individuelle sont évalués. Ces modèles prennent en compte les principaux processus impliqués dans le métabolisme carboné (assimilation photosynthétique, respiration, dynamique des réserves, allocation des assimilats et croissance). Les concepts communs à tous ces modèles sont discutés. Il est montré que l'échelle d'espace et la représentation de l'architecture utilisées dépendent principalement des objectifs du modèle. Au-delà de concepts communs, les modèles évalués utilisent des représentations très différentes pour chacun des processus impliqués dans le métabolisme carboné. Les différentes représentations de ces processus sont présentées et discutées en termes de simplicité de formulation, de capacité à prendre en compte la réponse aux variables environnementales, et de capacités prédictives. La représentation des gains de carbone va de relations purement empirique calculant la production annuelle de photosynthétats jusqu'à des modèles de photosynthèse foliaire à bases mécanistes prenant explicitement en compte les effets des principales variables environnementales. La respiration est souvent décrite de façon empirique comme la somme de deux composantes (maintenance et croissance). La demande de maintenance est calculée à partir de coefficients dépendant de la température, alors que l'efficience de croissance est calculée à partir de coefficients de conversion indépendant de la température. Les réserves carbonées sont généralement représentées comme des boîtes noires, et leur dynamique est rarement prise en compte. La mise en réserve et l'utilisation des réserves sont souvent traitées comme des processus passifs, les réserves servant souvent de compartiment tampon absorbant les assimilats produits en excès sur une base journalière ou saisonnière. De nombreuses approches ont été utilisées pour modéliser l'allocation de carbone, telles que l'utilisation de coefficients d'allocation empiriques, l'application des principes de l'équilibre fonctionnel et d'optimisation, l'utilisation de schémas flux-résistance, ou des approches sources-puits. Les sorties des modèles simulant le bilan carboné et la croissance de plantes ligneuses à l'échelle individuelle sont présentées, et leurs implications en foresterie et en écologie sont discutées. Trois points particulièrement critiques actuellement pour ces modèles sont identifiés : (i) la représentation de l'allocation du carbone et des effets de l'architecture sur la croissance de l'arbre est le talon d'Achille de la majorité de ces modèles ; (ii) la dynamique des réserves est toujours faiblement représentée ; (iii) la représentation du fonctionnement racinaire et de la gestion des nutriments dans l'arbre est absente dans presque tous les modèles évalués. Une meilleure prise en compte de ces points critiques devrait fortement améliorer la fiabilité et les capacités prédictives des modèles de croissance d'arbres à l'échelle individuelle dans le futur.

allocation du carbone / bilan carboné de l'arbre / dynamique des réserves / photosynthèse / respiration

1. INTRODUCTION

Mathematical modelling has been used as a powerful tool in many fields of scientific activity. A model is usually a simplification of the real system, and is in some respect more convenient to work with [127]. In particular, simulation models offer a convenient way to represent current scientific understanding and theory in complex biological systems such as trees. During the last two decades, emphasis on tree growth modelling has changed from merely statistical (i.e. descriptive and predictive under particular conditions) models, to mechanistic (i.e. explanatory) process-based models [45]. The latter are often based on a detailed description of physiological processes. Thus, they are complex and mostly restricted to research and educational applications, while statistical models are usually devoted to management applications [63, 83, 128]. Neither empirical nor mechanistic formulations are a priori preferable. The kind of formulation should be chosen according to the modeller's objectives. Furthermore, purely mechanistic tree growth models are scarce. Generally, depending on the purpose of the model and the level of understanding of the processes involved, model designers concentrate more or less on a few particular processes, and mix both process-based and statistical formulations.

For these reasons, there are many tree growth models of different types, and the ongoing development of new models without a clear knowledge of the existing ones may be a waste of research resources [15]. Thus, it is highly useful to assess the range of models currently existing, and identify key strategies of model structure and development. A critical evaluation of carbon-based tree growth models has already been published by Bassow et al. [7]. However, the authors only reviewed a few simulation models, and focused exclusively on their suitability for assessing the effects of pollution on growth of coniferous trees. Furthermore, the analysis was concentrated on a particular model of forest growth in stands [80]. Recently, Ceulemans [15] reviewed ten models of tree and stand growth. However, most of the models reviewed did not treat important processes involved in tree growth (e.g. carbon allocation) and were designed to simulate only carbon and/or water exchanges between tree stands and the atmosphere.

The present paper is a critical analysis of twenty-seven carbon-based growth models of individual woody plants, and of their ability to predict plant response to various environmental conditions. Reference is also made to a generic model of plant growth that could provide a useful framework for individual tree growth models [128]. By contrast, models that are beyond the scope of this review are: (i) models of radiation and gas exchange between trees and the atmosphere that do not

focus on carbon processes driving tree growth (e.g. MAESTRO [135]; CANLIP [17]; PGEN [35]; RATP [118]), (ii) models of forest growth in stands that are not explicitly based on individual tree growth (e.g. [12, 27, 64]; see also the review by Tiktak and van Grinsven [131]), (iii) models that were used to simulate shoot growth without integrating carbon balance and growth at the whole-tree scale [11, 33, 49] and (iv) individual-based forest models or morphological tree growth models that do not explicitly represent the major processes involved in tree growth and carbon balance (e.g. SORTIE [89]; FRACPO [18]; [57, 101]). It should be mentioned that our paper does not aim at providing an extensive review of all the models of individual tree growth published to date, but rather a comprehensive and critical view (from a sample of models) of what has been done and remains to be done in this research area.

The twenty-seven carbon-based models of individual tree growth that were reviewed are presented in *table I*. Typically, these models operate at a time step ranging from one hour to one year, and either deal with whole-tree processes (e.g. whole tree photosynthesis) or sum processes that occur at spatial scales smaller than a single tree (e.g. shoot or leaf photosynthesis). The individual tree is often divided into a number of compartments (i.e. organ classes) and/or individual organs. The objectives of the models range from simulating tree growth and wood production of a single tree representative of a stand, to simulating fruit production, tree architecture dynamics, or individual tree function within a vegetation dynamics framework (*table I*). In a first section, we present the common framework and rationales shared by all the models. The dependence of the time and space levels used and representation of tree architecture employed on model objectives is analysed. The way all the models represent, to a certain extent, the relationships between tree structure and function is also studied. In a second section, the different approches used to model each process involved in tree carbon metabolism (photosynthate production, respiration, carbon allocation and growth, storage and reserve mobilisation) are reviewed. We discuss these different treatments in terms of formulation simplicity, ability to account for response to environmental variables, and explanatory or predictive capacities. For each process, the correlation between the formulation chosen and the time and space levels used is studied. In a third section, the outputs of carbon-based models of individual tree growth are reviewed, and their ecological implications are discussed. In the last section, major critical issues for individual tree growth models to date are identified.

2. GENERAL FRAMEWORK OF CARBON-BASED MODELS OF INDIVIDUAL TREE GROWTH

2.1. Processes accounted for and common rationales used

Whatever their objectives and levels of application, the carbon-based models of individual tree growth reviewed generally encompass different sub-models, each describing one of the main carbon processes, i.e. photosynthate production, respiration, reserve dynamics and allocation of assimilates within the tree (*figure 1*). Indeed, the processes driving the carbon dynamics and growth remain fundamentally identical between different tree species, and only differ in their species- and site-specific parameters [62]. Thus, although many models have been developed for one or several particular species (*table I*), most of them can be applied to a range of tree species when suitably parameterised.

To a certain extent, all these models can be viewed as mechanistic models of tree growth that formulate rates of change in several state variables of the tree system by using differential (or difference) equations, in contrast to purely empirical models that translate empirical observations into suitable mathematical relationships (such as yield tables for instance). Because all these models try to correctly capture the relevant processes involved in tree growth, they thus all exhibit potential to be applied under a range of novel environmental conditions [12]. To a certain extent, all the models reviewed use this potential for assessing the effect of changes in environmental conditions (e.g. changes in water or nutrient availability, increase in CO_2 level, temperature, or pollutant load), predicting the impact of changes in disturbance regime (herbivory intensity or pruning practice), or matching clones to sites and predicting their potential growth, among other issues (*table I*). However, such predictive potential outside the range of data used for model development is more or less important according to the formulations used for the key carbon processes (see Sect. 3).

At least, even models using different formulations for a given process can use common rationales to represent this process. For instance, tree models represent carbon allocation by very different approaches, ranging from "morphological" modules predicting the result of translocation without any reference to the underlying mechanisms (e.g. functional balance approach) to simplified representations of the basic translocation mechanisms (namely transport resistance modules)

Table I. The 27 carbon-based models of individual tree growth reviewed. The generic model of forest growth proposed by Thornley [128] is included because it provides a useful framework for individual tree growth models.

Model	Main references	Major objectives	Tree species	Single tree representation	Time step
–	Promnitz (1975)	Simulating tree growth response to changes in nutrient and moisture regimes (greenhouse conditions)	*Populus* sp.	4 organ classes	Hour/Day
PT	Ågren and Axelsson (1980)	Simulating the growth of a 15-year old Scots pine throughout one year	*Pinus sylvestris*	8 organ classes	Day
–	Valentine (1985)	Modelling growth rates of tree basal area and height	–	3 organ classes (active and disused pipes between foliage and roots)	Year
–	Mäkelä and Hari (1986)	Individual tree-based stand growth simulation	*Pinus sylvestris*	4 organ classes	Year
FORSKA	Prentice et al. (1990; 1993)	Simulation of natural forest dynamics in a current or changing environment	–	2 organ classes (only aboveground)	2 years
ECOPHYS	Rauscher et al. (1990); Host et al. (1990)	Simulation of first-year poplar clones under near-optimum conditions	*Populus* sp.	Individual leaves and internodes + total root system	Hour/Day
–	Thornley (1991)	Forest growth model	–	5 organ classes × 4 tissues/bioch. pools	Day
–	Webb (1991)	Predicting the growth of tree seedlings under high CO_2 levels	*Pseudotsuga menziesii*	5 organ classes	5 min to 1 h
VIMO	Wermelinger et al. (1991)	C and N assimilation and allocation, and impact of herbivory	*Vitis vinifera*	4 organ classes × n age subclasses × 2 bioch. pools	Day
TREGRO	Weinstein et al. (1992)	Simulating tree physiological responses to multiple environmental stresses	*Picea rubens Picea ponderosa*	12 organ classes × 3 bioch. pools	Hour/Day
WHORL	Sorrensen-Cothern et al. (1993)	3D development of tree crown structure	*Abies amabilis*	Parts of the crown, i.e. whorl sectors (only aboveground)	Year
–	West (1993)	Predicting annual above-ground tree growth in even-aged forest monoculture	*Eucalyptus regnans*	3 organ classes (only aboveground)	Year
PEACH	Grossman and DeJong (1994)	Simulating vegetative and reproductive growth through carbon supply and demand	*Prunus persica*	6 organ classes	Hour/Day
–	Takenaka (1994)	Simulating 3D tree architecture dynamics	–	Individual shoots (only aboveground)	Year
–	Zhang et al. (1994)	Predicting the response of young red pines to environmental conditions	*Pinus resinosa*	6 organ classes	Hour/ Day
–	Deleuze and Houllier (1995)	Predicting wood production and stem form under field conditions	*Picea abies*	3 organ classes	Year

Table I. (continued).

TRAGIC	Hauhs et al. (1995)	Linking structural and functional views of forest ecosystems	*Picea abies*	6 organ classes	Year
–	Kellomäki and Strandman (1995)	Simulating the structural growth of young tree crown	*Pinus sylvestris*	Individual shoots (only aboveground)	Year
FORDYN (modes 2, 3 or 4)	Luan et al. (1996)	Predicting the impact of the environment on the structure and function of forest ecosystems	*Pinus* sp.	5 organ classes	Hour/Day
LIGNUM	Perttunen et al. (1996, 1998)	Expert system for forestry problems, simulation of tree architecture dynamics	*Pinus sylvestris*	Individual shoots × 4 organ/tissues + total root system	Year
ARCADIA	Williams (1996)	Individual-based forest stand model simulating establishment, growth and mortality of mixed tree species	US old-growth forest	5 organ classes	A few months
SIMFORG	Berninger and Nikinmaa (1997)	Simulating pine tree growth	*Pinus sylvestris*	5 organ classes	Day*/Year
–	de Reffye et al. (1997)	Simulating tree growth and tree architecture dynamics	–	Individual leaves, terminal growth units, sapwood units and root hairs	Cycle of growth
–	Deleuze and Houllier (1997)	Simulating wood production and wood distribution along the stem	Conifers	3 organ classes	Year
SIMWAL	Le Dizès et al. (1997); Balandier et al. (2000)	Simulating young walnut tree growth and architecture dynamics (including response to pruning)	*Juglans* sp.	Individual shoots, leaves and internodes + 3 root classes × 2 bioch. pools	Hour/Day
CROBAS	Mäkelä (1997)	Simulating tree growth and self-pruning	*Pinus sylvestris*	5 organ classes	Year
–	Escobar-Gutiérrez et al. (1998)	Studying the transition between heterotrophy and autotrophy for tree seedlings	*Juglans* sp.	4 organ classes × 2 bioch. pools	Day

Bioch = biochemical; * the time step of the model SICA, coupled to SIMFORG, is one day.

(see Sect. 3.4). However, as discussed in Section 3.4.5, all these approaches account, explicitly or implicitly, for the effect of distance on carbon allocation. Furthermore, all the tree growth models reviewed represent, to a certain extent, the effect of tree architecture on tree growth.

2.2. Representing the effects of architecture on tree growth

Interactions between tree structure and functioning are of paramount importance in the context of individual tree growth. At a given time, tree geometry is the result of carbon allocation to the formation of structure that has occurred in the past, and the resulting new structure has an impact on the local environments experienced by tree parts and the ability of the tree to conduct its metabolic functioning (resource acquisition and storage) in the future. These feedback loops between the accumulated growth over many years and the quasi-instantaneous metabolic reactions involved in tree growth are the essence of the interaction between tree structure and functioning [88].

All the models of individual tree growth reviewed treat these interactions, but the ways to represent structure-function relationships differ according to the space and time levels that characterise each model. On the one hand, when trees are considered in one (vertical)
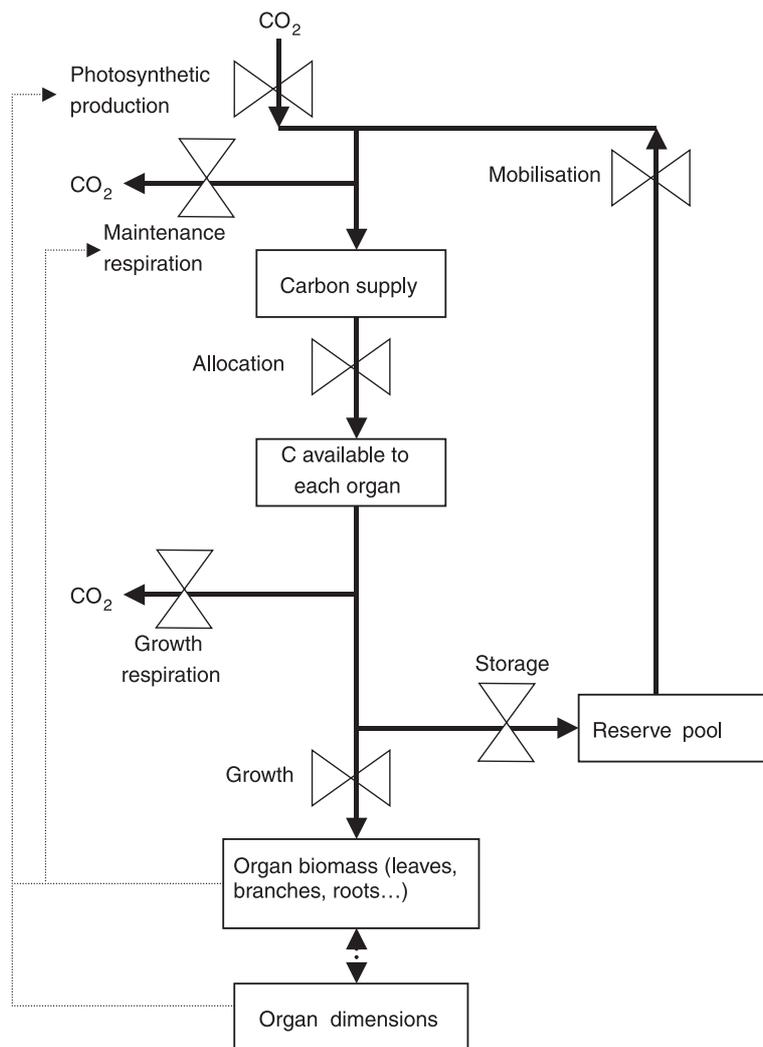
Figure 1. Schematic representation of a typical carbon-based model of tree growth in terms of carbon (━) and information (---) flows. Boxes and valves represent state variables and carbon processes, respectively.

dimension, their structure is often described in terms of basic indicators such as diameter at breast height, stem height, crown diameter, height of crown base, or foliage density in the crown. Then, a description of how these indicators develop concurrently in time must be provided. In this case, allometric or functional relationships can be used to co-ordinate the growth of the different tree parts. In this context, the relative allocation to height growth is of vital importance for the future carbon economy of the tree. This is an example of the way the interaction between tree structure and function can be represented in a model using a coarse resolution. On the other hand, 3D models with detailed shoot structure must provide a method of simulating carbon allocation at shoot level, including, e.g., the shape and location of new shoots. In

order to be operational, such detailed models must also represent the environmental factors driving shoot growth in three dimensions. This can be achieved by (i) representing carbon gain by individual shoots, (ii) applying a carbon allocation module using individual shoot carbon gains and the distance between tree parts (typically individual shoots, trunk, and root classes), (iii) simulating the increase of individual shoot dimensions, and (iv) simulating the appearance of new shoots on mother shoots. This is a typical example of the way the interaction between tree structure and function can be represented in a fine resolution model.

