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Forest carbon allocation modelling under climate change

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Abstract

Carbon allocation plays a key role in ecosystem dynamics and plant adaptation to changing climate. Hence, proper description of this process in dynamic vegetation models is crucial for the simulations of the impact of environmental conditions on carbon cycling in forests under ongoing climate change. Here we review carbon allocation modelling in 31 dynamic vegetation models and address main knowledge gaps in the modelled description. We found that although the number of carbon allocation studies emerging over the last 10 years has substantially increased, some background processes are still insufficiently understood, and some issues in models are frequently oversimplified or even omitted. Hence, current challenges for carbon allocation modelling in forest ecosystems are (i) to overcome remaining limits in process understanding, particularly regarding the impact of disturbances on carbon allocation, accumulation and utilisation of non-structural carbohydrates, and carbon use by symbionts, and (ii) to implement existing knowledge to mechanistic description of carbon allocation in models that would integrate the impact of environmental conditions, disturbances, and seasonal variation in carbon allocation, or (iii) to improve more simplistic models by accounting for the impact of crucial factors affecting carbon allocation in particular environment.

Keywords: carbon partitioning, fixed ratio, natural resources, natural disturbances, non-structural carbohydrates, reproduction, mycorrhiza, repair and defence function, temporal resolution, model calibration

THE1

1. Introduction

Process-oriented ecosystem models are widely and intensively used for simulating long-term tree and/or forest stand growth (Bohn et al. 2014, Lonsdale et al. 2015), as well as for forecasting carbon and vegetation dynamics using different climate scenarios (Peters et al. 2013, Gutiérrez et al. 2014, Sánchez-Salguero et al. 2016), because they can predict water, carbon and nutrient flows within ecosystems. However, our understanding of the processes governing these flows is patchy (Garcia et al. 2016), with some being understood in much more detail than others. Carbon accumulation in the structural and non-structural components of vegetation, for example, depends on a variety of processes such as photosynthesis, respiration, and allocation into different compartments, including those for defence and reproduction (Xia et al. 2017). In particular regarding the latter aspect, it has been noted that ecosystem models often use rather simple descriptions of carbon allocation based on a huge array of principles (Franklin et al. 2012, Mäkelä 2012).

However, carbon allocation of vegetation plays a critical role for the carbon exchange between atmosphere and biosphere (Litton et al. 2007). It is considered one of the most important plant adaptation mechanisms to environmental changes (Yan et al. 2016). Although the processes driving carbon partitioning to individual plant organs are still not thoroughly understood, experimental results suggest that carbon allocation depends on species, environmental conditions, and stand structure (Poorter et al. 2011, Vicca et al. 2012). The carbon that vegetation allocates to structural components has longer residence time compared to those that are allocated to leaves and fine roots (Campioli et al. 2008). Hence, if the ratio between fast and slow turnover compartments changes in response to altered resource availability and stress intensity, future predictions of carbon feedbacks between biosphere and atmosphere that do not account for this change may be biased (Friend et al. 2013, Lehtonen and Heikkinen 2015). Therefore, sophisticated carbon allocation modelling approaches are required to better understand the effects of changes in climate, air chemistry and forest management on terrestrial ecosystems.

In the presented study we analyse the results from a questionnaire-based survey of 31 dynamic vegetation models (DVM) from forest stand-scale to global models. Our specific objectives are (i) to review the current state of art in carbon allocation modelling in dynamic vegetation models, and (ii) to highlight challenges and possibilities to improve carbon allocation in DVMs in the context of climate change.

2. Material and Methods

In our study we adopted a general view on the carbon allocation terms presented by (Litton et al. 2007), which encompass both the pattern of biomass distribution among individual tree components and the process of carbon partitioning, i.e. the flux of carbon to a particular tree component per unit time defined as biomass increment.

2.1. Questionnaire survey and database creation

The questionnaire (Supplementary A) was prepared by a working group of the COST Action network project “Towards robust PROjections of European FOrests UNDer climate change” (PROFOUND) as a web based survey. It consisted of both open-ended and closed-ended questions divided into three main parts.

The first part of the questionnaire dealt with the general description of the whole modelling system, which comprises the carbon allocation model. It consisted of 14 questions including the queries about the applied modelling concept, simulated ecosystems, modelled object, and temporal and spatial resolution. The questions were based on the forest growth model classification (Fabrika and Pretzsch 2011).

The second part comprised 25 questions about the allocation model implemented in the modelling system, gathering information about the applied principles and types of carbon allocation modelling, temporal and spatial scales of the models, compartments used for carbon allocation in the models, factors affecting carbon allocation in the model, model sensitivity to environmental conditions, the reasons for selecting a particular approach to modelling carbon allocation, and the main issues of carbon allocation modelling the researchers have identified when simulating forest ecosystems. The principles and the types of carbon allocation models were taken from the previous works (Lacointe 2000, Fabrika and Pretzsch 2011, Franklin et al. 2012, de Kauwe et al. 2014).