Thus, the representation of tree structure and modelling of carbon allocation and structure-function relationships can hardly be separated. The next section reviews
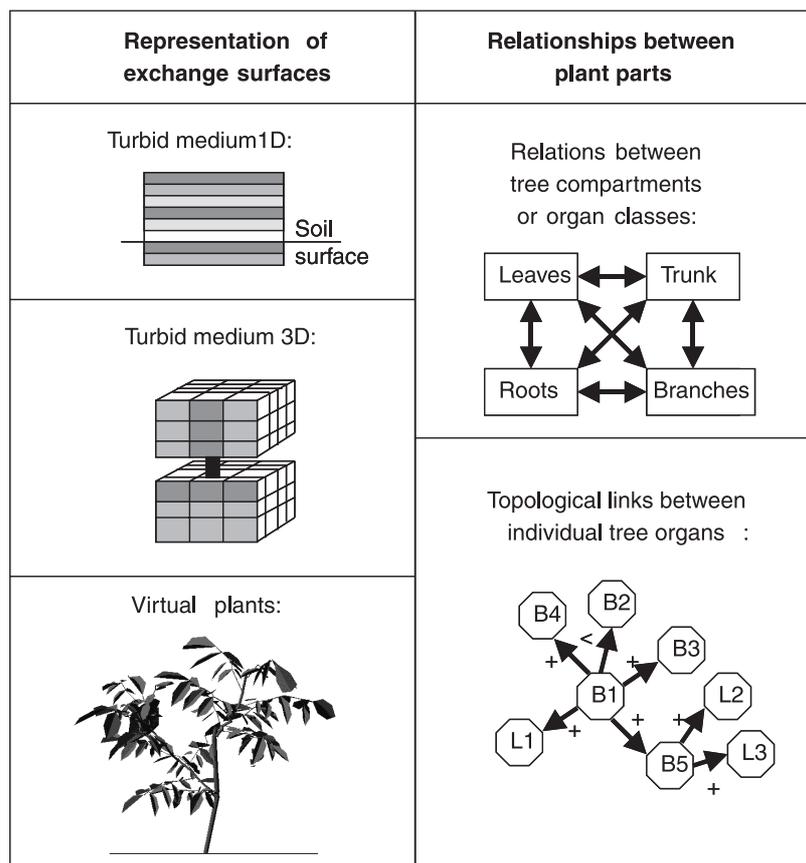
Figure 2. Different approaches used in carbon-based models of tree growth to represent (i) the spatial distribution of exchanging surfaces, i.e leaves and roots, which determines the way to simulate foliage-atmosphere or root-soil exchanges, and (ii) the links between tree organ classes or individual organs, which determine the way to simulate internal fluxes. Theoretically, each approach for (i) can be coupled with each approach for (ii). Topological links are represented according to Godin et al. [39] (B = branches; L = leaves).

the ways tree structure can be represented, and analyses to what extent the space and time resolutions chosen for a given model are constrained by model objective.

2.3. Representation of tree structure: A problem of model objective?

2.3.1. Range of representations of tree structure

Tree growth models may exhibit several different representations of plant structure. All representations encompass two components defining tree architecture: geometry and topology. Geometry deals with the dimensions and locations of plant parts in a coordinate system, while topology describes the physical links between them. In the context of tree growth modelling, both

components are important. Indeed, the geometrical representation of the tree determines the way the exchange surfaces such as leaves and roots are located, and thus the way the model can represent the interactions between the tree and its above- and below-ground environments [32, 117]. Similarly, the representation of topological links between tree parts strongly determines the way the model can simulate internal processes such as allocation of assimilates. The different representations of plant architecture used in the tree growth models reviewed are presented in *figure 2*.

Firstly, most of the models reviewed in this paper describe tree geometry by dividing the surrounding space into grid cells and locating each tree part in a given cell. This approach can be used either for a 1D-representation of the plant defined as vertical vectors (e.g. different foliage layers), or a 3D-representation in which a given

elementary volume is assigned for each tree part. Only a few models use the "virtual plant" approach to represent the location of each shoot or each organ such as leaves and buds (e.g. ECOPHYS and SIMWAL).

Secondly, most of the models reviewed represent the tree as root-, trunk-, branch- and/or leaf- compartments, sometimes distinguishing sub-compartments (e.g. age classes) (table 1). Due to the small number of compartments defined, topological relationships within the plant are very simplified (figure 2). In some cases, functional relationships between compartments (e.g. the pipe model, see below) can be included in order to structure compartments to some extent [23, 73, 75, 133, 142]. A refinement of tree architecture representation is proposed in the compartmental model WHORL [120] that abstracts the tree crown as a series of 3D-whorls stacked along the tree trunk. Each whorl is radially divided into 4 arbitrary segments that are assumed to represent individual branches. However, this strong assumption does not allow an accurate representation of the actual location and topological characteristics of tree organs. An important feature of compartmental models is that they cannot assign resource acquisition to a given growth unit or organ, or treat processes involving relationships between individual organs (e.g. carbon allocation between individual shoots).

In contrast to compartmental models, some models use a very detailed representation of tree architecture based on the description of individual organs [4, 51, 93, 102, 123]. Among these models, the most detailed three-dimensional geometric representation of tree crown can be found in the models ECOPHYS [102] and SIMWAL [4, 65] in which the size, shape and orientation (azimuth and inclination) of each leaf and shoot are specified. In the models of Takenaka [123], Kellomäki and Strandman [51] and Perttunen et al. [93, 94], crown structure is based on a simpler 3D-representation of shoots and associated leaf clusters.

Regardless of the approach used, root geometry is never taken into account except in the model TREGRO [139, 140] that uses soil layers and associated root biomasses to simulate nutrient uptake more realistically, and in the most recent version of ECOPHYS that uses a 3D-representation of the root system (Host and Isebrands, personal communication). The root compartment is sometimes divided into fine- and coarse-root compartments, but individual roots are never represented. Thus, no topological links can be assigned between them, in contrast to the above-ground growth units. This inconsistency of tree architecture representa-

tion for above- and below-ground parts is often not deliberate because process-based models should emphasise the interaction between architecture and function in determining the response to environmental variables for both shoots and roots [20, 32, 90]. Actually, this inconsistency reflects the fact that roots have partly escaped due attention by soil scientists, plant physiologists and ecologists because they are more difficult to study than shoots.

2.3.2. Link between the representation of tree structure and model objective

One can wonder to what extent the space level (for representing tree structure) and time level (model time step) chosen depend on model objectives. When locating the twenty-seven models reviewed in a time x space domain (figure 3), the time level used (hourly to annual time step), that can be tightly linked to the way the carbon processes are represented (see Sect. 3), appears to be largely independent of model objective (note that, among the models used in forest management, those that do not explicitly represent the major processes involved in tree carbon balance generally run at large temporal scale, but these models are beyond the scope of this review). In contrast, the space level chosen (representation of individual organs such as leaves and buds, organ clusters such as leafy shoots, or big compartments such as leaf, stem and root compartments), that is crucial for the way tree topology/geometry is described, largely depends on model objectives (figure 3). On the one hand, a fine spatial resolution (i.e. accurate representation of tree architecture) is required if the model actually aims at simulating individual tree architecture dynamics. On the other hand, a coarse spatial resolution (and thus crude representation of tree architecture) is often adequate if the model aims at simulating the growth (in terms of biomass accumulation) of individual trees at plot level. In an intermediate position are models that aim at simulating tree dynamics in heterogeneous stands or forest growth models that focus on the heterogeneity of individual trees within a stand. In this case, modellers generally represent an individual tree as an ensemble of growth units or more often clusters of growth units such as leafy shoots or branches. This representation can capture essential features of the competition between trees in stands without using a complex, organ-based approach. Indeed, very high resolution models are often difficult to parameterise. Thus, despite the more detailed structure they use to represent trees and structure-function relationships, their predictions may prove to be less reliable
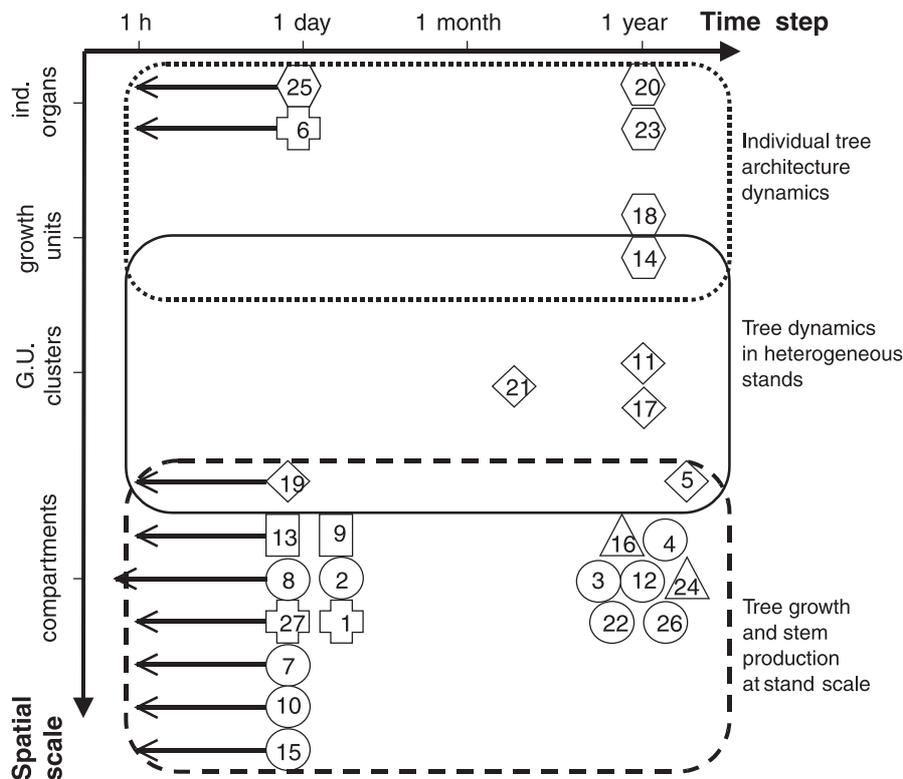
Figure 3. Schematic location of each tree growth model reviewed in a space-time domain. Each symbol corresponds to a major model objective (◯: simulation of individual tree architecture dynamics; ○: prediction of tree growth and stem production; △: prediction of stem profile; ⬡: research tool; ◇: simulation of tree dynamics in forest stands; □: prediction of fruit yield at tree level). Arrows indicate the range of time steps used for the different processes represented. Numbers in symbols refer to models (1: [100]; 2: [1]; 3: [132]; 4: [73]; 5: [97]; 6: [102]; 7: [128]; 8: [138]; 9: [141]; 10: [139]; 11: [120]; 12: [142]; 13: [40]; 14: [123]; 15: [147]; 16: [23]; 17: [41]; 18: [51]; 19: [71]; 20: [93]; 21: [144]; 22: [9]; 23: [103]; 24: [24]; 25: [4]; 26: [75]; 27: [29]).

in the long term. In contrast, lower resolution models provide coarser estimates but are much easier to parameterise/calibrate and test.

2.3.3. Conclusion

Carbon-based models of individual tree growth (i) represent the same main carbon processes driving tree growth and (ii) share common rationales for modelling carbon allocation and structure-function relationships. In contrast, the way the models represent tree architecture and structure-function relationships differ according to the objective-dependent, spatial resolution used. However, it should be noted that fine- and coarse-resolution approaches are not fundamentally exclusive. For instance, a promising approach for simulating individual tree growth is to combine the high- and low-resolution approaches by using the high-resolution models as

sources of parameter values [9, 71] or as a basis for "summary models" that can be used by lower resolution models as proposed by Sinoquet and Le Roux [117]. For instance, the instantaneous calculations of the photosynthesis and transpiration model SICA are converted into yearly values that are used as inputs by the tree growth model SIMFORG [9]. Such an approach is worthy, but implies to devise appropriate interfaces between the different modules using strict modular design rules [106]. Similarly, a mechanistic model computing instantaneous photosynthesis for individual growth units within an individual tree growth has been used to show that the daily light use efficiency is constant whatever the growth unit location and light regime [117], so that the light use efficiency approach can be used with confidence to compute the carbon gain of foliage entities at different scales (growth units, shoots or arbitrary crown sectors).

Beyond the common framework and common rationales presented in this section, carbon-based models of individual tree growth use strongly different approaches to compute each carbon process they account for. Such a diversity is obviously necessary because no one model or modelling approach is likely to be suitable for all purposes and applications [45].

3. RANGE OF APPROACHES AVAILABLE TO MODEL CARBON PROCESSES INVOLVED IN TREE GROWTH

3.1. Modelling photosynthate production

Published carbon-based models simulating the growth of woody plants all include a module that provides estimates of carbon gain for the plant as a function of climatic parameters and the physiological state of the leaves. These estimates are then used as inputs by the other modules. However, the models differ markedly in (i) the way they formulate photosynthetic carbon assimilation and the effects of environment on this process, and (ii) the way they consider the spatial distribution of carbon gain within the foliage.

3.1.1. Formulation of photosynthate production

Three model classes can be distinguished as far as photosynthesis formulation is concerned (*table II*). The first class encompasses models that do not calculate leaf photosynthesis but instead compute photosynthate production proportional to leaf mass or area, or to absorbed radiation. These models generally do not represent explicitly the effects of important environmental variables on production. The second class includes tree growth models that represent the effects of environmental variables on photosynthesis by empirical relationships. The third class corresponds to tree growth models that use a biochemically-based approach to account for the effects of environment on leaf photosynthesis.

3.1.1.1. Modelling photosynthate production without treatment of leaf photosynthesis

Most tree growth models (or generic models of plant growth) that do not deal with leaf photosynthesis compute a net rate of carbon uptake P (g C unit time^{-1}) assumed to be proportional to leaf weight W_l or area A_l [23,

24, 73, 100] or shoot or leaf structural dry matter W_s (g C) [75]:

$$P = \sigma_s\, W_l \quad or \quad P = \sigma_s\, W_s \qquad (1)$$

where σ_s is the shoot or leaf specific activity (unit time^{-1}). The time step of this photosynthate production module is generally one year [23, 73, 75].

P can also be assumed to be proportional to the amount of photosynthetically active radiation (PAR) absorbed by the foliage (PAR$_a$, J unit time^{-1}) according to Monteith's model [85]:

$$P = \varepsilon_c\, PAR_a \qquad (2)$$

where ε_c is the conversion efficiency of PAR$_a$ into dry matter (g C J^{-1}). This model was used by West [142] to simulate annual production of individual trees. Sorrensen-Cothern et al. [120], Takenaka [123] and Kellomäki and Strandman [51] used this approach to compute the production of tree parts or individual shoots according to their local light environment.

A third approach is found in the model developed by de Reffye et al. [103] where P is assumed to be proportional to transpiration (E, g H$_2$O unit time^{-1}):

$$P = WUE\, E \qquad (3)$$

where WUE is a prescribed water use efficiency (g C g H$_2$O^{-1}). This approach was used because the model is based on a detailed description of tree hydraulic architecture and computes water flows (note that all the other models reviewed do not account for tree hydraulic architecture despite its importance for coupling carbon and water fluxes). However, models using equation 1, 2 or 3 assume that plant productivity on a leaf mass, leaf area, PAR$_a$ or leaf transpiration basis is constant, or only age-dependent as in the model of Sorrensen-Cothern et al. (consistent with field observations e.g. [146]). In particular, Sorrensen-Cothern et al. [120], Takenaka [123] and Kellomäki and Strandman [51] assumed that ε_c is constant for all the shoots within tree foliage. This assumption is consistent with recent conclusions drawn from conceptual [26] or simulation [117] models that found that time-integrated leaf photosynthetic efficiency is highly conservative within a canopy. In contrast, WUE was assumed to be constant for all the shoots within tree foliage in the model of de Reffye et al. [103], but was found to strongly vary with light regime within an individual tree crown in the field [117].

Some authors modified the basic relationships 1 or 2 to account for the effects of carbon demand or photosynthate accumulation in leaves. For instance, Wermelinger et al. [141] simulated P as a function of

Table II. Formulations used and environmental factors taken into account in the photosynthate production submodels of the carbon-based models of individual tree growth reviewed.

Authors	Formulation	PAR	Ta	CO_2	VPD	Ψ	N	Age	Others
					Factors taken into account				
Leaf photosynthesis not explicitly described									
*$P = \sigma_s W$ or $P = \sigma_s A$									
Promnitz (1975)	$P = \sigma_s W_l$ with constant σ_s								
Deleuze and Houllier (1995)	id								
Deleuze and Houllier (1997)	id								
Ågren and Axelsson (1980)	$P = \sigma_s W_l$ with $\sigma_s = \sigma_{s0}$ f (age, soil water and T_l)		X			X		X	
Valentine (1985)	$P = \sigma_s W_l$ with $\sigma_s = \sigma_{s0}$ f(PAR)	X							
Hauhs et al. (1995)	id	X							
Perttunen et al. (1996)	id	X							Tree age
Mäkelä and Hari (1986)	$P = \sigma_s A_l$ with $\sigma_s = \sigma_{s0}$ f (PAR)	X							
Mäkelä (1997)	$P = \sigma_s W_s$ with $\sigma_s = \sigma_{s0}$ f(PAR)f(H_c)	X							
*$P = \varepsilon_c PAR_a$									
West (1993)	$P = \varepsilon_c PAR_a$ with constant ε_c	X							
Takenaka (1994)	id	X							
Kellomäki and Starndman (1995)	id	X							
Sorrensen et al. (1993)	$P = \varepsilon_c PAR_a$ with $\varepsilon_c = f$ (relative tree height)	X							
Wermelinger et al. (1991)	$P = Dem[1–exp(–\varepsilon_c PAR_a/Dem)]$ and $\varepsilon_c = f(age)$	X					(X)	X	
*$P = WUE\ E$									
de Reffye et al. (1997)	$P = WUE\ E$	(X)	(X)		(X)	(X)			
Empirical leaf photosynthesis formulation									
*Rectangular hyperbola : $P = P_{max} [\alpha\,PAR / (\alpha\,PAR + P_{max})]\ g_1(T_a)\ g_2(CO_2)\ g_3(VPD)\ g_4(\Psi)\ g_5(N)\ g_6(age)$									
Rauscher et al. (1990); see Host et al. (1990b)	$g_1(T_a)$: defined for 8 temperature classes $g_6(age)$: α and P_{max} defined for each age class	X	X					X	
Zhang et al. (1994)	$g_1(T_a)$: parabolic function; $g_4(\Psi)$: linear function under threshold Ψ, $g_6(age)$: multiplier for each age class; (g_1, g_4 and g_6 applied to P_{max}); $\alpha = \alpha_{max}\ g_1(T_a)$	X	X			X		X	

Table II. (continued).

Authors	Formulation	Factors taken into account							
		PAR	Ta	CO_2	VPD	Ψ	N	Age	Others
*$P = P_{max} (PAR-c) / (PAR+\alpha -c)\ g_1(T_a)\ g_4(\Psi)$									
Prentice et al. (1993)	P_{max} and α: functions of air CO_2 concentration; $g_1(T_a)$: symmetrical parabola; $g_4(\Psi)$: function of soil moisture	X		X		X			
*$P = \{g\ Ca\ \alpha\ PAR / (PAR + \gamma)\} / \{g + \alpha\ PAR / (PAR + \gamma)\}$									
Berninger and Nikinmaa (1997)	g: stomatal conductance function of air VPD and soil water content	X		X	X	X			
*Non-rectangular hyperbola: $\theta P^2 - (\alpha\ PAR + P_{max})P + \alpha\ PAR\ P_{max} = 0$ with $P_{max} = P_{max0}\ g_1(T_a)\ g_2(CO_2)\ g_5(N)\ g_6(age)$									
Thornley (1991)	$g_1(T_a)$: quadratic function; $g_5(N)$: linear relationship; $g_2(CO_2)$: linear relationship and $\alpha = \alpha_{max}\ g(CO_2)$	X	X	X			X		
Grossman and DeJong (1994)	$g_1(T_a)$, $g_5(N)$, $g_6(age)$: not detailed; N function of light exposure	X	X				X	X	
Luan et al. (1996) in mode 3	Functions g not detailed	X	X		X				
Williams (1996)	$g_1(T_a)$: empirical function; $g_4(\Psi)$: function of evaporative deficit	X	X			X			
*The Lohammar (1980) formulation: $P = (C_a - C_c): (r_s + r_m)$ with $r_s = r_{smax}\ f_1(PAR)\ g_3(VPD)\ g_4(\Psi)$ and $r_m = r_{mmax}\ f_1(PAR)\ g_1(T_a)\ g_5(N)\ g_6(age)\ g_7(M_g)\ g_8(O_3)$									
Weinstein et al. (1992); Weinstein and Yanai (1994)	$g_4(\Psi)$: actually function of soil water Determination of C_c not detailed	X	X		X	X	X	X	Mg, O_3
Mechanistic leaf photosynthesis formulation Farquhar's model $P = min\ (P_c, P_j)$ **$P_c = f\ (V_{cmax}, R_d, C_i, T)$ and $P_j = f\ (J_{max}, R_d, PAR, C_i, T)$ with V_{cmax}, J_{max}, R_d function of N and T**									
Webb et al. (1991)	stomatal conductance $= f\ (\Psi, CO_2, VPD, PAR)$	X	X	X	X	X			
Luan et al. (1996) in mode 4	Computation of stomatal conductance not detailed	X	X	X		X			
Balandier et al. (2000)	$C_i/C_c = f\ (PAR)$	X	X	X			X		

NB: The model of Escobar-Gutiérrez et al. [29] uses measured photosynthesis as an input; Luan et al. [71] in mode 2 use an hyperbolic light response curve but its equation is not detailed.

carbon demand (Dem), PAR absorbed by the foliage, and an age-dependent conversion coefficient ε_c, as:

$$P = Dem. \ [1 - exp(-\varepsilon_c\ PAR_a / Dem)]. \quad (4)$$

In this case, carbon uptake is sink-dependent (i.e. a function of carbon demand). Nitrogen supply indirectly influences photosynthate production in this model because nitrogen restriction would have a negative feedback on carbon demand.

However, for all these models, σ_s or ε_c is not explicitly influenced by environmental variables and rarely by leaf status variables *(table II)*. Generally, such a simple treatment of photosynthate production is deliberate since these models were designed (i) to simulate tree growth under well-characterised environmental conditions, or (ii) to address very specific aspects of plant growth, e.g. to test a postulated partitioning function. Nevertheless, such a simple treatment of photosynthate production is

sometimes not consistent with the objectives of the tree growth models. For instance, the major objective of the model of Deleuze and Houllier [23] was to describe radial and height growth for trees and to extrapolate tree growth to varying conditions. However, such an extrapolation to different environments should be done with extreme caution since the model uses a constant specific leaf activity that is not influenced by climatic parameters and leaf state.

Only three models reviewed [73, 93, 133] expressly state the effect of an environmental parameter in the context of this approach. The leaf specific activity approach was used in these models of Scots pine tree growth to compute photosynthate production as a function of the local radiation regime. In this case, the leaf specific activity is modulated by a so-called photosynthetic light ratio $f(PAR)$ (*i.e.* the ratio between the actual leaf specific activity σ_s observed in a given shaded environment within the tree foliage and the leaf specific activity σ_{s0} exhibited in sunlit conditions), so that:

$$P = \sigma_s \, W_s \qquad (5)$$

with:

$$\sigma_s = \sigma_{s0} \, f(PAR) \qquad (6)$$

where $f(PAR)$ is not directly a function of PAR but a function of the leaf area index above a given location.

3.1.1.2. Empirical modelling of leaf photosynthesis

Most tree growth models simulate leaf photosynthesis by empirical relationships that include sensitivity to some environmental variables (*table II*). Typically, leaf photosynthesis P is represented as:

$$P = P_{max} \, f(PAR) \, g_1(T_a) \, g_2(C_a) \, g_3(VPD) \, g_4(\Psi) \, g_5(N) \, g_6(age) \qquad (7)$$

where P_{max} is the maximum photosynthetic rate observed at high leaf irradiance PAR and in optimal environmental conditions, $f(PAR)$ is the key empirical function of leaf irradiance, and g_i's are multiplicative functions that account for the effects of air temperature (T_a), air CO_2 concentration (C_a), air water vapour pressure deficit (VPD), plant water potential (Ψ) or soil moisture, leaf nitrogen content (N) and leaf age. P_{max} generally depends on light regime [10]. The most common functions for $f(PAR)$ encountered in the models reviewed are the rectangular [44, 102, 147] and non rectangular [40, 128] hyperbolae. The parameters used in these relationships (*table II*) are generally physiologically sound (e.g. the initial slope of the hyperbolic function represents quantum yield).

An alternative, empirical approach is used in the model TREGRO [139]. In this case, leaf photosynthesis P is computed using the equation form of Lohammar etal. [70]:

$$P = (C_a - C_c) / (r_s + r_m) \qquad (8a)$$

with:

$$r_s = r_{smax} \, f_1(PAR) \, g_1(\Psi) \, g_2(VPD) \qquad (8b)$$

$$r_m = r_{mmax} \, f_1(PAR) \, g_1(T_a) \, g_2(y) \, g_3(N) \, g_4(Mg) \, g_5(ozone) \qquad (8c)$$

where C_a and C_c are the CO_2 concentrations in ambient air and at the carboxylation sites, respectively, and r_s and r_m are the stomatal and mesophyll resistances to CO_2 transfer, respectively. Environmental variables are taken into account when computing stomatal and mesophyll resistances. However, this sole equation is not sufficient to determine P since C_c is not a constant. Because the authors do not explain how C_c is computed or prescribed, it is difficult to evaluate whether the use of equation 8a is straightforward.

At least, it should be noted that the empirical photosynthesis model used in the SICA/SIMFORG model (*table II*) is coupled to a stomatal conductance model that presents the optimal scheduling of water use during a drought period [8]. This is the sole case where a teleonomic approach is used to compute leaf gas exchanges in the tree growth models reviewed.

3.1.1.3. Mechanistic modelling of leaf photosynthesis

The photosynthesis model proposed by Farquhar et al. [30] represents the most physiologically sound approach presently available. This model simulates the photosynthetic rate of C_3 species as a function of leaf irradiance, intercellular CO_2 concentration and leaf temperature. It distinguishes two factors that can limit leaf photosynthesis P ($\mu mol \, CO_2 \, m^{-2} \, s^{-1}$):

$$P = min \, (P_c, P_j) \qquad (9)$$

where P_c and P_j are the photosynthetic rates limited by (i) the amount, activation state and/or kinetic properties of Rubisco, or (ii) the rate of RuP_2 regeneration, respectively. The effect of nitrogen on photosynthesis can be easily introduced in the model because the three key parameters of the model (the maximum carboxylation rate, the light-saturated rate of electron transport, and the dark respiration rate) are proportional to the amount of leaf nitrogen on an area basis [31, 66, 68]. This latter variable can be linked to local radiation regime experienced by the leaves [67, 68]. However, predicting tree growth according to soil fertility would imply to account for tree nutrient economy (see Sect. 5.3).

Because the CO_2 partial pressure in sub-stomatal cavities (C_i) or at the carboxylation sites is an input of Farquhar's model, an estimate of stomatal conductance is required. The most common modules available are the multiplicative approach proposed by Jarvis [46] and the semi-empirical equation developed by Ball et al. [5] (for a review, see [117]). However, most of published tree growth models that use a mechanistic approach of photosynthesis exhibit a crude treatment of stomatal functioning. For instance, C_i is computed by an empirical function of PAR and C_a in the model SIMWAL [65], although the latest version of the model can also use the Jarvis approach to compute stomatal conductance [4].

3.1.1.4. Choice of a formulation for photosynthate production: implications for model applications, parameterisation and computation requirements

Models using the specific leaf activity approach do not represent explicitly the effects of several important environmental variables and leaf characteristics on photosynthate production (*table II*). This restricts their ability to predict tree function beyond their initial do-

main of application (i.e. a given species, in a given location). For instance, the empirical photosynthetic light ratio function *f*(PAR) has to be calibrated for each particular stand because it depends on both structural factors (tree architecture and tree density in the stand) and biological factors (shading effect on photosynthesis and respiration for the species studied). Such a calibration would be tedious and time-consuming. Thus, if a carbon-based model of tree growth is to be used for different species and/or in contrasting environments, an explicit consideration of the effects of environmental constraints on leaf photosynthesis is necessary. Empirical leaf photosynthesis models offer a good potential to analyse tree photosynthate production in response to environmental stimuli. However, when using empirical formulations, the mechanisms involved in response of photosynthetic rates to environmental variables are hidden. This is not a problem in many cases, such as when the tree growth model has been designed for a specific purpose (e.g. management of young trees for a given species under given range of environmental conditions). For other applications, empirical formulations could restrict the
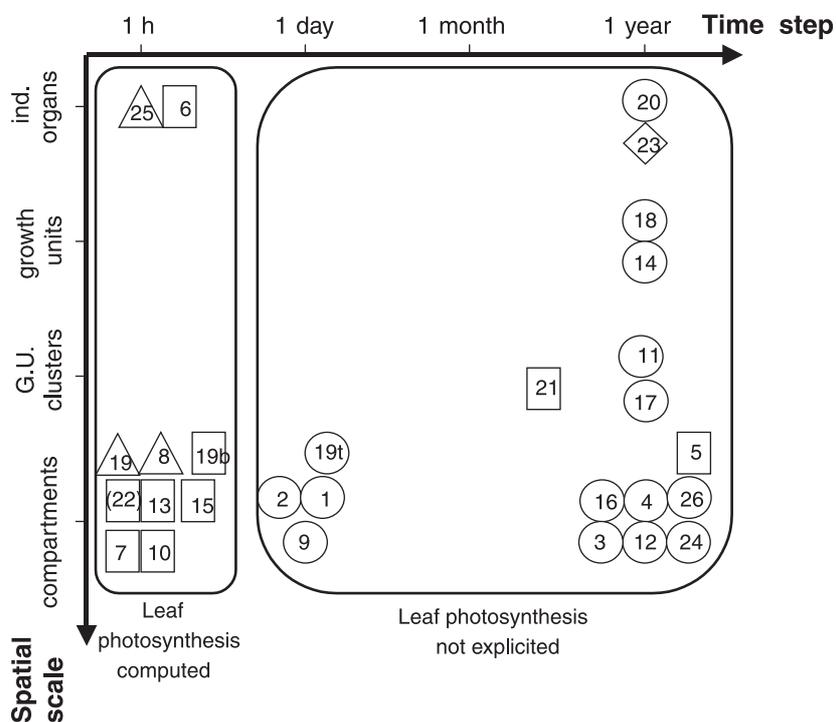

Figure 4. Schematic location of the photosynthate production module of each tree growth model in a space-time domain. Each symbol corresponds to a given approach to represent photosynthate production (△: Farquhar et al.'s photosynthesis model; □: empirical formulation of leaf photosynthesis; ○: leaf specific activity approach; ◇: water use efficiency approach). Numbers in symbols refer to models (see legend of *figure 3*; 19, 19b and 19t refer to FORDYN in its mode 4, 3 and 2, respectively).

predictive capacity of the model beyond its initial scope (e.g. tree functioning in contrasting or changing environmental conditions). In this context, a more mechanistic formulation of leaf photosynthesis is probably required. For instance, using the Farquhar approach in the tree seedling model of Webb [138] is consistent with the model's objective, i.e. predicting seedling growth under increased CO_2 levels. However, despite its great predictive potential, a mechanistic approach of photosynthesis is not the panacea for modelling photosynthate production by trees. It is only required when a comprehensive understanding of photosynthetic processes is necessary (which can sometimes be the case for generalisation or educational needs) and when a complex formulation of photosynthesis is consistent with the complexity of the other modules used by the tree growth model.

Beyond their ability to explicitly represent environmental effect on photosynthesis and to be applied under new environmental conditions, the different formulations of photosynthate production have to be evaluated from a pragmatic point of view in the context of computation requirements and model parameterisation. Due to the non-linearity of the leaf photosynthesis-light response, models that compute leaf photosynthesis cannot be utilised unless a physiologically sensible time step is applied. The different formulations of photosynthate production used by the models reviewed are located in a time-space domain in *figure 4*: this shows that models using an empirical or biochemically based approach to simulate the effects of environment on leaf photosynthesis are all run at a time step of one hour or less. The only exceptions are the models FORSKA and ARCADIA that compute monthly or annual carbon gain using a formulation usually devoted to represent instantaneous leaf photosynthesis. In this case, the model is parameterised from coarse scale data rather than leaf gas exchange data [97], and the formulation has not the same meaning as its original form. In addition, using an empirical or biochemically based formulation of leaf photosynthesis requires a detailed description of the variations of the environmental driving variables inside the canopy (vertical profiles or 3D distribution of relevant environmental variables according to the spatial representation used). In contrast, models that only assume a dependence of shading on photosynthate production (equation 5) look at longer time scales [133] or situations where the rest of environmental variables can be controlled. In this case, the integrated effect of the environmental variability can be incorporated in the input parameter σ_s.

Combining a temporal coarse approach (such as the leaf specific activity or conversion efficiency approach)

to a higher temporal resolution approach representing leaf photosynthesis is a good means to solve this dilemma. Berninger and Nikinmaa [9] used this method where a high resolution model (flux model SICA) provides annual photoproduction to SIMFORG. The approach used by the model FORDYN [71] to simulate tree carbon gain is even more flexible. A key feature of this model is that users can choose a particular approach, among different available, to simulate photosynthate production (i.e. tree annual photosynthate production by a species-dependent hyperbolic light response curve vs. hourly or instantaneous leaf photosynthesis by a non-rectangular hyperbola or by the Farquhar's model). Such an approach greatly enhances model versatility.

3.1.2. Representation of the distribution of photosynthate production within the tree crown, and associated radiation transfer modules

In addition to the various ways of formulating photosynthesis, carbon-based models simulating the growth of woody plants also differ in their representations of the spatial distribution of carbon gain within tree foliage. This is related to the way tree architecture is accounted for (Sect. 2.3) and implies the use of specific radiation transfer modules.

Whatever the method used for representing leaf distribution (that determines the spatial distribution of simulated carbon gain), models using the compartmental approach cannot assign carbon assimilation rates to individual shoots or leaves (*table III*). Most of the compartmental models reviewed simulate total carbon gain at the individual tree scale [23, 75, 100, 133], or represent the vertical distribution of carbon sources within the foliage [139]. In the later case, provided that the vertical distribution of foliage is known, Beer's law is applied to compute the vertical distribution of leaf irradiance and then total photosynthate production or the vertical profile of carbon gain. The photosynthetic light ratio approach (equation 5) can also be applied to simulate the effect of PAR on carbon gain as an alternative to traditional modules simulating leaf irradiance effect on photosynthesis [73]. In contrast, even compartmental models would need a very detailed representation of crown structure and a complex radiation interception module if they aim to accurately represent competition between individual trees in complex forest stands (several tree species, several tree sizes). For instance, although West [142] uses a complex submodel of light interception, his compartmental model aims only at computing total carbon gain by individual trees within a forest stand.

Table III. Foliage representation and radiation module used to compute photosynthetic production and its spatial distribution. Models computing whole tree carbon gain or local carbon gains within the tree crown are distinguished.

Authors	Foliage representation	Radiation module
Models computing total carbon gain at the individual tree scale		
Promnitz (1975)	One compartment	None
Ågren and Axelsson (1980)	id	id
Valentine (1985)	id	id
Webb (1991)	id	id
Deleuze and Houllier (1995)	id	id
Deleuze and Houllier (1997)	id	id
Escobar-Gutiérrez et al. (1998)	id	id
Zhang et al. (1994)	One compartment	Same incident PAR for all the needles
Mäkelä (1997)	One compartment (canopy horizontally homogeneous)	Beer's law used to compute the average-tree photosynthesis
Thornley (1991)	id	id
Berninger and Nikinmaa (1997)	id	id
Wermelinger et al. (1991)	Age classes	Beer's law; age-specific photosynthetic efficiencies modulate effective LAI
Mäkelä and Hari (1986)	One compartment (foliage distributed within a cylindrically symetrical crown)	Photosynthetic light ratio function of leaf biomass above a given location
Grossman and DeJong (1994)	One compartment	Empirical data on daily light interception in orchards used to adjust an effective LAI
Prentice et al. (1993)	One compartment (leaf area of each tree uniformly distributed between top and bole heights at the patch scale)	Beer's law applied at the patch scale
Luan et al. (1996)	One compartment (cylindrical crown divided into arbitrary layers)	Beer's law
Weinstein et al. (1992)	Sunlit and shaded leaves in the inner and outer parts of the conical crown	Same PAR for all the leaves of a given age class and position, empirically determined
West (1993); see West and Wells (1992)	One compartment; Crown is ellipsoidal; random leaf location and orientation; constant leaf area density	Interception of direct and diffuse PAR (Beer's law along beam path)
3D distribution of carbon sources within the crown		
Sorrensen et al. (1993)	Series of discs stacked along stem axis; 4 sectors of discs assumed to represent branches	Interception of radiation coming from the vertical only (Beer's law in each cell of a 3D-grid)
Hauhs et al. (1995)	Foliage distribution within a 2D cross section of the forest stand (0.1×0.15 m² cells)	Beer's law applied to the 2D cross section
Takenaka (1994)	3D distribution of shoots and associated spherical clusters of leaves	Interception of diffuse PAR by leaf clusters (Beer's law along beam path)
Kellomäki and Strandman (1995)	3D distribution of shoots and associated foliage (cylinders)	Interception of direct and diffuse PAR by leaf clusters (Beer's law along beam path)
Williams (1996)	3D distribution of sun and shade leaves	Interception of direct and diffuse PAR in each cell (Beer's law along beam path)

Table III. (continued).