The third part served for collecting the data on reference sources and comprised 11 questions. Hence, in total the questionnaire consisted of 50 questions. Out of 33 closed-ended questions 6 were dichotomous and 27 were multiple choice questions, while in 10 cases a single answer was required, and in the remaining 17 questions multiple answers were allowed. The whole questionnaire is presented in Supplementary Material A.

The invitations to participate in the survey were distributed by email using the initial list of the participants of the PROFOUND COST Action as well as the COST Action "Climate Change Manipulation Experiments in Terrestrial Ecosystems - Networking and Outreach" (ClimMani) and further forwarded to relevant model developers and model users based on personal contacts of participants. In total we invited approximately 260 scientists. The participation to the survey was voluntary. The survey was open from November 11, 2016 to January 31, 2017.

In total, we gathered 40 responses with the information about carbon allocation modelling approaches implemented in 31 different models (Table 1). This number of models reflects the number of complex vegetation based models found in preceding studies focusing on a similar pool of models (Fontes et al. 2010). At the time of the survey, the models were applied in 17 different countries around the world (Figure 1). The applied modelling approaches varied from the point of temporal, spatial and modelled units defined by Fabrika and Pretzsch (2011, see Figure 2).

The collected responses were checked for consistency and stored in Microsoft Access database. In the case of ambiguous replies, these were cross-checked with references and model developers and/or users who had filled in the questionnaire.

Table 1. List of examined models

Name of the model	Modelling approach	Dominant modelling concept	Applied types of carbon allocation	References
3D-CMCC FEM	hybrid	process-based	allometry, resource limitation	(Arora and Boer 2005), (Lüdeke et al. 1994), (Collalti et al. 2014)
3PG-BW	hybrid	process-based	allometry, resource limitation	(Landsberg and Waring 1997)
ANAFORE	hybrid	process-based	pipe model, resource limitation, source-sink model	(Deckmyn et al. 2008)
BALANCE	hybrid	process-based	pipe model, source-sink model, root-shoot functional balance	(Rötzer et al. 2010), (Rötzer et al. 2012), (Grote and Pretzsch 2002)
BASFOR	hybrid	process-based	fixed ratios, resource limitation, source-sink model, root-shoot functional balance	(Van Oijen et al. 2005)
Biome-BGC	process-based	process-based	fixed ratios	(Thornton et al. 2005)
Biome-BGCMuSo	process-based	process-based	fixed ratios	(Hidy et al. 2016), (Running and Hunt 1993)
CARAIB	process-based	process-based	fixed ratios	(Warnant et al. 1994)
CASTANEA	process-based	process-based	allometry, pipe model, resource limitation	(Dufrêne et al. 2005), (Guillemot et al. 2016)
CENTURY	process-based	process-based	fixed ratios, resource limitation	(Parton et al. 1987), (Allister et al. 1993)
Community Land	hybrid	process-based	allometry, resource limitation	(Oleson et al. 2013), (Fan et al. 2015)

Model (CLM4.5)				
CoupModel	hybrid	process-based	allometry, fixed ratios, optimal response, resource limitation, transport-resistance	(Eckersten and Jansson 1991), (de Willigen 1991), (Jansson and Karlberg 2004), (Svensson et al. 2008)
ED2	hybrid	process-based	allometry, fixed ratios, pipe model	(Medvigy et al. 2009), (Hurtt et al. 2013)
FORESEE (4C)	hybrid	process-based	allometry, pipe model	(Bugmann et al. 1997)
ForGEM	empirical	empirical	allometry	(Kramer et al. 2015), (Kramer and Werf 2010), (Kramer et al. 2008)
FORMIND	process-based	process-based	allometry	(Bohn et al. 2014)
GO+	hybrid	process-based	allometry, optimal response, resource limitation	(Loustau 2010)
GO+TreeStabd	hybrid	structural	allometry	(Bosc 2013), (Loustau et al. 2005)
GOTILWA+	process-based	process-based	pipe model, source-sink model	(Keenan et al. 2009), (Shinozaki et al. 1964)
Heterofor	hybrid	empirical	allometry, root-shoot functional balance	(Jonard and André 2018)
iLand	hybrid	process-based	allometry, root-shoot functional balance	(Seidl et al. 2012)
Klein & Hoch	process-based	process-based	source-sink model	(Klein and Hoch 2014)
LANDIS-II	hybrid	process-based	allometry, fixed ratios, resource limitation	(Scheller et al. 2011)
LandscapeDNDC	hybrid	process-based	pipe model, source-sink model	(Grote et al. 2011), (Grote and Reiter 2004), (Grote 1998)
LIGNUM	hybrid	process-based	allometry, pipe model, source-sink model	(Sievänen et al. 2008), (Perttunen et al. 1998)
LPJ-GUESS	hybrid	process-based	allometry, fixed ratios, pipe model, resource limitation, root-shoot functional balance	(Smith et al. 2001), (Smith et al. 2014), (Sitch et al. 2003)
ORCHIDEE-CAN	hybrid	process-based	allometry, pipe model, source-sink model	(Naudts et al. 2015)
PICUS	hybrid	process-based	allometry, pipe model, source-sink model	(Lexer and Hönninger 2001), (Seidl et al. 2007), (Seidl et al. 2009), (Seidl et al. 2005)
PnET	hybrid	empirical	fixed ratios, pipe model	(Aber and Federer 1992)
SIBYLA	empirical	empirical	allometry	(Fabrika 2005), (Fabrika and Ďurský 2006), (Fabrika and Pretzsch 2011)
TreeMig	hybrid	process-based	fixed ratios	(Lischke et al. 2006), (Bugmann 1994)