Authors	Foliage representation	Radiation module
Perttunen et al. (1996)	3D distribution of tree segments and associated foliage	PLR function of leaf biomass above a given location
Rauscher et al. (1990)	3D geometric model of tree crown : size, orientation and area of each leaf specified	Direct and diffuse PAR on both sunlit and shaded leaf portion (geometric model)
Balandier et al. (2000)	mixed 3D geometric/turbid medium approach	Direct and diffuse PAR interception by each leaf (geometric model for young trees ; Beer's law along beam path for old trees)

NB: The model of de Reffye et al. [103] computes photosynthesis indirectly by a tree hydraulic architecture approach that does not use foliage representation.

Models using the organ-based approach to simulate individual organ growth must simulate carbon gain by different tree parts (branches or growth units and associated foliage clusters, or the individual leaves). Thus, these models include a light interception submodel that computes light regime for each leaf or shoot within the tree crown canopy (e.g. models ECOPHYS, WHORL and SIMWAL, Takenaka's model, Kellomäki and Strandman's model) (*table III*). Most of these models compute incoming direct and diffuse photon flux densities from different elevation angles. PAR interception is then computed by the turbid medium analogy, i.e. applying Beer's law to leaf cluster volumes associated to each shoot or tree parts according to leaf area density, and leaf orientation and distribution [51, 123]. In the case of the model WHORL, interception of only vertically incoming radiation is considered, which is a deterrent for an accurate representation of local radiation regimes within the tree crown [120]. In contrast to models using the turbid medium analogy, the model ECOPHYS simulates direct and diffuse PAR interception by each individual leaf using a geometrical approach. A mixed, turbid medium/geometric approach was used in SIMWAL where a geometric model is used for young trees exhibiting a negligible self-shading between leaves, and Beer's law is applied for bigger trees [4]. Some organ-based models use cruder approaches. In LIGNUM [93], the photosynthetic light ratio approach is used rather than a radiation transfer module.

3.1.3. Summary

Tree growth models exhibit different formulations for photosynthate production and different representations of the spatial variability of carbon gain. However, the use of a particular photosynthesis function does not require

or preclude a particular method for representing the spatial distribution of carbon gain. For instance, the model LIGNUM [93] uses the empirical photosynthetic light ratio approach to simulate annual carbon gain; the model ECOPHYS [102] simulates leaf photosynthesis with a rectangular hyperbola function; and the model SIMWAL [4] uses the mechanistic Farquhar model to simulate the leaf photosynthetic rate. However, all these models use an organ-based approach and represent the 3D–distribution of carbon gain at the shoot- or leaf-level. Thus, despite different representations of carbon assimilation, the models all exhibit a good potential to analyse in details structure-function relationships involved in tree architecture dynamics. Therefore, model objectives strongly constrain the method used to represent the spatial distribution of carbon gain (e.g. computation of total carbon gain for simulating wood production vs. computation of the 3D-distribution of carbon gain at the organ scale for predicting architecture dynamics), and constrain the choice of a photosynthesis formulation to a weaker extent (use of empirical photosynthate production modules to describe the tree functioning in the long term vs. use of mechanistic leaf photosynthesis modules to provide rationales for predicting tree responses to future environmental changes).

3.2. Modelling respiration

Net production of plant biomass strongly depends on carbon losses resulting from respiration. For example, in herbaceous plants, respiratory losses were estimated to be 50% of the photosynthetically fixed carbon [3]. Similarly, respiration losses may account for 40–60% of gross photosynthesis of cool temperate forests [122]. However, reliable measurements of whole-plant carbon

balance and its components are scarce. Consequently, most carbon-based models of tree growth use a simplified, theoretical representation of respiratory processes, i.e. either a two-component approach or a global, non-explicit treatment of respiration (*table IV*).

3.2.1. The two-component model

It is widely accepted that plant respiration has at least two components, growth and maintenance. Growth respiration is defined as the respiration associated with the

Table IV. The respiration submodels of the 27 models reviewed. W : dry matter (DM); R_T : total respiration; R_M or R'_M : maintenance-associated component of R_T; R_G, or R'_G : growth-associated component of R_T; P : gross photosynthesis; n.a. : not available. Unless otherwise specified, W stands for total DM (living + inert); R_T, R_M, R_G, W and P are expressed as equivalent C units.

Model class and reference	Specificities	Parameter[1] ranges [min : max]	Temperature dependence (R_M)
2-component formulations			
Thornley [124] or equivalent : $R_T = R_G + R_M$ with $R_M = m \cdot W$ and $R_G = [(1 - Y_G) / Y_G] \cdot (\Delta W / t)$			
Ågren and Axelsson (1980)	R_M includes a specific, delocalized protein metabolism	$m_i (20^{\circ}C)^{(2)} = [0.3 : 1.2]\ 10^{-3}\ d^{-1}$ $Y_{Gi} = 0.70$ [2]	winter woody tissue : $m_i = 0$; other cases : $Q_{10}(m_i) = 2$
Valentine (1985)		n.a.	
Mäkelä and Hari (1986)	R_M considers only sapwood, itself assumed as proportional to tree height $\times$ total leaf area	'm' $= 0.016\ kgCO_2\ m^{-1}\ m^{-2}\ y^{-1}$ $Y_G = 0.90$ [2]	
Thornley (1991)	For woody tissues, R_M is proportional to bark area	for woody tissues : 'm_i' $(20^{\circ}C) = 0.5\ gC\ m^{-2}\ d^{-1}$ else: $m_i (20^{\circ}C) = 0.001\ d^{-1}$ $Y_{Gi} = 0.75$	2nd order parabolic function
Webb (1991)	For R_M, W is expressed as g DM	$m (20^{\circ}C) = 0.33\ gC\ gDM^{-1}\ d^{-1}$ $Y_G = 0.75$ [2]	$Q_{10}(m_i) = 2$ [2]
Wermelinger et al. (1991)	For R_M of woody tissues, only the non-lignified part of DM is considered as W	$m_i (25^{\circ}C) = [0.01 : 0.03]\ d^{-1}$ $Y_{Gi} = 0.70$ [2]	$Q_{10}(m_i) = 2.3$
Weinstein et al. (1992)	For R_M, W is expressed as g structural C	$m_i (20^{\circ}C) = [0.8 : 20]\ 10^{-4}\ h^{-1}$ $Y_{Gi} = 0.80$	user-defined function (default : $Q_{10}(m_i) = 2$)
Grossman and DeJong (1994)	For R_M, W is expressed as g DM	'm_i' $(20^{\circ}C)^{(2)} =$ $[1 : 42]\ 10^{-9}\ gC\ gDM^{-1}\ s^{-1}$ $Y_{Gi} = 0.83$ [2, 3]	$Q_{10} (m_i) = 2$ (on the [20 : 30] $^{\circ}$C range)
Hauhs et al. (1995)	For R_M, W is expressed as g DM (for stem, only sapwood is considered)	$m_i = [0.01 : 0.07]\ gC\ gDM^{-1}\ y^{-1}$ $Y_{Gi} = 0.63$ [2, 3]	
Luan et al. (1996)	includes the model of Thornley (1991)	(see above, Thornley, 1991)	
Williams (1996)	For foliage, W is expressed as m^2 leaf surface area For fine roots, total cost ($R_T + \Delta W / \Delta t$) is prop. to leaf construction cost and relative nutrient availability For woody organs, W is expressed as g living parenchyma tissue (itself assumed as prop. to supported leaf area)	*Foliage :* $m_i(5^{\circ}C) =$ $[1.0 : 2.6]\ \mu g\ C\ m^{-2}\ s^{-1}$ [2] $Y_{Gi} = [0.56 : 0.73]$ [2, 3] *Fine roots: n.a.* *Woody organs:* $m_i = 1.1\ 10^{-8}\ gC\ gDM^{-1}\ s^{-1}$ [2] $Y_{Gi} = 0.59$ [2, 3]	$Q_{10}(m_i) = 2.3$

Table IV. (continued)

Model class and reference	Specificities	Parameter[1] ranges [min : max]	Temperature dependence (R_M)
Deleuze and Houllier (1997)	For R_M, W is expressed as: • g DM for leaves and roots • m^2 bark area for stem; R_G is ignored for stem	'm_i' = 0.1 gC gDM^{-1} y^{-1} for leaves, roots; 'm_i' = 10 gC m^{-2} y^{-1} for stem Y_{Gi} = 0.92[2, 3] for leaves, roots	
Berninger and Nikinmaa (1997)		m_i: n.a. Y_{Gi} = 0.80	$Q_{10}(m_i)$ = 2
Mäkelä (1997)	For R_M, W is expressed as g DM	'm_i' = [0.02 : 0.2] gC gDM^{-1} y^{-1} Y_{Gi} = 0.75[2]	
Escobar-Gutiérrez et al. (1998)	For R_M, W is expressed as g structural C	m_i = 0.016 d^{-1} Y_{Gi} = 0.75	
Balandier et al. (2000)	For R_M, W is expressed as g DM; Fine root R_G implicitly includes turnover losses	'm_i' = [6 : 50] 10^{-4} g CO_2 gDM^{-1} h^{-1} Y_{Gi} = 0.50 for fine roots Y_{Gi} = 0.75 for other organs	$Q_{10}(m_i)$ = 2

McCree (1970) or equivalent: $R_T = R'_G + R'_M$ with $R'_M = c \cdot W$ and $R'_G = (1 - Y_G) \cdot P$			
Promnitz (1975)	For R'_M, W is expressed as g DM	'c_i' = 2 mg CO_2 gDM^{-1} h^{-1} Y_{Gi}: n.a.	
Rauscher et al. (1990)	diurnal net photosynthesis used in calculation of R'_G	c_i = 0.015 d^{-1} Y_{Gi} = 0.75[2]	user-defined
Zhang et al. (1994)		'c_i'(20ºC)[2] = [1.6 : 22] 10^{-5} h^{-1} Y_{Gi} = [0.67 : 0.73][2, 3]	simplified Arrhenius function
Deleuze and Houllier (1995)	For the stem, R_M is proportional to bark area	c_i = 0.1 y^{-1} for leaves, roots; 'c_i' = 10 gC m^{-2} y^{-1} for stem Y_{Gi} = 0.81[2]	

One-component formulation (R_G ignored or implicit): $R = k \cdot W$			
Prentice et al. (1993)	Only sapwood maintenance respiration computed, using the pipe model	k: n.a.	Q_{10} = 2.3
Takenaka (1994)	only leaf maintenance cost is explicitly computed.	k_{leaf} = 0.25 y^{-1}	
Perttunen et al. (1996)		k_i = [0.02 : 0.2] y^{-1}	

Respiration ignored or implicitly taken into account in a global light conversion efficiency (see *table II*)			
Sorrensen-Cothern et al. (1993)			
West (1993)			
Kellomäki and Strandman (1995)			
De Reffye et al. (1997a,b)			

[1] Indexed parameters refer to specific tissue components (e.g. branches, stems, coarse roots...).
[2] Recalculated from related parameter values.
[3] Recalculated assuming a DM C content of f_c = 0.42 gC gDM^{-1}.

synthesis of new biomass, while maintenance respiration is defined as that required for maintenance and turnover of existing biomass [2, 3, 48, 79, 107, 124]. Most of the tree growth models reviewed here use one of the two formalisms that were developed concurrently in 1970, one by McCree and the other by Thornley. Each formulation

is used to split total respiration into its growth and maintenance components.

The formulation proposed by McCree [78] relies on a relationship between photosynthesis and respiration:

$$R_T = k \cdot P + c \cdot W \qquad (10)$$

where R_T and P are, respectively, the integrated total respiration and gross photosynthesis (less photorespiration), both expressed as g C unit time^{-1}, and W is the dry mass of living tissue (g C equivalents). Coefficient k (dimensionless) is associated with growth and coefficient c (unit time^{-1}) with maintenance activity, so that term $k \cdot P$ can be referred to as "growth-associated respiration" and term $c \cdot W$ as "maintenance-associated respiration".

In the approach of Thornley [124], the photosyntates (P) produced during a time interval Δt are utilised (for a plant having no change in storage material over Δt) either as evolved as CO_2 in total respiration (R_T), or as incorporated into new structure (ΔW) (g C equivalents):

$$P = R_T + \Delta W / \Delta t. \qquad (11)$$

In this two-component partitioning of total respiration, the maintenance-associated component (R_M) is assumed to be proportional (constant m) to the living tissue biomass (W):

$$R_T = R_G + R_M \quad \text{with} \quad R_M = m \cdot W \qquad (12)$$

Thornley [124] further introduced the concept of growth efficiency or yield (Y_G), as the ratio of the weight of new structural dry matter (ΔW) built up as growth during Δt to the total amount of assimilates required for this new growth, which includes both ΔW itself and growth respiration ($R_G \cdot \Delta t$), both expressed as g C equivalents:

$$Y_G = \Delta W / (\Delta W + R_G \Delta t). \qquad (13)$$

This equation can be rewritten as a definition of the growth-associated component of respiration:

$$R_G = \{(1 - Y_G) / Y_G\} (\Delta W / \Delta t). \qquad (14)$$

Although both McCree and Thornley's approaches yield a two-component partitioning of total respiration, one component being associated with growth and the other with maintenance, it must be pointed out that these two ways of decomposing R_T are not equivalent. By combining equations (11) through (13), Thornley [124] derived a new decomposition of R_T formally equivalent to equation (10):

$$R_T = (1 - Y_G) \cdot P + m \cdot Y_G \cdot W. \qquad (15)$$

Hence, identifying expressions (10) and (15):

$$k = 1 - Y_G \quad \text{and} \quad c = m \cdot Y_G. \qquad (16)$$

The maintenance- and growth-associated components of respiration in McCree's formulation are not the same as those in Thornley's original formulation. Thus, for a given set of data, the growth-associated respiration will be computed as higher and the maintenance component as lower in McCree's approach than in Thornley's, although the sum of both components will be the same [2, 3, 48, 79, 107]. Hence, the choice of a particular formulation for growth respiration (i.e., as a function of photosynthesis or of growth) imposes the type of coefficient for maintenance respiration (m or c). If experimental data are available, a regression analysis will yield correct values for both parameters. However, one must be careful about the consistency of formulation for both components when deriving the coefficients from literature, as inconsistency could generate a significant error in total respiration. This point should be emphasised, because most of the models reviewed here (with very few exceptions, e.g. PEACH) used respiration coefficients borrowed from the literature, with maintenance and growth components generally not taken from the same reference.

Generally, tree growth models use the formulation proposed by Thornley [124] (*table IV*). The McCree formulation [78] has been used mainly for long term periods by models run at yearly time steps [23, 147], although it could be used for shorter time-steps as well [100]. In the model ECOPHYS [102], the respiration formulation is analogous to McCree [78], but for experimental reasons the photosynthesis taken into account to compute the growth-associated respiration is the diurnal net photosynthesis of leaves instead of the gross photosynthesis which can generally not be determined directly.

In the tree models computing carbon balance at the organ (or organ class) level, the growth respiration of each organ is computed after running the assimilate partitioning routine. Maintenance respiration, however, is in most cases subtracted from gross photosynthesis prior to partitioning photoassimilates among the different organs. In contrast, in a few models [4, 23, 29, 128] maintenance respiration is computed after allocating photosynthates within the plant. The underlying assumptions are different in both cases, and so are generally the results, as both the total amount of assimilates to be allocated and the relative sink demands are different (see Sect. 3.4).

3.2.2. Practical application of the two component-approach in tree growth models

Given a particular two-component-approach (i.e. either McCree or Thornley's approach), tree growth models can still significantly differ (1) by the values of

parameters used, (2) by the definition applied to biomass W, (3) by the way they consider temperature dependence, and (4) by the priority assigned to growth respiration, maintenance respiration, and photosynthate partitioning.

Y_G is generally expressed directly as a dimensionless coefficient between 0 and 1 (g C new DM per g C photoassimilate) [23, 102, 141]. Alternatively, growth efficiency can be expressed as a global coefficient integrating also the carbon concentration of dry matter f_c [24, 40, 73, 75, 147]. Y_G can then be derived assuming a value for f_c (generally f_c ranges between 0.4 and 0.5 g C per g DM). In the models reviewed, the values of Y_G range from 0.6 to 0.9, with most of them around 0.75 (*table IV*). This value is generally assumed to be the same for all organs. However, Y_G actually depends on the chemical composition of the biomass produced because the synthesis of protein requires a higher input of respiratory energy than that of an equivalent (in C terms) amount of cellulose or starch [61, 91]. Thus, values of growth efficiency should depend on the type of organ [107]. Only Zhang et al. [147] and Williams [144] actually used different values of Y_G. In a few cases, growth respiration is ignored (i.e. Y_G apparently = 1), either for specific organs or tissues such as woody organs [24], or for the whole plant [93], presumably because growth respiration is low compared to maintenance respiration at the time scale considered (one year) or because it is in some way integrated in another component of the whole-plant C balance (see below).

Maintenance respiration, which provides the energy required for the turnover of cellular constituents and for the maintenance of pH and solute gradients [92], is correlated to temperature and the amount of living biomass, i.e. total organ biomass or nitrogen content for leaves, twigs or fine roots [109, 110], and sapwood volume for woody organs [110, 111, 121]. Some growth models applied to young trees [29, 102, 138] assume that maintenance respiration is proportional to the total dry mass of the tree, including both living and dead cells. However, this approach should be used carefully when working with older trees. Early studies on maintenance respiration using this approach led to aberrant results of carbon balance (more respiration than photosynthesis) as discussed by Jarvis and Leverenz [47]. The tree growth models reviewed use different approaches to give an approximate estimation of the amount of living biomass, in particular for the woody components (stemwood, branches and coarse roots). In the models developed by Thornley [128] and Deleuze and Houllier [23, 24], a correlation between stem respiration and wood surface area is used. In the models of Mäkelä and Hari [73] and Wil-

liams [144], the amount of sapwood is approximated by using leaf area values, as assumed in the "pipe model" (see Sect. 6.2.). As an alternative approach, maintenance respiration can be simulated as a function of total biomass of each plant part, with different coefficients for each one [4, 9, 40, 75, 93, 141, 147]. All these considerations result in large differences in m or c values used in the different process-based models (*table IV*).

When respiration is computed on a yearly basis, the parameter values can be considered as averages integrating the seasonal temperature variations. When the time step is a day or lower, however, the values are generally given for a given temperature. The temperature dependence of maintenance respiration is in most cases taken into account, by using a constant Q_{10} value [4, 9, 40, 138, 139, 141, 144] or a more complex function of temperature [1, 128, 147]. In ECOPHYS [102] and TREGRO [139], users can enter their own temperature dependence functions. In the model of Thornley [128], the rate of maintenance is further limited by the local substrate C availability, according to a Micheailis-Menten law. In the year-based model of Mäkelä and Hari [73], the light environment modulates respiration in a similar way as it does photosynthesis.

3.2.3. Potential extensions of the two-component model

In addition to the two-component model, there are extended, more refined, respiration models such as those proposed by Thornley [127] and Johnson [48]. The three-compartment model of Thornley [127] includes storage, degradable and non-degradable structures whereas Johnson [48] extended the basic growth and maintenance compartments model to incorporate three additional processes associated with ion uptake and N assimilation. However, these models require more information and have thus not been widely used so far in tree growth models.

Among the models reviewed in this paper, only the theoretical plant model of Thornley [128] explicitly assigns ion uptake a respiratory cost. Yet, nutrient uptake has been suggested to be the process that requires most of the respiratory energy in roots of herbaceous species, with the amount of energy needed increasing with increasing relative growth rates [95]. Thus, Poorter et al. [95] suggested that the specific cost associated with ion uptake differs between fast- and slow-growing herbaceous species. In contrast, respiration costs for nutrient uptake have not been accurately determined for tree roots [77]. However, in woody plant growth models, the lack

of the ion uptake component of respiration can often be acceptable as a first approximation considering the importance of recycled nitrogen [81] and perhaps other minerals. In this case, it seems difficult to separate energetic cost due to maintenance from that associated with nutrient recycling.

3.2.4. Simpler approaches to modelling respiration

As an alternative approach to the multi-component approach of respiration, some tree growth models consider C acquisition as a net process, and the amount of assimilates allocated by the model is gross photosynthesis less total respiration [51, 142]. These models do not explicitly include respiratory losses because they approximate annual net gain of aboveground organic matter with the help of the annual PAR_a conversion efficiency approach, which aggregates many other factors operating at shorter time steps. In the model of Takenaka [123], only the maintenance respiratory cost of leaves is explicitly computed; the other components of total respiration are integrated in the conversion efficiency. Using a constant R/P ratio could be a more simple and accurate way of modelling respiration than the growth-maintenance paradigm, at least for computing whole tree carbon balance at an annual time step [38]. The theoretical, substrate-based model developed by Dewar et al. [25] provided some support to this view (Dewar, unpublished results). However, for similar reasons as above (end of Sect. 3.2.2), this global approach would generally not lead to the same quantitative results as if respiration was explicitly taken into account. Despite this flaw, a simple, physiologically sound approach avoids the critical problem of parameterisation of the component parts of respiration. As noted by Weinstein et al. [138], "accurate values for the respiration of each tissue are critically needed". Furthermore, such values are needed for each tree species studied because process rates such as maintenance respiration can exhibit significant variations among species (e.g. for woody-tissue respiration even when expressed per volume of living tissue: [108]). Such information is also needed for other causes of carbon loss such as leaf shedding, self-pruning, root turnover and exudation, which are in most cases ignored or modelled with parameter values borrowed from the literature. Thus, improving the accuracy of modelling C input by photosynthetic assimilation (Sect. 3.1) is pointless unless the accuracy of modelling C outputs is significantly improved.

3.2.5. Link between respiration formulation and time/space scale

The simplified ways of accounting for respiration (Sect. 3.2.4) have been used only in models that use yearly time steps to simulate tree growth on the long term, generally throughout the tree's lifetime (*figure 5*). This is consistent with the global and simple approaches used to represent carbon processes in these models, such as the use of modules that do not explicit leaf photosynthesis (Sect. 3.1.1). In contrast, models using a daily time step apply one of the explicit, more analytical two-component formulations (*figure 5*), in most cases that of Thornley [124]. In addition, most of them apply a temperature correction of the maintenance component, which is often operated at the hourly time scale. However, the link between respiration formulation and time/space scale is far from absolute, as many (actually, most) of the models using a yearly time step apply the 2-component approach (*figure 5*).

3.3. Modelling reserve dynamics

The dynamics of storage and mobilisation of carbon reserves in trees have been investigated for a long time, resulting in a considerable amount of data. In particular, the main features of the annual cycle, including reserve deposition in late summer and fall, partial starch-sugar interconversion in winter, and massive mobilisation in spring, are qualitatively well known [36, 54, 55, 59, 132, 148]. Yet, carbon-based models generally ignore, or treat very briefly, this aspect of the tree carbon balance. Of the twenty-seven models reviewed in this paper, only seven consider some mobile carbon other than current photosynthates. Of these seven, only five [4, 29, 128, 139, 141] include a specific reserve carbohydrate pool separate from the rest of dry matter. In the other two, mobilisable C is simply a proportion of the total dry matter of specific organs, which is mobilised to complement the photosynthetic sources at specific times of the year [40, 147].

When attempting to simulate reserve dynamics, one of the main open questions regards the driving force of reserve deposition. In the models considering specific pools of reserve carbon, each pool is assigned a specific storage capacity or demand, which is assumed to be a function of leaf demand [141] or of carbon saturation deficit [4, 139]. Alternatively, reserve deposition can follow a Michaelian kinetic rule [29]. However, the models greatly differ in the way they include this demand in the
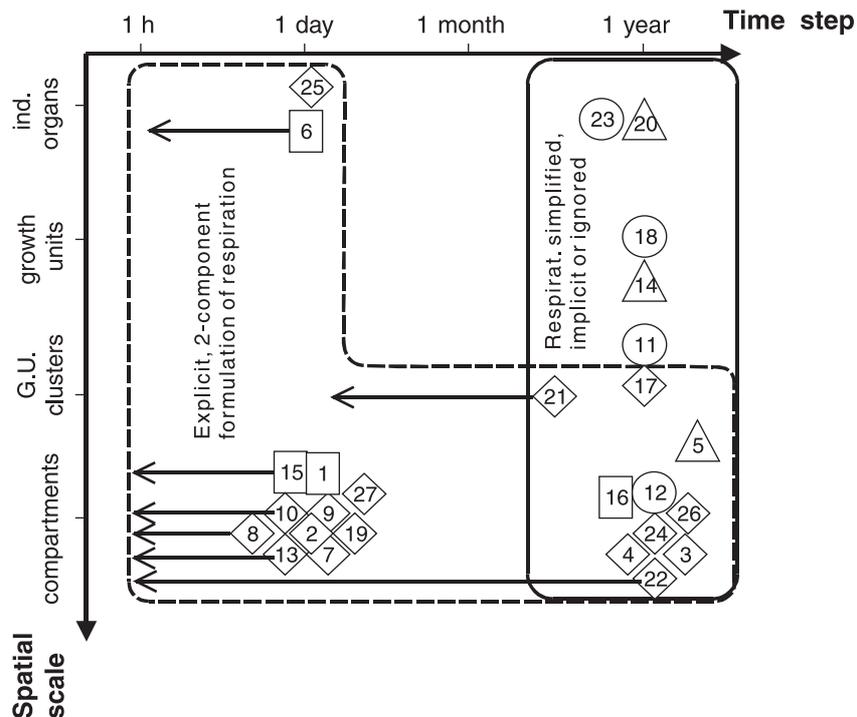
Figure 5. Schematic location of the respiration module of each tree growth model in a space-time domain. Each symbol corresponds to a given approach to represent respiration ($\diamond$: 2-component formulation of Thornley [124] or equivalent; $\square$: 2-component formulation of Mc Cree [78] or equivalent; $\triangle$: 1-component formulation (R_0 ignored or implicit); $\bigcirc$: respiration ignored or implicit). Numbers in symbols refer to models or model versions (see legend of *figure 3*). Arrows indicate that maintenance respiration is computed at a finer time step than growth respiration.

general carbon economy. In TREGRO [139], where the available C is allocated among sinks according to priority rules (see Sect. 3.4 below), non-leaf reserve pools are assigned the lowest priority level. In other words, they are modelled as passively absorbing any assimilates available in excess of the active growth demand. The model of Wermelinger et al. [141] regards reserve areas as passive overflow buffers during most of the season (like TREGRO), but the priority orders shift at harvest so that reserve storage gets a higher priority level than growth in fall. In contrast, in the models of Balandier et al. [4] and Escobar-Gutiérrez et al. [29], no priority order is set a priori. Reserve storage is regarded as an active process alongside structural growth and can compete efficiently with it. The view of reserve areas as short-term buffers is supported to some extent by experimental data [112]. However, this might not hold in the long term or on a wide range of disturbance. An increasing body of evidence supports the view that storage areas might actually be active sinks with their own strength [14], so that a tree would normally "manage" to store some reserves, at the expense of growth, in sustained conditions of low carbon

availability. Given the importance of reserves for tree survival in difficult conditions, more quantitative knowledge is needed in this area.

A similar problem arises regarding reserve mobilisation. When taken into account, reserves are in most cases modelled as a supplemental source, providing for a limited period of time (generally in spring, during the intense growth of new shoots and leaves) the missing C when current photosynthesis is not sufficient to meet the carbon requirements [4, 40, 139]. Alternatively, the models of Wermelinger et al. [141] and Escobar-Gutiérrez et al. [29] simulate the rate of mobilisation as proportional to the existing reserve pool size, hence independent of the demand. Zhang et al. [147] made no particular assumption but just derived the rates of mobilisation from experimental measurements of the variations in the dry weight of reserve organ. Computing, as most models do, the rate of mobilisation in spring as the mere difference between current photosynthetic supply and total carbon demand involves a very strong assumption: i.e. that the bulk of reserves would be immediately available on request, or that carbon availability would never be

limiting growth in spring (except in pathological conditions severely affecting the total amount of reserves at the plant level). Such an assumption could be easily accepted for short periods and/or for moderate amounts of C. However, it should be questioned for the massive spring mobilisation, both at the quantitative (total amount of carbon released from reserve pools in spring) and dynamic (rate of mobilisation) levels. Actually, the driving force of spring mobilisation (whether sink-driven or induced by external conditions regardless of demand) is poorly known. A few experiments involving bud removal [37] support the assumption that mobilisation is a demand-driven process. On the other hand, there is also evidence for a direct role of temperature on the conversion of starch to sugars within the parenchyma cells and their subsequent release into the conducting systems ([59] and references therein). More information is required in this field, particularly regarding the fine-scale and quantitative dynamics of mobilisation in relation to early spring growth.

3.4. Modelling carbohydrate allocation

Carbohydrate allocation currently represents a central problem of process-based models of tree growth, because carbon allocation and growth cannot be dissociated. However, formulation of allocation remains an unsolved issue of current tree (and more generally plant) modelling. Among plant growth models, some have been exclusively devoted to test hypotheses concerning carbon allocation [82]. Wilson [145], Mäkelä [74], Marcelis [76], Cannell and Dewar [14] and Lacointe [60] presented and discussed the main concepts used to build or constrain models of carbon allocation in plants. The reviews by Mäkelä [74], Cannell and Dewar [14] and Lacointe [60] made special reference to trees.

Four main approaches have been used to simulate carbon allocation in tree growth models (*table V*): (i) the use of empirical allocation coefficients, (ii) functional balance and other allometric relationships between different plant parts, (iii) the use of transport resistance models, and (iv) the interactions among sinks with different C demand and import capacities.

3.4.1. Empirical allocation coefficient approach

In 1962, Brouwer [13] stated that, under constant environmental conditions, allocation coefficients between above- and below-ground parts could roughly be considered as constant. This assumption has given some

Table V. The four main classes of assimilate allocation modules used in the carbon-based models of individual tree growth reviewed. T_a : air temperature; T_s : soil temperature; cT, cumulative air temperature; N : soil nitrogen; N_i : internal tissue N content.

Model reference	Subclass / specificities	factors taken into account (through their impact on growth dynamics)
Empirical models		
Promnitz (1975)	seasonal variation of allocation coeffs.	
Ågren and Axelsson (1980)	seasonal variation of allocation coeffs.	T_a, T_s, cT, daylength, tree water content
Mäkelä and Hari (1986)		PAR
Rauscher et al. (1990)		
Webb (1991)	compartment model with seasonal variation of transfer coefficients	
Zhang et al. (1994)	seasonal variation of allocation coeffs.	soil water potential
Functional balance (FB) and other allometric relationships		
Valentine (1985)	FB : pipe model + root : shoot activities	
Prentice et al. (1993)	pipe model + other allometric rules	
Sorrensen-Cothern et al. (1993)	architectural growth rules	local C production
West (1993)	allometric rules + FB : pipe model includes allometric inequations	
Takenaka (1994)	architectural growth rules	local PAR

Table V. (continued).

Model reference	Subclass / specificities	factors taken into account (through their impact on growth dynamics)
Deleuze and Houllier (1995)	allometric + growth rules	
Kellomäki and Strandman (1995)	architectural growth rules	local PAR
Hauhs et al. (1995)	FB : pipe model + architectural growth rules	Tree age, abstract representation of local environment resources other than PAR
Perttunen et al. (1996)	FB : pipe model + root : shoot activities + architectural growth rules	
Williams (1996)	FB : pipe model + root : shoot activities + allometric rules	
Berninger and Nikinmaa (1997)	FB : pipe model + root : shoot activities (modified for N retranslocation) + allometr. and architectural growth rules	light environment, potential evapotranspiration, soil water capacity, N_i
de Reffye et al. (1997a,b)	architectural + allometric growth rules	
Mäkelä (1997)	FB : pipe model + root : shoot activities + allometric rules	
Transport resistance models		
Thornley (1991)	bisubstrate (C–N)	T_a, N_i
Luan et al. (1996)	includes the model of Thornley (1991)	
Deleuze and Houllier (1997)	1-substrate (C) reaction-diffusion	
Interactions among sinks with different carbon demands and/or import capacities		
Wermelinger et al. (1991)	hierarchical	N_i, cT
Weinstein et al. (1992)	hierarchical	N_i
Grossman and DeJong (1994)	hierarchical with proportional submodel embedded within 1 priority level	cT
Escobar-Gutiérrez et al. (1998)	proportional, modified with 2-component sink strength : affinity and maximum import rate	
Balandier et al. (2000)	proportional, modified as above, with explicit involvement of within-tree distances	previous growth rate

reasonable predictions [73, 74, and references therein], and a number of models [1, 73, 100, 102, 147] use allocation coefficients, also referred to as partitioning coefficients, to assign a given part of total photosynthates to each organ. The model ECOPHYS [102] includes a very detailed, experiment-derived allocation coefficient matrix that gives the proportion of assimilate flowing from each source into each sink. In the models of Promnitz [100], Ågren and Axelsson [1] and Zhang et al. [147], the allocation parameters vary during the season to account

for experimentally observed time variations in growth allocation. This is also the case in the compartment model of Webb [138], which can be classified as an empirical model for this reason.

Although the allocation coefficients can be modulated by external conditions such as PAR [73], temperature or soil water potential [1, 147], empirical models can only be applied over a limited range of conditions, regarding both the plant material and the environment or man-induced perturbations. However, when such conditions are

actually met, these models can be very efficient to simulate tree growth.

3.4.2. Functional balance and other allometric relationships

In the functional balance approach, carbon allocation is described so as to maintain a balance between the different growing parts of a tree. It is assumed that the carbohydrate investment is driven according to the external conditions by allocating the assimilates in an "optimal" way among the different organs, i.e. so that the total growth of the plant is maximised in a given environment. These considerations are based mainly on the principles of the shoot-root functional balance [22] and of the pipe model [114, 115].

3.4.2.1. Shoot: root functional equilibrium

The underlying assumption of this approach is that, in the long term, the assimilation of carbon by foliage and the acquisition of nutrients by fine roots must be in balance with the utilisation of carbon and nutrients for plant growth. This functional balance was described mathematically by Davidson [22] as:

$$(\sigma_s \, W_s) \, / \, (\sigma_r \, W_r) = \pi \qquad (17)$$

where σ_s and σ_r are the specific C and N assimilation rates per unit mass, respectively, W_s and W_r are the shoot and root biomass, respectively, and π is a constant. Allowing σ_r to vary with external N availability provides a convenient way to account qualitatively for the effects of soil conditions on C partitioning among organs. Similarly, σ_s can vary as a function of above-ground environment (e.g. atmospheric CO_2 concentration, see Sect. 3.1).

Interest in Davidson's balanced activity hypothesis has led to many theoretical whole-plant allocation models [42, 50, 82] and more particularly to a number of teleonomic (apparently goal-seeking) models developed by Thornley and co-workers. Hypotheses used in this approach are summarised and detailed in the reviews by Mäkelä [74] and Cannell and Dewar [14]. Allocation is based on a coefficient defined as a function of the substrate concentrations, the current shoot and root fractions, and the fractional carbon and nitrogen content of shoot and root dry matter. This coefficient could be defined to constrain the substrate C/N ratio to a target value in balanced exponential growth, independent of the external environment [105], or to allow varying C/N ratios [42], or to maximise plant relative growth rate [50, 105]. Practically, the models of Valentine [133], Deleuze and Houllier [23], Perttunen et al. [93], Williams [144] and

Mäkelä [75] include the shoot: root functional balance principle.