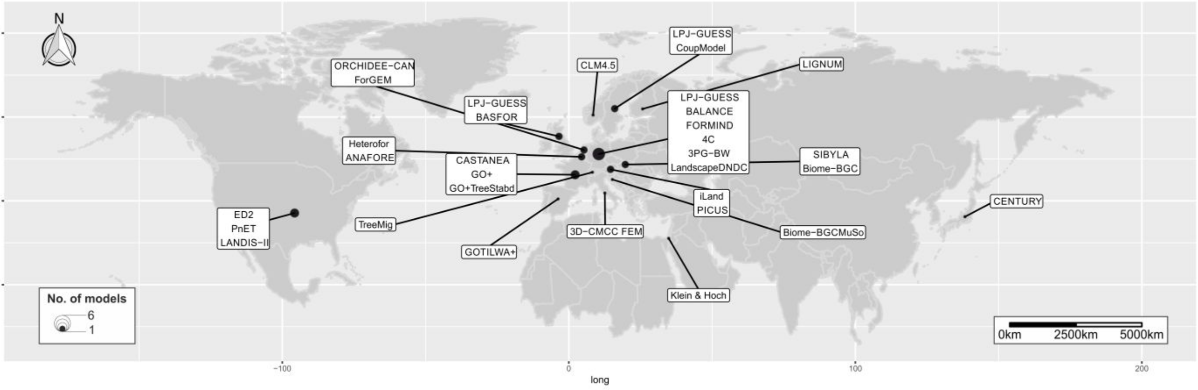


Figure 1. Distribution of the models included in our analysis on the base of their application in particular countries.