3.4.2.2. The pipe-model approach

In its original formulation [114], the pipe model states that a given unit area A of water-conducting tissue (sapwood) at any height in the tree is necessary to supply water to the foliage biomass W_f above that height. A species-specific parameter η relates these two variables, so that:

$$W_f = \eta \, \cdot \, A. \qquad (18)$$

This principle has been used as a framework for the derivation of growth models for tree height and basal area, often associated with the shoot: root functional balance principle [9, 75, 93, 133, 144]. In several of them, the parameter η is assigned different values at different height levels within the tree, which is more consistent with experimental data [72]. Although the pipe model approach is interesting for many purposes, it is probably inadequate to predict tree response to disturbances such as pruning or thinning.

3.4.2.3. Other growth relationships

Different kinds of allometric relationships or growth rules, generally without an explicit functional or adaptive value, have been used to set constraints on the relative dimensional sizes or weights of the tree parts. Some are intended to reflect experimental relationships among large compartment dimensions, e.g. between crown size and stem height or diameter [23, 142]. Others can be more specifically referred to as architectural growth rules describing the geometrical and dimensional relationships between stem growth units of successive branching orders [41, 51, 93, 103, 104, 120, 123], sometimes according to mechanical constraints [34]. Although they can include some stochastic variability [103, 104], the degree of flexibility of these models is similar to that of basic empirical models. However, it can be improved through a modulation of the architectural parameters by external factors, e.g. local light conditions [51, 123]. Furthermore, some of these models [23, 41, 93, 142, 144] combine architectural growth rules or mere allometric relationships with one or more of the functional balance concepts, which can provide convenient ways to introduce environmental effects.

3.4.2.4. A discussion of goal-seeking approaches

The functional balance approach, based on optimality principles, may be chosen for conceptual or practical

reasons such as simplicity, utility, or ability to represent growth strategies selected by evolutionary pressures [129]. In addition, it may provide a connection between the formation of structure and the metabolic process considered [74]. Although the mechanisms underlying optimality principles are not well understood (but see Sect. 3.4.5), this approach has often appeared to give an acceptable approximate description of experimental data on dry matter distribution between tree compartments. However, functional balance models cannot take into account a complex and dynamic plant architecture, as they are defined by strong integrative constraints that allow few possibilities for changes in the structure they represent. Thus, most tree growth models applying this approach deal with biomass allocation into bulk compartments.

3.4.3. Interactions among sinks with different demands and/or import capacities

3.4.3.1. The proportional and hierarchical approaches

In a number of recent tree growth models, the allocation of photosynthates to new and existing parts of the tree is based on the hypothesis that trees grow as a collection of semi-autonomous, but interacting "sinks" (e.g. fruits, growing shoots and leaves, roots, cambium) that compete for the supply of photosynthate coming from "sources" (i.e. photosynthesising leaves, or reserve organs during remobilization). The competitive ability of a sink to accumulate assimilates per unit time defines its strength [137]. This capacity, or demand, has two or three elementary components: maintenance respiration, growth (and the respiratory cost of that growth) (see Sect. 4) and, in just a few of these models (see Sect. 5), carbohydrate reserve storage. The carbohydrate requirement for growth is generally quantified as the genetic potential growth rate of a sink, i.e. the maximum growth rate achieved by the growing organ under non-limiting environmental conditions. In a few cases, this concept is made more flexible through modulating the current demand according to external conditions such as temperature or nitrogen or water availability [40, 139, 141], and/or to the previously achieved growth [4].

Although the demand function can be quantified in different ways, the problem of allocation is generally solved by similar approaches in the different models. Each day, the allocation module has to process a given daily supply (leaf photosynthesis and/or reserve mobilisation) on one hand, and a set of demands for each of the tree components on the other hand. When the total daily demand is less than the daily supply, each component gets its own demand, i.e. grows at its potential rate, and the excess supply goes to the reserves and/or photosynthesis is reduced. In case of shortage, a decision has to be made as to the amount each component will be allocated. There are two solutions in the literature to that problem. In the "proportional" approach, each component gets the same proportion of its demand, which then must be the supply/demand ratio. According to the "hierarchical" approach, the component with the highest priority is "fully served" first, and only then the component with the next priority level is considered, and so on. Maintenance respiration requirements are assigned the highest priority level because they are vital for the organ (or even the plant) survival.

The combination of the "proportional" and "hierarchical" approaches has led to various models (*table V*), based on daily potential growth rates, priorities in assigning resources and affinities for substrates by the sinks [4, 29, 40, 139, 141]. In the model developed by Wermelinger et al. [141], reproductive and vegetative demands for C and N have equal priority before blooming. After blooming, reproductive growth is assigned the highest priority for both resource allocation, followed by vegetative growth. The lowest priority level is assigned to the nutrient reserves. In the model PEACH [40], sink priority is implicitly based on proximity to sources. Fruits, leaves, stems and branches are modelled as being closest to the source, followed by the trunk, and finally the roots. In the model TREGRO [139], aboveground parts of the plant have first access to newly fixed C, while below-ground parts have first access to nutrients for growth. Each sink gets different proportions of its demand based on the phenology of growth through the year and the availability of other resources, or environmental conditions.

The model SIMWAL [4] explicitly refers to individual source-sink distances, depending on the geometrical properties of each organ and their topological links, in the calculation of the allocation coefficients. No priority levels for carbon allocation are assigned a priori between organs; within each sink maintenance respiration is given the highest priority for carbohydrate use. This approach enables simulation of the tree architectural development on an organ-basis.

Marcelis [76] suggested that the use of potential demand and priority functions is the most valuable approach for simulation of dry matter distribution between plant parts under a wide range of experimental

conditions, and this approach has shown some promising results. However, the limitation of these models is mainly the problem of estimating the various sink demands, which are hypothetical quantities that can, at best, be indirectly approximated. In most cases, the "non-limiting conditions" used to define potential growth are actually the upper limit of a particular range of conditions, e.g. when all fruits are removed; however, it is very difficult to be sure that this upper limit cannot be exceeded in extreme or uncommon cases, e.g. after severe pruning.

3.4.3.2. A mechanistic attempt to model interactions among sinks: Resistance models of sugar transport

Using simplified models derived from the theory proposed by Münch [87], Thornley [125, 126] and Minchin et al. [82] showed that processes of transport and utilisation alone are sufficient to predict a wide range of allocation responses. The transport and resistance model of Thornley [125, 126], combining C and N movements in opposite directions with bi-substrate dry matter growth kinetics, provides an explanation for the functional balance in terms of substrate fluxes and dynamics, and can predict shoot-root responses under various conditions. For plants undergoing steady-state growth, it predicted the ratio of shoot to root activities to be constant, which is similar to predictions of functional equilibrium models. When applied over decades, the transport resistance model of Thornley [128] gives a realistic simulation of forest growth, although it does not account for the annual cycle exhibited by tree growth; it has been included in the model FORDYN [71]. Deleuze and Houllier [24] developed a particular version of the transport resistance model (reaction-diffusion model) to simulate C allocation to the diffuse sink of radial growth. This model is able to account for experimental profiles of wood distribution along the stem. Beside these few cases, the mass-flow/resistance approach has not been used extensively in tree growth models, due to its complexity and difficulties to determine its parameters. However, it has so far not been replaced by an alternative mechanistic theory [130].

3.4.4. Tentative classification of carbon allocation modules to assist the choice of a given formulation

Although not always explicit, all classes of models involve some growth rules to some extent because carbon allocation cannot be dissociated from organ growth. Even the most mechanistic, carbon-based models, namely transport-resistance (TR) and between-sink interaction models, include some basic assumptions about growth patterns. For instance, formulating the sink metabolic or carbon import rates as constant or Michaelian has strong implications, although not explicit, on growth pattern. However, the extent or prevalence of growth rules relative to carbon-based processes differs greatly among the different classes, with architectural/allometric rule-based models on one side, the TR/sink interaction – based models on the other, empirical models in the midpoint and functional balance models closer to architectural/allometric models. Such a classification can also be understood to some extent as a structure (growth rules) vs. function (carbon-based processes) prevalence ranking.

As can be seen from *figure 6*, these different model classes have often been used for specific time scales. All models where allocation is driven primarily by growth rules are run on a yearly time step, whereas all between-sink interaction models typically have a 1-day time step, as do most empirical and TR models with few exceptions. It can be noticed that TR models have been used only at the coarse scale of organ classes or compartments, presumably because of the difficulty to assign different local values for parameters. However, as TR models involve continuous fluxes, this allows a structuring of the longitudinal dimension, as achieved by the model of Deleuze and Houllier [24] in the form of a longitudinal profile of radial growth.

Beyond this apparent diversity, the different approaches to modelling carbon allocation are actually closer to each other than is immediately visible because they all take into account, to a certain extent, the effect of distance on carbon allocation. From a wide body of experiments, it is well known that the assimilate fluxes from a given source to a given sink decrease with increasing distances between both partners [28]; this is properly accounted for by the Münch mass-flow theory of assimilate transport (see Sect. 3.4.3). As they are an approximation of that theory, TR models include the impact of distance explicitly as the pathway resistance; some recent models of other classes like SIMWAL also include it explicitly. But many models include it implicitly as, e.g., the priority level orders in hierarchical models like PEACH, TREGRO or VIMO where the sinks closest to leaf sources have the highest priority levels and the farthest sinks have the lowest priority.
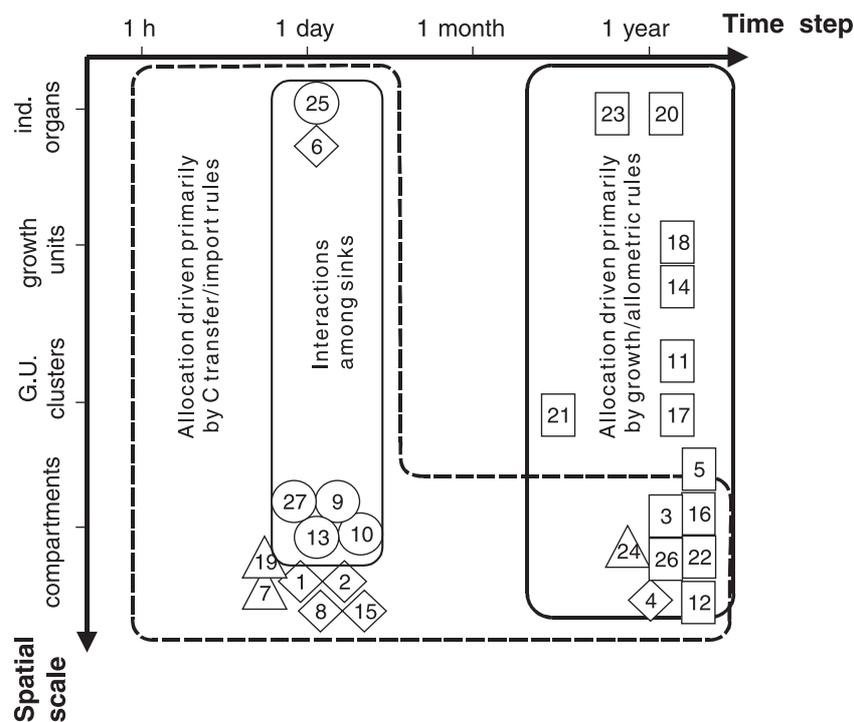
Figure 6. Schematic location of the carbon allocation module of each tree growth model in a space-time domain. Each symbol corresponds to a given approach to represent carbon allocation (◇: empirical; □: functional balance and other allometric relationships; △: transport-resistance; ○: interactions among sinks). Numbers in symbols refer to models or model versions (see legend of *figure 3*).

## 4. MODEL OUTPUTS AND IMPLICATIONS FOR FORESTRY AND TREE ECOLOGY

Given their different objectives and representation of tree architecture (Sect. 2) and the range of approaches they use to model processes involved in tree growth (Sect. 3), the models reviewed differ in their typical outputs and end-uses (*figure 7*). This section gives a short overview of the range of outputs and implications of the models for forestry and tree ecology.

Firstly, the majority of the models reviewed are used to provide estimates of tree growth in terms of biomass increments for different tree parts (*figure 7a*), and particularly stem production. In addition to a better understanding of the determinants of tree growth, predicting forest ecosystem and stem productions over long term periods, and sometimes under changing conditions, is the main end-use of the models developed by Agren and Axelsson [1], Berninger and Nikinmaa [9], Weinstein et al. [139], West [142], Zhang et al. [147] or Mäkelä

[75]. Some models can even be used to predict the stem taper of forest trees [23, 24] which is important for timber quality. All these models aim at providing biologically-sound predictions of tree growth in stands under various conditions, thereby reducing the need of costly calibrations. They are thus useful tools for forest management. From an ecological point of view, such models are mainly useful (i) to compare tree functioning under different environmental conditions [9], and (ii) to anticipate the effects of changing environmental conditions (acidification, fertilisation by nitrogenous deposits, raising air CO_2 concentration) on forest ecosystem production [139].

Secondly, some models provide predictions of tree dynamics in heterogeneous woody ecosystems [41, 71, 97, 144] (*figure 7b*). They are fruitful tools for ecologists in assessing the competitive ability of different tree species. Such models can be used to identify the key features of a given tree species that allow it to out-compete other species under certain circumstances. For instance, the species-specific plasticity of crown growth patterns was

(a) Biomass increment per organ class (Webb, 1991)
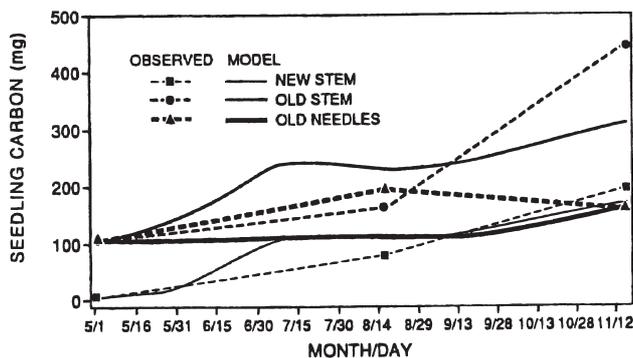
(b) Tree species dynamics in heterogeneous forests (Williams, 1996)
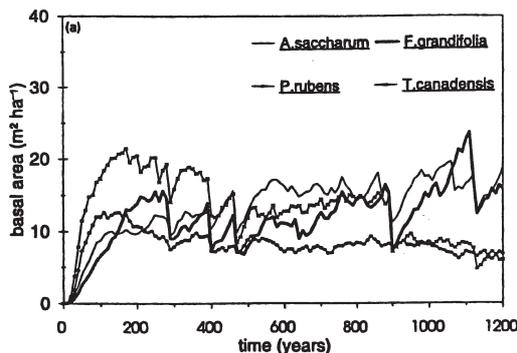
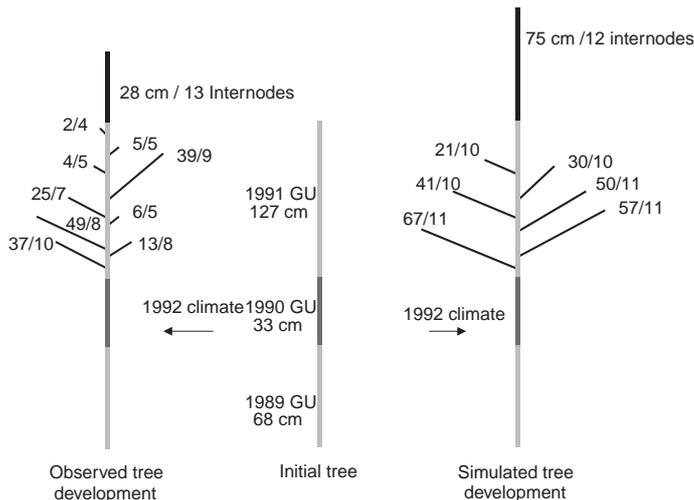(c) Individual tree architecture dynamics (Balandier et al., 2000)

Figure 7. Three typical examples of outputs of carbon-based models of individual tree growth: (a) seasonal evolution of the amount of carbon in different compartments of Douglas-fir seedlings in their second year of growth [138]; (b) stand development (i.e. changes of basal area for each species) over 1200 years for a site seeded with Acer saccharum, Fagus grandifolia, Picea rubens and Tsuga canadensis [144]; (c) comparison of the observed and simulated architecture dynamics of a young walnut tree during one year: the length (cm) and the number of internodes are given for each new growth unit [4].

found to largely determine the competitive ability of hardwood vs. more productive coniferous tree species [144].

Thirdly, other models provide predictions of the temporal evolution of the detailed tree structure (number, location and size of individual organs or growth units) in response to changing environmental conditions or cultural practices (*figure 7c*). This is needed for assessing the importance of structural development as an acclimation mechanism in trees [56]. Indeed, the fine tree structure (e.g. location of leafy shoots and number of buds) at a given time can constrain tree response to an abrupt change in environmental conditions (e.g. light regime after gap formation) [119]. These models are also useful when a detailed representation of tree structure is needed to predict the effect of disturbances like pruning or browsing on tree growth.

Thus, models of individual tree growth presently available cover a wide range of outputs and exhibit good potential for predicting forest yield and testing ecological hypotheses dealing with tree functioning in response to its physical, chemical and biotic environment, as well as disturbances. However, most of these models are not really accurate and exhibit weak predictive capacities at present time. In particular, models using a detailed representation of tree structure are still in their infancy and cannot accurately predict tree architecture dynamics or the growth of individual organs according to the environment and cropping practices. Important lacks in the representation of tree growth in many models still need to be addressed before these models can provide biologically-sound outputs in a large range of environmental conditions.

5. CRITICAL ISSUES FOR INDIVIDUAL TREE GROWTH MODELS TO DATE

5.1. Carbon allocation and interactions between tree structure and function: Achillie's heel of most tree growth models

As outlined in Section 2.2, the interactions between tree structure and function are of paramount importance in the context of individual tree growth. In particular, the dynamic and feedback aspects of carbon allocation on tree structure and resource acquisition make allocation a very sensitive point regarding the reliability and predictive capacity of individual tree growth models in the long-term. Unfortunately, the carbon allocation module is generally the weakest point of all models, either because (i) it cannot simulate a wide range of conditions and will fail in out-of-standard conditions, which inevitably do occur at some time during long periods (this is particularly true for empirical and growth-rule based models), or because (ii) carbon import / metabolic rates (and their regulation) are not sufficiently well known in the sinks to simulate properly the functioning of each organ (this is particularly relevant for TR- and sink-interaction models).