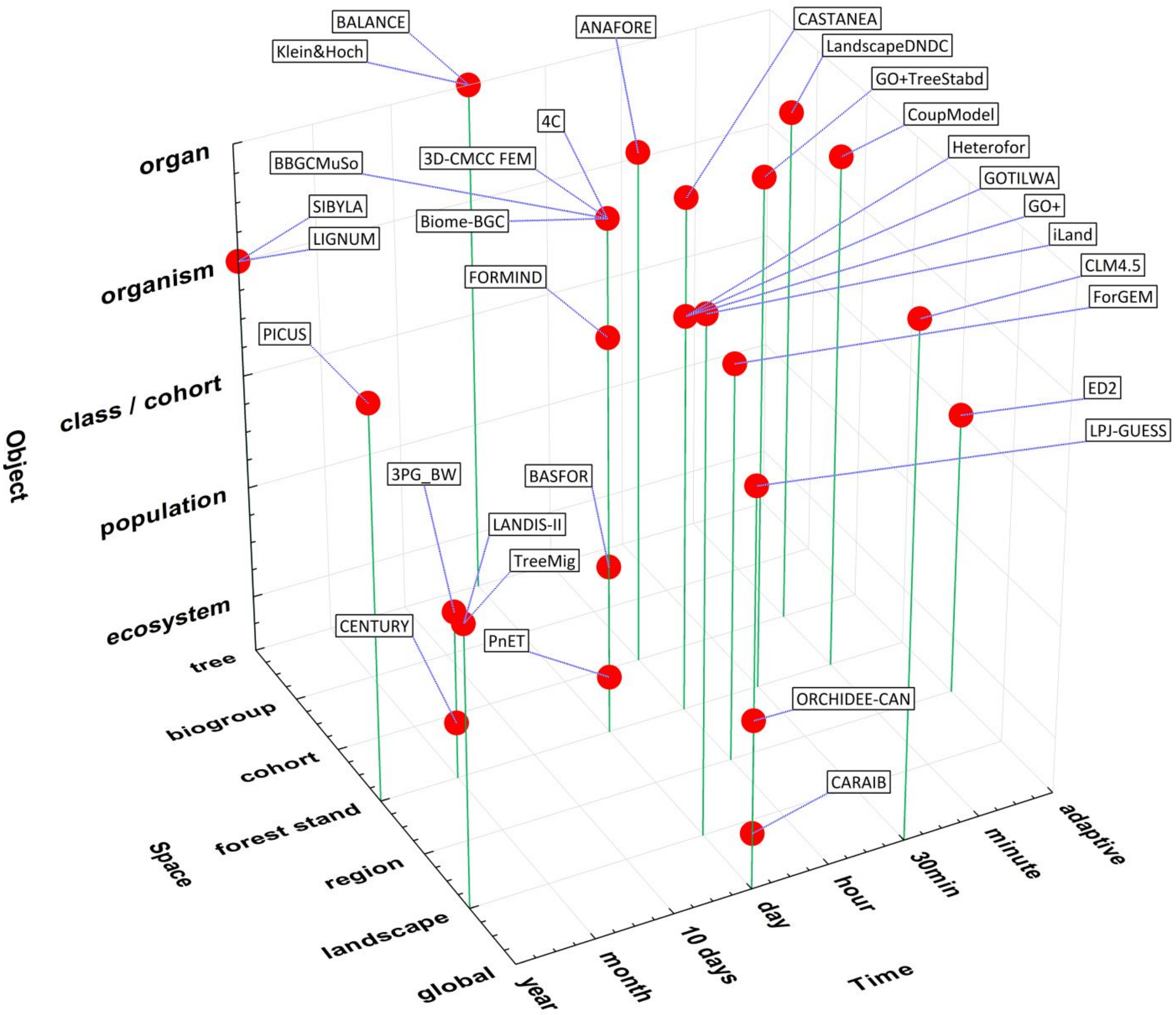


Figure 2. Model classification based on their temporal and spatial modelling scale and the modelled object.

2.2. Analysis of the gaps

The questionnaire contained two questions (2.13. and 2.13.1. in Supplementary A), asking the respondents to specify any problems and knowledge gaps they have encountered when modelling carbon allocation. From all the entries to question 2.13.1. (Supplementary A) we selected the most frequent gaps in the representation of carbon allocation in forest growth models identified by the respondents, and analysed them in 3 steps:

I. Identification of the gap
II. Evidence to prove the gap
III. Approaches and examples to overcome the gap

The existence of the gap was further examined using the responses on other related questions from the second part of the questionnaire (questions 2.1. to 2.12.). We were primarily concerned with the frequency of the gap, i.e. in how many models the identified problem may potentially occur because of the model settings. The evidence of the identified gaps was justified by a literature review to independently confirm the relevance of each modeling gap for accurate modeling of carbon allocation using published empirical evidence. In the next step we examined possible modelling approaches to overcome the identified gaps. This was performed based on the characteristics of the models in the database in combination with the literature review of other existing modelling approaches. The relevant literature sources were searched online using the databases of Elsevier Scopus©, ISI Web of Knowledge©, CAB Abstract©, and Google Scholar©. The material was selected by searching for the term "carbon allocation" and its synonyms identified by Litton et al. (2007) in combination with the terms "model or modelling" in the title, abstract, and/or keywords of published papers, and further examining the references in the selected papers. We selected only works referring either to experimental studies or to modelling experiences that justified and/or solved one or more identified gaps in carbon allocation modelling.

3. Results

3.1. Approaches of carbon allocation modelling

We found that 15 models (i.e. 48%) out of the total 31 models used a single principle of carbon allocation modelling defined by Franklin et al. (2012, Table 2), while 16 models were hybrid ones. Out of these, 11 models combined two principles, 4 models combined three principles, and 1 model (CoupModel) combined four different principles of carbon allocation modelling (Figure 3). Combining more principles of carbon allocation is not new, as it has already been reported by Lacointe (2000). Empirically defined carbon allocation was the most common principle used in 19 models (61%), followed by the principles of functional relationship and functional balance applied in 16 models (52%) each. Eco-evolutionarily-based types of carbon allocation modelling were used in three models (CLM 4.5, CoupModel, GO+), and the thermodynamic principle was not used in any of the investigated models. The use of individual types of carbon allocation modelling, which represent a lower level of carbon allocation modelling classification is presented in Figure 4. Note that the number of models based on a single type of carbon allocation modelling is lower than those based on a single principle of carbon allocation modelling, as in some models more types of the same principle were applied (for an example see Figure 3).

Table 2. Description of principles and types of carbon allocation modelling

ID of carbon allocation principle	**Principle of carbon allocation modelling**	**Basic description**	**Computation efficiency**	**Variation of carbon allocation with size/age**	**Variation of carbon allocation with environment**	**Feedback between plant´s strategy and environment**
1	Empirical	carbon allocation is based on constant statistical relationships among individual organs	high	no	no	no
2	Functional relationship	carbon allocation is defined by allometric functions describing relationships among plant organs	high	yes	no	no
3	Functional balance	carbon is allocated to maintain internal balance between organs according to an optimum internal status of resource or element ratio	moderate	yes	yes	no
4	Eco-evolutionarily-based	carbon is allocated in order to maximise a fitness proxy	low	yes	yes	yes
5	Thermodynamic	carbon is allocated in order to maximise entropy or entropy production	moderate	yes	yes	yes
	Type of carbon allocation modelling					

1	Fixed ratios	fixed fractions of assimilated carbon are allocated to individual organs	high	no	no	no
1 (2)	Allometry	carbon is allocated to a particular organ according to mass and size relationships	high	yes	no	no
2 (3)	Pipe model	carbon is allocated in order to provide the (sapwood) conductance necessary to support foliage	high	yes	no/yes	no
3	Root-shoot functional balance	carbon is allocated to individual organs to ensure a balanced supply of resources from foliage and fine roots	moderate	yes	yes	no
3	Resource limitation	allocation of assimilated carbon to individual organs is driven by the most limiting source to growth	moderate	no/yes	yes	no
3	Source-sink model	allocation of assimilated carbon to individual organs is driven by the demands of individual organs and the availability of assimilates	moderate	yes	yes	no
3	Transport resistance	allocation of assimilated carbon is controlled by concentration gradients of elements/compounds between plant parts	low	yes	yes	no
4	Optimal response	selects an optimal allocation strategy that maximises a predefined goal (fitness proxy) when there is a significant competition only for one resource	low	yes	yes	no
4	Game-theoretic optimisation	selects an optimal allocation strategy that maximises a predefined goal (fitness proxy) when there is a significant competition for more than one resource	low	yes	yes	yes
4	Adaptive dynamics	selects an optimal allocation strategy that maximises a goal (fitness proxy), which is dynamically selected	low	yes	yes	yes
5	Maximum entropy production	selects the most probable allocation strategy that maximises entropy under given environmental and internal constraints	moderate	yes	yes	yes
5	Maximum entropy	predicts the most probable allocation strategy and the frequency distribution of different strategies (allocation patterns) around the most probable strategy under given environmental and internal constraints	moderate	yes	yes	yes

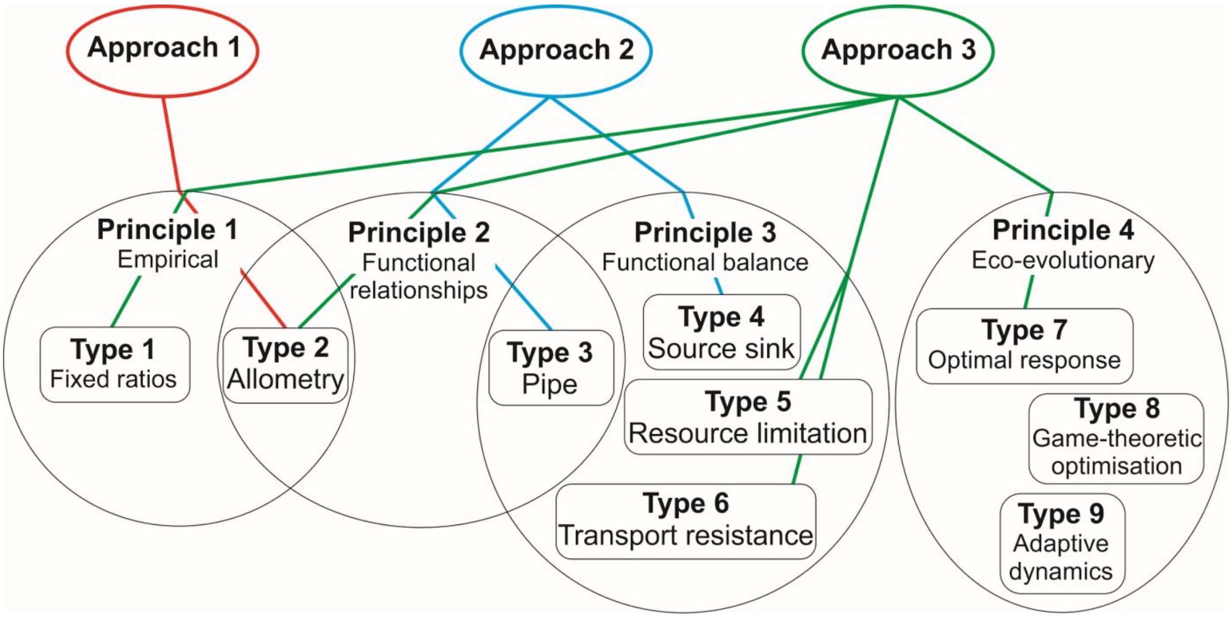


Figure 3. Examples of applied approaches using different principles and types of carbon allocation modelling in three different models: approach 1 applied in SIBYLA, approach 2 in LANDSCAPE DNDC, and approach 3 in CoupModel. Approaches 2 and 3 are examples of applied combinations of more carbon allocation types.