Point (i) illustrates the dilemma regarding growth rules: whereas they can usefully keep things within realistic ranges in normal ("standard") conditions, they may also prevent an efficient simulation of "non-standard" situations and miss some important aspects of the tree response to significant, "non-standard" environmental changes. Hence, the extent of growth rule inclusion should (and generally does) depend on the major objective of the model, whether research- or current production-oriented.

Point (ii) is obviously a major challenge for the future. Progress in assessing the "sink strength" or growth demand and its variations and feedback responses to external and internal conditions would be very fruitful, particularly regarding the early spring growth of buds and new shoots, radial growth and root growth.

5.2. Carbon storage/remobilisation

As pointed out in Section 3.3, carbon reserves are poorly considered, if at all, in most carbon-based tree growth-models. One reason for this is that the change in total reserves during the modelling period is often assumed to be negligible. This assumption may be acceptable over short periods in particular conditions for trees exhibiting continuous growth [100], e.g. fast-growing one-year-old poplar [102]. It is certainly more questionable on longer terms because the total reserves of a tree normally increase every year in proportion to their living cells. However, this proportionality allows models simulating tree biomass increment to include reserve pools in bulk tree compartments. Nevertheless, the functional role of reserve dynamics should not be underestimated. Indeed, carbon reserves are a means by which trees cope with environmental hazards [6, 58, 136]. More generally, reserve dynamics should be considered when analysing tree ecological plasticity or adaptation to particular environments. For instance, shade-tolerant deciduous species growing in forest understorey can gain large fractions of

their total growing season carbon during short periods when the overstorey is leafless, and then allocate this carbon to storage [134]. Hence, reserve dynamics should receive as much consideration as other processes if tree growth models are to account for environmental changes. However, this is not an easy task because the current status of knowledge in this area makes it very difficult to represent reserve dynamics efficiently. Indeed, the published information, however abundant and accurate for particular cases as mentioned in Section 3.3, has so far not revealed a general, simple organising principle, which would account for the observed dynamics, not to mention the variability between locations or years. The current ignorance of the mechanisms driving reserve deposition and remobilisation, is a major obstacle for evaluating the carbon substrate (other than direct photosynthate) actually available at any given time, and more generally for relating reserve dynamics with different internal or external variables in tree growth models. Future progress in this area can be expected to allow significant improvement of tree growth models.

5.3. Below-ground processes and tree nutrient economy: The missing module of many tree growth models

A striking feature of most of the models reviewed is that they do not represent below-ground processes and water and nutrient economy of the tree. Only a few models account for tree nutrient budget, using generally crude formulations for nutrient uptake, allocation and use, and losses [9, 41, 139, 141]. This is surprising because tree growth is often limited by soil nitrogen availability [21]. Indeed, nitrogen and other nutrients are of paramount importance for biological processes. As noticed above, leaf photosynthetic capacity is strongly correlated to the amount of nitrogen per unit leaf area [31], while maintenance respiration is well correlated to nitrogen content for leaves, twigs and fine roots [109, 110]. Thus, representing nutrient cycle in the soil-plant system is warranted for several applications, particularly for predicting tree growth on the long term and under changing
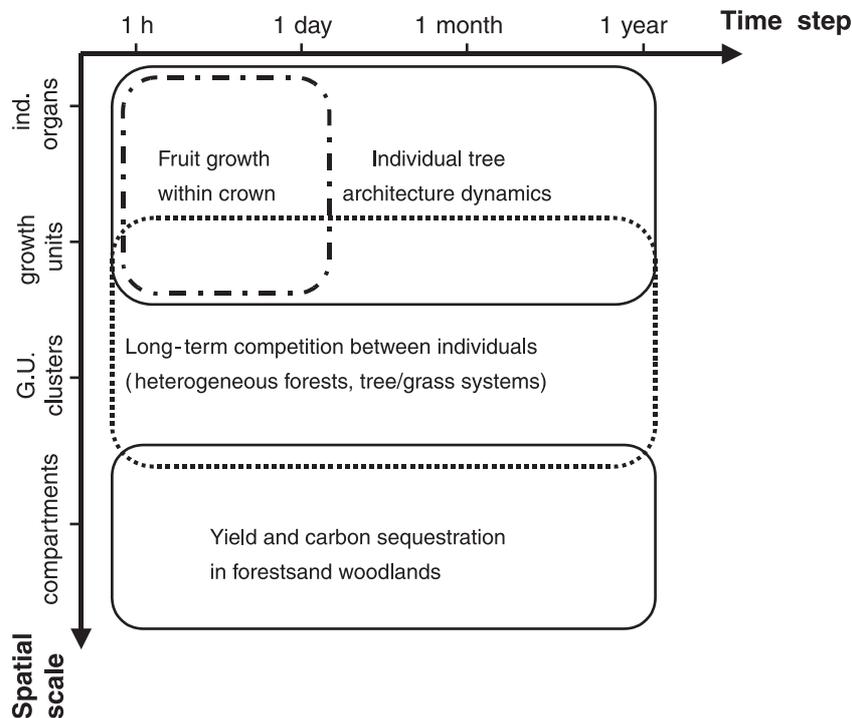

Figure 8. Schematic location, in a space-time domain, of some selected objectives that will be increasingly addressed by carbon-based models of individual tree growth in the near future.

environmental conditions (e.g. under high CO_2 levels: [52]). Similarly, various soil moisture regimes should be accommodated so that the models are applicable to a wider range of growing conditions, in particular to account for drought effect on tree growth.

As for aboveground parts (Sect. 2.3), the representation of the structure of the root system and the scale at which tree nutrient/water economy is simulated should be chosen according to model objectives. For instance, the approaches used to couple the soil- and plant-functioning in forest growth models [16, 53, 84] are generally adequate for individual tree growth models operating at coarse spatial scales. In contrast, according to their objectives, individual tree growth models operating at fine spatial scales should sometimes represent the development of the root system and account for the importance of root architecture dynamics for water and nutrient uptake, including carbon cost of such a dynamics. This is particularly true for models simulating competition between tree individuals, because both shoot and root development and competition play a significant part in determining the growth of coexisting individual plants [145]. This is readily feasible because some models are now available to link the 3D root architecture dynamics and carbon allocation [19, 90].

In addition to the structure and function of the root system, internal cycling of nutrients should also be represented in tree growth models because it allows the seasonal growth pattern of trees to be largely independent of nutrient uptake [99] and can determine the long-term growth response of trees to fertiliser application [98]. The representation of tree nutrient economy could range from nutrient budget in coarse tree compartments (for, e.g., simulating biomass increments) to the representation of nutrient fluxes and storage within a detailed tree structure (to assess the impact of local defoliation or pruning for instance). For many applications, and whatever the level of representation of the tree structure, accounting for the delayed response of tree growth and development to nutrient supply via the storage process is worth being modelled.

5.4. Conclusion

This review shows that we have come a long way in modelling individual tree growth, but further model improvement is hindered by the weakness of the representation of several aspects of tree functioning such as carbon allocation, reserve dynamics and the interactions between carbon economy and water/nutrient economy in trees. Like for models developed in other scientific fields, the overall accuracy of tree growth models is limited by the least well understood or ill-represented processes. Thus, the key modelling issues identified above should be major goals for researchers in the future.

New or increasingly important questions should spur on the development of individual tree growth models in the next decade (*figure 8*). Models operating at the coarser spatial scales will be increasingly used to improve predictions of yield and carbon sequestration for non-homogeneous forests and woodlands (e.g. to assess the frequency distribution of stem biomass increments in forest stands rather than whole stem yield, or to quantify the impact of tree species composition on stand carbon sequestration). When operating at intermediate spatial scales, these models will be of particular interest for simulating long-term competition between individual plants in the framework of models simulating plant dynamics in complex ecosystems. This is particularly the case for heterogeneous forests where the size and spatial distribution of tree individuals strongly determine gap phase dynamics, while plant competition largely depends on the location and shape of individuals [86, 96, 144]. This is also the case for savanna-like ecosystems where the spatial structure of the vegetation cannot be neglected for predicting its functioning and dynamics [113, 116]. At least, among other issues, the need to model individual tree architecture dynamics accurately (because of its ecological importance for tree response to local disturbances or changing environment, and its economical importance in ornamental horticulture for instance) and to quantify the heterogeneity of fruit growth within individual tree crowns (because fruit size distribution is becoming an increasingly important aspect of fruit quality in horticulture, see references in Lescourret et al. [69]) will spur on the development or refinement of individual tree growth models operating at fine scales. Thus, individual tree growth models will undoubtedly have an important role in addressing many new or increasingly important ecological and agronomic questions in the near future.

REFERENCES

[1] Ågren G.I., Axelsson B., PT – A tree growth model, in: Persson T. (Ed.), Structure and function of Northern coniferous forests, an ecosystem study, Ecol. Bull., Stockholm, 1980, pp. 525–536.

[2] Amthor J.S., The role of maintenance respiration in plant growth, Plant. Cell Env. 7 (1984) 561–569.

[3] Amthor J.S., Respiration and crop productivity, Springer-Verlag, New York, 1989, 180 p.

[4] Balandier P., Lacointe A., Le Roux X., Sinoquet H., Cruiziat P., Le Dizès S., SIMWAL: a structure-function model simulating single walnut tree growth according to climate and pruning, Ann. For. Sci. 57 (2000) 571–585.

[5] Ball J.T., Woodrow I.E., Berry J.A., A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions, in: Biggins I. (Ed.), Progress in photosynthesis research, Martinis Nijhoff Publishers, Dordrecht, 1987, pp. 221–224.

[6] Bamber R.K., Humphreys F.R., Variations in sapwood levels in some Australian forest species, Aust. For. 29 (1965) 15–23.

[7] Bassow S.L., Ford E.D., Kiester A.R., A critique of carbon-based tree growth models, in: Dixon R., Meldahl R., Ruark G., Warren W. (Eds.), Process modelling of forest growth responses to environmental stress, Timber press, Portland, Oregon, 1990, pp. 50–57.

[8] Berninger F., Effects of drought and phenology on GPP in Pinus sylvestris: a simulation study along a geographical gradient, Funct. Ecol. 11 (1997) 33–42.

[9] Berninger F., Ninkinmaa E., Implications of varying pipe model relationships on Scots pine growth in different climates, Funct. Ecol. 11 (1997) 146–156.

[10] Boardman N.K., Comparative photosynthesis of sun and shade plants, Ann. Rev. Plant. Physiol. 28 (1977) 355–377.

[11] Bosc A., EMILION, a tree functional-structural model: presentation and first application to the analysis of branch carbon balance, Ann. For. Sci. 57 (2000) 555–569.

[12] Bossel H., TREEDYN3 forest simulation model, Ecol. Modelling 90 (1996) 187–227.

[13] Brouwer R., Distribution of dry matter in the plant, Neth. J. Agr. Sci. 10 (1962) 361–376.

[14] Cannell M.G.R., Dewar R.C., Carbon allocation in trees: a review of concepts for modelling, in: Begon M., Fitter A.H. (Eds.), Advances in Ecological Research, Academic Press, London, 1994, pp. 59–104.

[15] Ceulemans R., An inventory of tree and stand growth models with potential application in short-rotation forestry, Biomass and Bioenergy 11 (1996) 95–107.

[16] Chen C.W., Tsai W.T., Gomez L.E., Modeling responses of Ponderosa pine to interacting stresses of ozone and drought, For. Sci. 40 (1994) 267–288.

[17] Chen S.G., Ceulemans R., Impens I., Is there a light regime determined tree ideotype?, J. Theor. Biol. 169 (1994) 153–161.

[18] Chen S.G., Ceulemans R., Impens I., A fractal-based *Populus* canopy structure model for the calculation of light interception, For. Ecol. Manage. 69 (1994) 97–110.

[19] Clausnitzer V., Hopmans J.W., Simultaneous modeling of transient three-dimensional root growth and soil water flown, Plant Soil 164 (1994) 299–314.

[20] Clothier B.E., Green S.R., Roots: the big movers of water and chemical in soil, Soil Sci. 162 (1997) 534–543.

[21] Cole D.W., Nitrogen uptake and translocation by forest ecosystems, in: Clark F.E., Rosswall T. (Eds.), Terrestrial nitrogen cycles, Ecol. Bull. 33 (1981) 219–232.

[22] Davidson R.L., Effect of root/leaf temperature differentials on root/shoot ratios in some pasture grasses and clover, Ann. Bot. 33 (1969) 561–569.

[23] Deleuze C., Houllier F., Prediction of stem profile of *Picea abies* using a process-based tree growth model, Tree Physiol. 15 (1995) 113–120.

[24] Deleuze C., Houllier F., A transport model for tree ring width, Silva Fennica 31 (1997) 239–250.

[25] Dewar R.C., Medlyn B.E., McMurtrie R.E., A mechanistic analysis of light and carbon use efficiencies, Plant Cell Env. 21 (1998) 573–588.

[26] Dewar R.C., Medlyn B.E., McMurtrie R.E., Acclimation of the respiration / photosynthesis ratio to temperature: insights from a model, Glob. Change Biol. 5 (1999) 615–622.

[27] Dixon K.R., Luxmoore R.J., Begovich, C.L., CERES – A model for forest stand biomass dynamics for predicting trace contaminants, nutrient and water effects. I-Model description Ecol. Modelling 5 (1978) 17–38.

[28] Donnelly J.R., Seasonal changes in photosynthate transport within elongating shoots of *Populus grandidentata*, Can. J. Bot. 52 (1974) 2547–2559.

[29] Escobar-Gutiérrez A.J., Daudet F.-A., Gaudillère J.-P., Maillard P., Frossard J.-S., Modelling of allocation and balance of carbon in walnut (*Juglans regia* L.) seedlings during the heterotrophy-autotrophy transition, J. Theor. Biol. 194 (1998) 29–47.

[30] Farquhar G.D., Caemmerer von S., Berry J.A., A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species, Planta 149 (1980) 78–90.

[31] Field C., Mooney H., The photosynthesis-nitrogen relationship in wild plants, in: On the economy of plant form and function, Cambridge University Press, 1986, pp. 25–55.

[32] Ford E.D., The control of tree structure and productivity through the interaction of morphological development and physiological processes, Int. J. Plant Sci. 153 (1992) 147–162.

[33] Ford E.D., Avery A., Ford R., Simulation of branch growth in the *Pinaceae*: Interactions of morphology, phenology, foliage productivity, and the requirement for structural support, on the export of carbon, J. Theor. Biol. 146 (1990) 15–36.

[34] Fournier M., Bailleres H., Chanson B., Tree biomechanics: growth, cumulative pre-stresses, and reorientations, Biomimetics 2 (1994) 229–251.

[35] Friend A.D., PGEN, an integrated model of leaf photosynthesis, transpiration and conductance, Ecol. Modelling 77 (1995) 233–255.

[36] Frossard J.S., Lacointe A., Les variations saisonnières de l'utilisation du carbone chez les arbres au stade végétatif, en zone tempérée, Bull. Soc. Bot. Fr. 135 (1988) 9–24.

[37] Gezelius K., Ericsson A., Hallgrem J.E., Brunes L., Effects of bud removal in Scots pine (*Pinus Silvestris*) seedlings, Physiol. Plant. 51 (1981) 181–188.

[38] Gifford R.M., Whole plant respiration and photosynthesis of wheat under increased CO_2 concentration and temperature: long-term vs. short-term distinctions for modelling, Glob. Change Biol. 1 (1995) 385–396.

[39] Godin C., Costes E., Caraglio Y. Exploring plant topological structure with the AMAPmod software: an outline, Silva Fennica 31 (1997) 357–368.

[40] Grossman Y.L., DeJong T.M., PEACH: A simulation model of reproductive and vegetative growth in peach trees, Tree Physiol. 14 (1994) 329–345.

[41] Hauhs M., Kastner-Maresch A. And Rost-Siebert K., A model relating forest growth to ecosystem-scale budgets of energy and nutrients, Ecol. Modelling 83 (1995) 229–243.

[42] Hilbert D.W., Reynolds J.F., A model allocating growth among leaf proteins, shoot structure, and root biomass to produce balanced activity, Ann. Bot. 68 (1991) 417–425.

[43] Host G.E., Rauscher H.M., Isebrands J.G., Dickmann D.I., Dickson R.E., Crow T.R., Michael D.A., The ECOPHYS user's manual, microcomputer scientific software series #6, USDA Forest Service, St Paul, MN, Gen. Tech. Rep. NC-141, 1990, 50 p.

[44] Host G.E., Rauscher H.M., Isebrands J.G., Michael D.A., Validation of photosynthate production in ECOPHYS, an ecophysiological growth process model of *Populus*, Tree Physiol. 7 (1990) 283–296.

[45] Isebrands J.G., Rauscher H.M., Crow T.R., Dickmann D., Whole-tree growth process models based on structural-functional relationships, in: Dixon R.K., Meldahl R.S., Ruark G.A., Warren W.G. (Eds.), Process modelling of forest growth responses to environmental stress, Timber Press, Portland, OR, 1990, pp. 96–112.

[46] Jarvis P.G., The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field, Phil. Trans. R. Soc. London B, 273 (1976) 593–610.

[47] Jarvis P.G., Leverenz J.W., Productivity of temperate, deciduous and evergreen forests, in: Lange O.L., Nobel P.S., Osmond C.B., Ziegler H. (Eds.), Physiological Plant Ecology IV, Springer-Verlag, Berlin, 1983, pp. 233–280.

[48] Johnson I.R., Plant respiration in relation to growth, maintenance, ion uptake and nitrogen assimilation, Plant Cell. Env. 13 (1990) 319–328.

[49] Johnson R.S., Lakso A.N., Carbon balance model of a growing apple shoot: I. Development of the model, J. Amer. Soc. Hort. Sci. 111 (1986) 160–164.

[50] Johnson I.R., Thornley J.H.M., A model of shoot-root partitioning with optimal growth, Ann. Bot. 60 (1987) 133–142.

[51] Kellomaki S., Strandman H., A model for the structural growth of young Scots pine crowns based on light interception by shoots, Ecol. Modelling 80 (1995) 237–250.