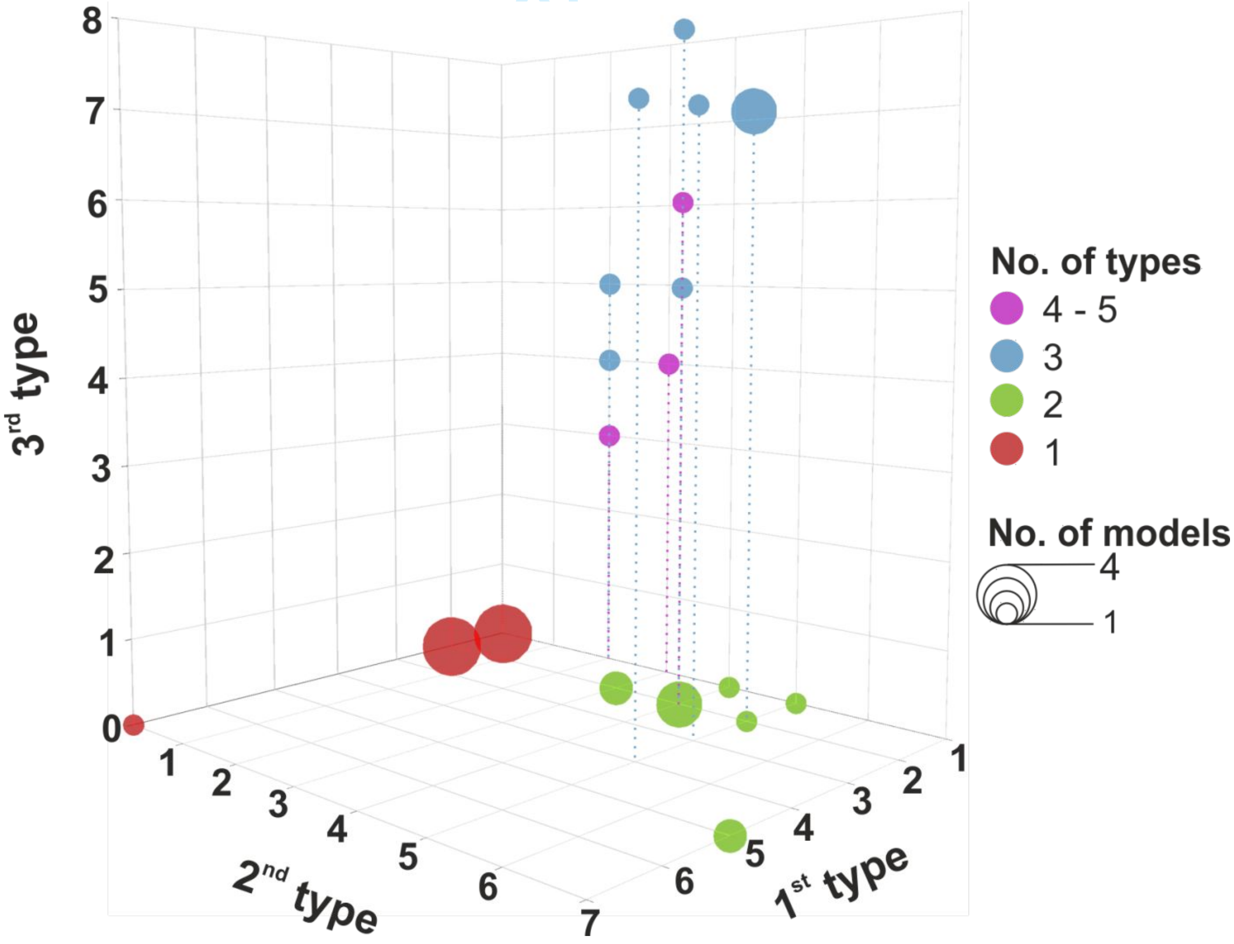


Figure 4. Applied combinations of different types of carbon allocation modelling (1 - fixed ratios, 2 - allometry, 3 - root-shoot functional balance, 4 - resource limitation, 5 - pipe model, 6 - transport

resistance, 7 - source-sink model, 8 - optimal response) in the investigated models. The size of the bubble indicates the number of models from our database that use a particular type or a combination of types for modelling carbon allocation, with the smallest size representing 1 model and the biggest size representing 4 models. Red colour indicates that only one type of carbon allocation modelling has been applied, green colour indicates the combination of two types, blue colour stands for the combination of three types and purple colour for four or five types of carbon allocation modelling, while only the first three types are presented in the graphs.

3.2. Identified gaps in carbon allocation modelling

The analysis of the questionnaire responses revealed that model developers and users identified 24 specific problems related to carbon allocation modelling in 17 out of 31 models (54.8%). The most commonly identified problems were (1) usage of fixed ratios despite known natural dynamics of carbon allocation, (2) lack of sensitivity of carbon allocation procedures to environmental conditions and (3) to natural disturbances, (4) missing pools that are likely to take up carbon or function as a buffer to withstand stress conditions, (5) allocation time steps that are too large to model the dynamics of resource acquisition, (6) lack of data for calibration of carbon allocation procedures. Below we analyse each gap using the three steps defined in Methods.

3.2.1. The use of fixed ratios for allocation

I. Identification of the gap

The term '*Fixed ratios*' refers to the method of carbon allocation that assumes fixed fractions of assimilated carbon to be allocated to individual organs/pools (Franklin et al. 2012). Models based on this approach use constant compartment carbon fractions or carbon allocation ratios and/or constant growth proportion. These parameters may be set in dependence to specific environmental conditions, e.g. vegetation group/biome/PFT/tree species, soil water and nutrient status, etc., but during a single simulation allocation fractions/ratios and/or growth proportion do not change in response to phenology, stand development, i.e. size or age of modelled objects, competition, compartment senescence or dynamically varying environmental conditions. According to the answers on the applied carbon allocation types (question 2.2, Supplementary A) and the use of constant values for specific carbon allocation characteristics (question 2.7, Supplementary A), more than a half of the investigated models (18 models, 58%) applied fixed allocation to a certain extent. Carbon allocation based solely on fixed ratios was used in four models (12.9%), while others used a hybrid modelling approach that combined fixed allocation with one or more other modelling types: usually allometry, resource limitation, or pipe model (Figure 3, 4). Models with fixed ratios have poor predictive power in capturing forest growth dynamics (Ostrogović Sever et al. 2017).

De Kauwe et al. (2014) showed that even the performance of the models that use fixed ratios in combination with other principles and/or types is at least partially negatively affected by the shortages of fixed coefficients.

II. Evidence to prove the gap

Carbon allocation is a highly dynamic process controlled by various plant functions driven by environmental factors (Wardlaw 1990). Its dynamics can be synthesised into: (1) seasonal - during the course of the year due to phenology (White et al. 1997, Collalti et al. 2014, 2016, Caldararu et al. 2014, Delpierre et al. 2015, Marconi et al. 2017); (2) periodical - during stand development due to age or size related parameters or processes (Franklin et al. 2012), e.g. age-dependent root-to-shoot ratio (Genet et al. 2009), age-dependent partitioning of carbon into foliage and wood (Litton et al. 2007), tree height-related dynamic of NSC (Sala and Hoch 2009), masting dynamics (Vacchiano et al. 2018, Chapter

3.2.4), stand density (Poorter et al. 2011, Krejza et al. 2013), competition (Vanninen and Mäkelä 2005); and (3) long-term - due to changes in the sensitivity of allocation processes to environmental conditions (Poorter et al. 2011).

Leaf phenology determines seasonal variations in leaf area as a direct result of carbon assimilation (White et al. 1997, Caldararu et al. 2014, Collalti et al. 2016). Klein et al. (2016) showed that leaf phenology of temperate deciduous tree species is tightly linked to their growth and carbon storage, and that their carbon alllocation strategies are species-specific. A number of research results on different scales corroborate that growth is often uncoupled from net photosynthesis, which would not be the case if allocation followed the principle of fixed ratios. For example, Muller et al. (2011) showed that growth is more sensitive to water limitation than photosynthesis. Water deficit can to a certain extent enhance fine root production in order to reach water reservoirs previously unavailable (Broeckx et al. 2013).

The allocation of carbon fluctuates with both size and age of a tree (Franklin et al. 2012). A positive linear correlation has been shown between stand age and partitioning of carbon into foliage and wood although the total net primary production tends to decrease with increasing stand age (Litton et al. 2007) because an increased amount of assimilates is allocated to non-structural compounds (Sala and Hoch 2009). Similarly, trees grown at high densities show an increase in stem biomass fraction (Sala and Hoch 2009). This influence is linked to environmental conditions, the impact of which is discussed in the next chapter (3.2.2).

III. Approaches and examples to overcome the gap

One of the simplest approaches of introducing seasonal dynamics in carbon allocation is to use a growing degree day threshold which controls fruit formation (e.g. CLM-Palm, Biome-BGCMuSo). A more complex dynamics can be introduced using a sink-source type which implies that sink demand of all plant compartments changes dynamically throughout phenological stages (e.g. LandscapeDNDC, CASTANEA, ANAFORE, CoupModel, 3D-CMCC FEM).

During stand development carbon allocation can be modified by implementing size related allocation ratios, often based on the notion that different compartments try to maintain a particular balance (e.g. 3PG, ForGEM, CoupModel, ORCHIDEE-CAN). This, however, still does not account for environmental changes as long as these balances do not vary with resource availability. If the allocation process is dependent on the time of the year (considered by 4 models, 12%) or is hierarchically organised (9 models, 29%), then environmental conditions also affect the partitioning into different compartments. Frequently, allocation is driven by the development of leaves, which is included in 16 models (52%), that requires carbon for flushing or disturbs the functional balance. In such cases, environmental conditions that drive phenology also drive allocation. Hybrid models, i.e. integration of empirical and process-based models (Fontes et al. 2010), try to account for this fact by introducing competition for resources (e.g. light, water) between individual model objects (organs, trees, and species, e.g. 4C, iLand, 3D-CMCC FEM, FORMIND). Nevertheless, the number of environmental factors considered is usually small although Poorter et al. (2011) provide dose-response curves of response of main plant fractions (i.e. leaf, stem and root) to 12 environmental factors. Most frequently soil water/drought stress and nitrogen availability/site fertility are incorporated (e.g. 3PG, FORESEE, ANAFORE, CoupModel, iLand, LPJ-GUESS). Furthermore, temperature limitation of growth (LPJ, Leuzinger et al. 2013), reserve pool estimated using allometry (iLand), and sink-controlled growth regarding water and low temperature stress (CASTANEA) can be found among the approaches used.

Our main recommendation to close the indicated gaps in carbon allocation modelling is to perform a revision of the model logic regarding the control of growth. This can be performed by implementing more sophisticated principles and/or types of carbon allocation modelling (Table 2) than fixed ratios. Using biomass relationships (e.g. root/foliage ratio) and/or allometric drivers (e.g. height/diameter ratio) that dynamically depend on environmental conditions such as light and water availability would increase the sensitivity to a changing environment (Lacointe 2000) including changes induced by management (e.g. as a mitigation strategy, Collalti et al. 2018). Furthermore, an uncoupling of photosynthesis and growth under stress conditions, e.g. the consideration of carbon storage/reserve pool dynamics during drought, would result in a more realistic representation of carry-over effects on growth due to stress periods.