[52] Kirschbaum M.U.F., King D.A., Comins H.N., McMurtrie R.E., Medlyn B.E., Pongracic S., Murty D., Keith H., Raison R.J., Khanna P.K., Sheriff D.W., Modelling forest response to increasing CO_2 concentration under nutrient-limited conditions, Plant Cell Env. 17 (1994) 1081–1099.

[53] Kirschbaum M.U.F., CenW, a forest growth model with linked carbon, energy, nutrient and water cycles, Ecol. Modelling 118 (1999) 17–59.

[54] Kozlowski T.T., Carbohydrate sources and sinks in woody plants, Bot. Rev. 58 (1992) 107–222.

[55] Kozlowski T.T., Keller T., Food relations of woody plants, Bot. Rev. 32 (1966) 293–382.

[56] Küppers M., Ecological significance of aboveground patterns in woody plants: a question of cost-benefit relationships, Tree 4 (1989) 375–379.

[57] Kurth W., Morphological models of plant growth: Possibilities and ecological relevance, Ecol. Modelling 75/76 (1994) 299–308.

[58] Lacointe A., Kajji A., Améglio T., Daudet F.A., Cruiziat P., Archer P., Frossard J.S., Storage and mobilization of carbon reserves in walnut and its consequences on the water status during dormancy, Acta Hort. 311 (1993) 201–209.

[59] Lacointe A., Sauter J.J., Améglio T., Harms U., Pellicer V., Frossard J.S., Carbohydrate and protein reserves in trees, in: Sandermann H., Bonnet-Masimbert M. (Eds.), EUROSILVA contribution to forest tree physiology, INRA (Les Colloques n°76), Paris, 1995, pp. 273–296.

[60] Lacointe A., Carbon allocation among tree organs: a review of basic processes and representation in functional-structural tree models, Ann. For. Sci. 57 (2000) 521–534.

[61] Lambers H., Szaniawski R.K., de Visser R., Respiration for growth, maintenance and ion uptake. An evaluation of concepts, methods, values and their significance, Physiol. Plant. 58 (1983) 556–563.

[62] Landsberg J.J., Physiological ecology of forest production, Academic Press, London, 1986, 198 p.

[63] Landsberg J.J., Kaufmann M.R., Binkley D., Isebrands J., Jarvis P.G. Evaluating progress toward closed forest models based on fluxes of carbon, water and nutrients, Tree Physiol. 9 (1991) 1–15.

[64] Landsberg J.J., Waring R.H. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning, For. Ecol. Manage. 95 (1997) 209–228.

[65] Le Dizès S., Cruiziat P., Lacointe A., Sinoquet H., Le Roux X., Balandier P, Jacquet P., A model for simulating structure-function relationships in walnut tree growth processes, Silva Fennica 31 (1997) 313–328.

[66] Le Roux X., Grand S., Dreyer E., Daudet F.A., Parameterization and testing of a biochemically-based photosynthesis model in walnut (*Juglans regia* L.) trees and seedlings, Tree Physiol. 19 (1999) 181–188.

[67] Le Roux X., Sinoquet H., Vandame M., Spatial distribution of leaf weight per area and leaf nitrogen concentration in relation to local radiation regime within an isolated tree crown, Tree Physiol. 19 (1999) 481–492.

[68] Le Roux X., Walcroft A.S., Daudet F.A., Sinoquet H., Chaves M.M., Rodriguez A., Osorio L., Photosynthetic light acclimation in peach leaves: importance of changes in mass: area ratio, nitrogen concentration, and leaf nitrogen partitioning, Tree Physiol. 21 (2001) 377–386.

[69] Lescourret F., Ben Mimoun M., Génard M., A simulation model of growth at the shoot-bearing fruit level. I. Description and parameterization for peach, Eur. J. Agron. 9 (1998) 173–188.

[70] Lohammar T., Larsson S., Linder S., Falk S.O., FAST–Simulation models of gaseous exchange in Scotch pine, in: Persson T. (Ed.), Structure and function of northern coniferous forests. An ecosystem study (Ecol. Bull. 32), Swed. Nat. Res. Counc., Stockholm, 1980, pp. 505–523.

[71] Luan J., Muetzelfeldt R.I., Grace, J., Hierarchical approach to forest ecosystem simulation, Ecol. Modelling 86 (1996) 37–50.

[72] Mäkelä A., Partitioning coefficients in plants models with turn-over, Ann. Bot. 57 (1986) 291–297.

[73] Mäkelä A., Hari P., Stand growth model based on carbon uptake and allocation in individual trees, Ecol. Modelling 33 (1986) 204–229.

[74] Mäkelä A., Modelling structural functional relationships in whole-tree growth resource allocation, in: Dixon R., Meldahl R., Ruark G., Warren W. (Eds.), Process modelling of forest growth responses to environmental stress, Timber press, Portland, Oregon, 1990, pp. 81–95.

[75] Mäkelä A., A carbon balance model of growth and self-pruning in trees based on structural relationships, For. Sci. 43 (1997) 1, 7–23.

[76] Marcelis L.F.M., Simulation of biomass allocation in greenhouse crops – a review, Acta Hort. 328 (1993) 49–68.

[77] Mata C., Scheurwater I., Martins-Louçào M.A., Lambers H., Root respiration, growth and nitrogen uptake of *Quercus suber* seedlings, Plant Physiol. Biochem. 34 (1996) 727–734.

[78] McCree K.J., An equation for the rate of respiration of white clover plants grown under controlled conditions, Proceedings of the technical meeting IBP, Trebon (CSK), 1969, Centre for Agricultural Publishing and Documentation, Wageningen, (NDL), 1970, pp. 221–229.

[79] McCree K.J., Measuring the whole-plant daily carbon balance, Photosynthetica 20 (1986) 82–93.

[80] McMurtrie R., Wolf L., Above and below ground growth of forest stands: a carbon budget model, Ann. Bot. 52 (1983) 437–448.

[81] Millard P., Ecophysiology of the internal cycling of nitrogen for tree growth, J. Plant. Nutr. Soil. Sci. 159 (1996) 1–10.

[82] Minchin P.E.H., Thorpe M.R., Farrar J.F., A simple mechanistic model of phloem transport which explains sink priority, J. Exp. Bot. 44 (1993) 947–955.

[83] Mohren G.M.J., Burkhart H.E., Contrasts between biologically-based process models and management-oriented growth and yield models, For. Ecol. Manage 69 (1994) 1–5.

[84] Mohren G.M.J., van de Veen J.R., Forest growth in relation to site conditions. Application of the model FORGRO to the Solling spruce site, Ecol. Modelling 83 (1995) 173–183.

[85] Monteith J.L., Solar radiation and productivity in tropical ecosystems, J. Appl. Ecol. 2 (1972) 747–766.

[86] Moravie M.-A., Pascal J.P., Auger P., Investigating canopy regeneration processes through individual-based spatial models: application to a tropical rain forest, Ecol. Modelling 104 (1997) 241–260.

[87] Münch E., Die Stoffbewegungen in den Pflanzen, Gustav Fischer, Jena, 1930, 234 p.

[88] Nikinmaa E., Analyses of the growth of Scots pine; matching structure with function, Acta For. Fennica 235 (1992) 1–68.

[89] Pacala S.W., Canham C.D., Silander J.A., Forest models defined by field measurements: I. The design of a northeastern forest simulator, Can. J. For. Res. 23 (1993) 1980–1988.

[90] Pagès L., Doussan C., Vercambre G., An introduction on below-ground environment and resource acquisition, with special reference on trees. Simulation models should include plant structure and function, Ann. For. Sci. 57 (2000) 513–520.

[91] Penning de Vries F.W.T., Brunsting A.H.M., van Laars H.H., Products, requirements and efficiency of biosynthesis: a quantitative approach, J. Theor. Biol. 45 (1974) 339–377.

[92] Penning de Vries F.W.T., The cost of maintenance processes in plant cells, Ann. Bot. 39 (1975) 77–92.

[93] Perttunen J., Sievänen R., Nikinmaa E., Salminen H., Saarenmaa H., Väkevä J., LIGNUM: A tree model based on simple structural units, Ann. Bot. 77 (1996) 87–98.

[94] Perttunen J., Sievänen R., Nikinmaa E., LIGNUM: A model combining the structure and functioning of trees, Ecol. Modelling 108 (1998) 189–198.

[95] Poorter H., van der Werf A., Atkin O.K., Lambers H., Respiratory energy requirements of roots vary with the potential growth rate of a plant species, Physiol. Plant. 83 (1991) 469–475.

[96] Prentice I.C., Leemans R., Pattern and process and the dynamics of forest structure: a simulation approach, J. Ecol. 78 (1990) 340–355.

[97] Prentice I.C., Sykes M.T., Cramer W., A simulation model for the transient effects of climate change on forest landscapes, Ecol. Modelling 65 (1993) 51–70.

[98] Proe M.F., Dutch J., Miller H.G., Sutherland J., Long-term partitioning of biomass and nitrogen following application of nitrogen fertilizer to Corsican pine, Can. J. For. Res. 22 (1992) 82–87.

[99] Proe M.F., Millard P., Relationship between nutrient supply, nitrogen partitioning and growth in young Sitka spruce (*Picea sitchensis* (Bong.) Carr.), Tree Physiol. 14 (1994) 75–88.

[100] Promnitz L.C., A photosynthate allocation model for tree growth, Photosynthetica 9 (1975) 1–15.

[101] Prusinkiewicz P., Remphrey W., Davidson C., Hammel M., Modeling the architecture of expanding *Fraxinus pennsylvanica* shoots using L-systems, Can. J. Bot. 72 (1994) 701–714.

[102] Rauscher H.M., Isebrands J.G., Host G.E., Dickson R.E., Dickmann D.I., Crow T.R., Michael D.A., ECOPHYS: An ecophysiological growth process model for juvenile poplar, Tree Physiol. 7 (1990) 255–281.

[103] Reffye (de) P., Fourcaud T., Blaise F., Barthélémy D., Houllier F., A functional model of tree growth and tree architecture, Silva Fennica 31 (1997a) 297–311.

[104] Reffye (de) P., Houllier F., Blaise F., Fourcaud T., Essai sur les relations entre l'architecture d'un arbre et la grosseur de ses axes végétatifs, in: Bouchon J., Reffye (de) P., Barthélémy D. (Eds.), Modélisation et simulation de l'architecture des végétaux, INRA Éditions, Paris, 1997, pp. 255–423.

[105] Reynolds J.F., Thornley J.H.M., A shoot-root partitioning model, Ann. Bot. 49 (1982) 587–597.

[106] Reynolds J.F., Acock B., Modularity and genericness in plant and ecosystem models, Ecol. Modelling 94 (1997) 7–16.

[107] Ruget F., Respiration de croissance et d'entretien: méthodes de mesure, comparaison des résultats, Agronomie 7 (1981) 601–610.

[108] Ryan M.G., Hubbard R.M., Clark D.A., Sanford R.L., Woody-tissue respiration for Simarouba amara and Minquartia guianensis, two tropical wet forest trees with different growth habits, Oecologia 100 (1994) 213–220.

[109] Ryan M.G., Foliar maintenance respiration of subalpine and boreal trees and shrubs in relation to nitrogen content, Plant Cell Env. 18 (1995) 765–772.

[110] Ryan M.G., Hubbard R.M., Pongracic S., Raison R.J., McMurtrie R.E., Foliage, fine-root, woody-tissue and stand respiration in Pinus radiata in relation to nitrogen status, Tree Physiol. 16 (1996) 333–343.

[111] Ryan M.G., Gower S.T., Hubbard R.M., Waring R.H., Gholz H.L., Cropper W.P., Running S.W., Woody tissue maintenance respiration of four conifers in contrasting climates, Oecologia 101 (1995) 133–140.

[112] Ryugo K., Nii N., Iwata M., Carlson R.M., Effect of fruiting on carbohydrate and mineral composition of stems and leaves of French prunes, J. Amer. Soc. Hort. Sci. 102 (1977) 813–816.

[113] Scholes R. J., Archer S. R., Tree-Grass interactions in savannas, Annu. Rev. Ecol. Syst. 28 (1997) 517–544.

[114] Shinozaki K., Yoda K., Hozumi K., Kira T., A quantitative analysis of plant form: the pipe model theory. I. Basic analyses, Jap. J. Ecol. 14 (1964) 97–105.

[115] Shinozaki K., Yoda K., Hozumi K., Kira T., A quantitative analysis of plant form: the pipe model theory. II. Further evidence of the theory and its application in forest ecology, Jap. J. Ecol. 14 (1964) 133–139.

[116] Simioni G., Le Roux X., Gignoux J., Sinoquet H., TREEGRASS: a 3D, process-based model for simulating plant interactions in tree-grass ecosystems, Ecol. Modelling 131 (2000) 47–63.

[117] Sinoquet H., Le Roux X., Short-term interactions between tree foliage and the aerial environment: an overview of modelling approaches available for tree structure-function models, Ann. For. Sci. 57 (2000) 477–496.

[118] Sinoquet H., Le Roux X., Adam B., Améglio T., Daudet F.A., RATP: a model for simulating the spatial distribution of radiation absorption, transpiration and photosynthesis within vegetation canopies: application to an isolated tree crown, Plant Cell Env. 24 (2001) 395–406.

[119] Sievänen R., Nikinmaa E., Nygren P., Ozier-Lafontaine H., Perttunen J., Hakula H., Components of functional-structural tree models, Ann. For. Sci. 57 (2000) 399–412.

[120] Sorrensen-Cothern K.A., Ford E.D., Sprugel D.G., A model of competition incorporating plasticity through modular foliage and crown development, Ecol. Monogr. 63 (1993) 227–304.

[121] Sprugel D.G., Components of woody-tissue respiration in young Abies amabilis trees, Trees 4 (1990) 88–98.

[122] Sprugel D.G., Benecke U., Woody-tissue respiration and photosynthesis, in: Lassoie J.P., Hinckley T.M. (Eds.), Technics and approaches in forest tree ecophysiology, CRC Press, Boca Raton, FL, USA, 1991, pp. 329–347.

[123] Takenaka A., A simulation model of tree architecture development based on growth response to local light environment, J. Plant Res. 107 (1994) 321–330.

[124] Thornley J.M.H, Respiration, growth and maintenance in plants, Nature 227 (1970) 304–305.

[125] Thornley J.H.M, A model to describe the partitioning of photosynthates during vegetative plant growth, Ann. Bot. 36 (1972) 419–430.

[126] Thornley J.H.M., A balanced quantitative model for root: shoot ratios in vegetative plants, Ann. Bot. 36 (1972) 431–441.

[127] Thornley J.H.M., Mathematical models in plant physiology, Academic Press, London, 1976, 318 p.

[128] Thornley J.H.M., A transport-resistance model of forest growth and partitioning, Ann. Bot. 68 (1991) 211–226.

[129] Thornley J.H.M., Shoot: Root allocation with respect to C, N and P: an investigation and comparison of resistance and teleonomic models, Ann. Bot. 75 (1995) 391–405.

[130] Thornley J.H.M., Modelling allocation with transport/conversion processes, Silva Fennica 31 (1997) 341–355.

[131] Tiktak A., van Grinsven H.J.M., Review of sixteen forest-soil-atmosphere models, Ecol. Modelling 83 (1995) 35–53.

[132] Tromp J., Nutrient reserves in roots of fruit trees, in particular carbohydrates and nitrogen, Plant Soil 71 (1983) 401–413.

[133] Valentine H.T., Tree growth models: Derivations employing the pipe model theory, J. Theor. Biol. 117 (1985) 579–585.

[134] Walters M.B., Reich P.B., Low-light carbon balance and shade tolerance in the seedlings of woody plants: do winter deciduous and broad-leaved evergreen species differ?, New Phytol. 143 (1999) 143–154.

[135] Wang Y.P., Jarvis P.G., Description and validation of an array model– MAESTRO, Agric. For. Meteorol. 51 (1990) 257–280.

[136] Wargo P.M., Starch storage and radial growth in woody roots of sugar maple, Can. J. For. Res. 9 (1979) 49–56.

[137] Warren-Wilson J., Control of crop processes in controlled environment, in: Rees A.R., Cockshull K.E., Hand D.W., Hurd R.G. (Eds.), Heinemann, London, 1972, pp. 76–88.

[138] Webb W.L., Atmospheric CO_2, climate change, and tree growth: a process model. I. Model structure, Ecol. Modelling 56 (1991) 81–107.

[139] Weinstein D.A., Yanai R.D., Beloin R., Zollweg C.G., The response of plants to interacting stresses: TREGRO Version 1.74 – description and parameter requirements, Electric Power Res. Institute, Palo Alto, CA, 1992, 73 p.

[140] Weinstein D.A., Yanai R.D., Integrating the effects of simultaneous multiple stresses on plants using the simulation model TREGRO, J. Env. Quality 23 (1994) 418–428.

[141] Wermelinger B., Baumbärtner J., Gutiérrez A.P., A demographic model of assimilation and allocation of carbon and nitrogen in grapevines, Ecol. Modelling 53 (1991) 1–26.

[142] West P.W., Model of above-ground assimilate partitioning and growth of individual trees in even aged forest monoculture, J. Theor. Biol. 161 (1993) 369–394.

[143] West P.W., Wells K.F., Method of application of a model to predict the light environment of individual tree crowns and its use in a eucalypt forest, Ecol. Modelling 60 (1992) 199–231.

[144] Williams M., A three-dimensional model of forest development and competition, Ecol. Modelling 89 (1996) 73–98.

[145] Wilson J.B., A review of evidence on the control of shoot: root ratio, in relation to models, Ann. Bot. 61 (1988) 433–449.

[146] Yoder B.J., Ryan M.G., Waring R.H., Schottle A.W., Kaufmann M.R., Evidence of reduced photosynthetic rates in old trees, For. Sci. 40 (1994) 513–527.

[147] Zhang Y., Reed D.D., Cattelino P.J., Gale M., Jones E.A., Liechty H.O., Mroz G.D., A process-based growth model for young red pine, For. Ecol. Manage. 69 (1994) 21–40.

[148] Ziegler H., Storage, mobilisation and distribution of reserve material in trees, in: Zimmermann M.H. (Ed.), The formation of wood in forest trees, Academic Press, New-York, 1964, pp. 303–320.