3.2.2. Direct sensitivity of allocation to environmental conditions

I. Identification of the gap

Allocation of carbon to individual tree components is affected by environment, phenology, ontogeny and many other factors (Litton et al. 2007, Ryan et al. 2010, Franklin et al. 2012, de Kauwe et al. 2014, Li et al. 2016). A descriptive sensitivity analysis based on the responses on question 2.9. (Supplementary A) identified 17 properties which influence simulated carbon allocation in the examined models, out of which 8 represented environment, i.e. climate and soil (Figure 5). The factors affect the dynamics of tree growth, the contribution of each tree component to autotrophic respiration, carbon transfer to the rhizosphere and carbon sequestration, which is explained by differences in lifespan and decomposition rates of tree components (Körner 2003, Epron, Nouvellon, et al. 2012).

The analysis revealed that in 11 models (35%) no climatic or soil conditions directly affected simulated carbon allocation (Figure S1B). From the models that accounted for some environmental conditions, most (14, 45%) considered air temperature, while precipitation affected carbon allocation only in four (13%) models (Figure 5).

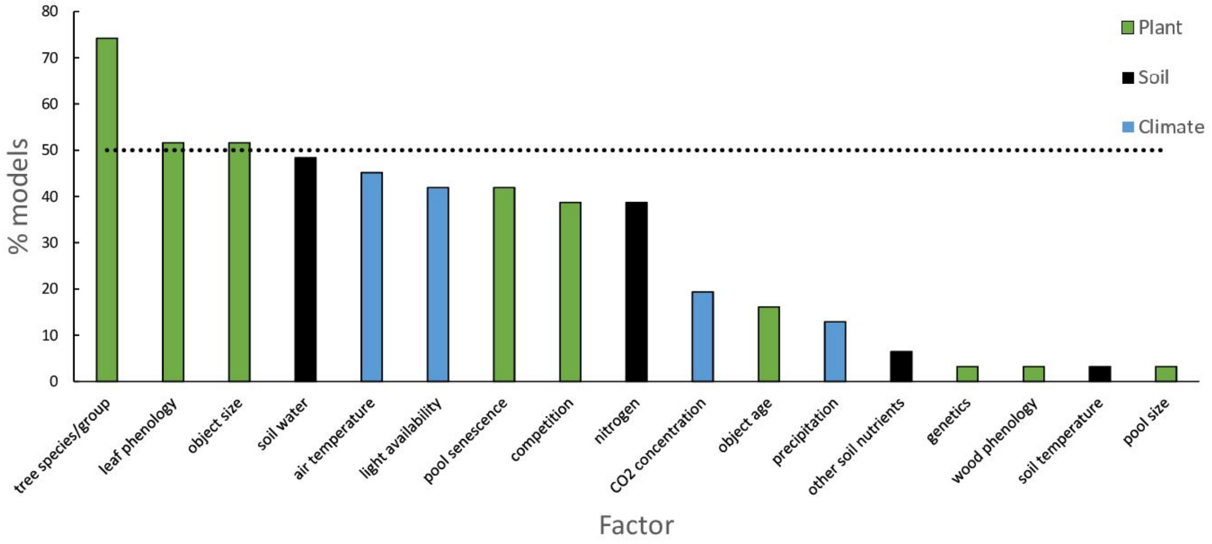


Figure 5. Percentage of models that account for the impact of a particular factor on carbon allocation (dashed line represents 50% of models).

Soil characteristics directly influenced carbon allocation in 20 models (65%), while none of the models included all four identified soil factors. Soil water was the most frequent soil factor affecting carbon allocation used in almost a half of the investigated models (15 models, 48%) followed by nitrogen (12 models, 39%). One third of the models (11, 35%) accounted only for one factor, either for soil water (7 models) or nitrogen (4 models). Two factors representing soil were included in eight models (26%), while the most common combination of factors comprised soil water and nitrogen (6 models, 19%). Only ANAFORE included the impact of three soil characteristics (soil water, nitrogen, and other soil nutrients). Although nitrogen was the most frequently included nutrient in models, still 38% of the models (i.e. 12 models) in our database do not simulate nitrogen cycling in ecosystems. Simulating cycling of other soil nutrients than nitrogen is very rare, as only two (i.e. 6%) of the investigated models (ANAFORE and Heterofor) included other elements apart from carbon and nitrogen.

II. Evidence to prove the gap

The meta-analysis of Poorter et al. (2011) confirmed that carbon allocation in plants changes with environment, plant size, competition and evolutionary history, while light, temperature, nutrients, and water were found to be the most influential factors. Decreasing light availability increases the fraction of whole-plant biomass allocated to leaves (Poorter et al. 2011, Konôpka et al. 2016). Several works (Usami et al. 2001, Overdieck et al. 2007, Kasurinen et al. 2012) showed that increasing temperature has the potential to increase carbon accumulation in aboveground biomass, while temperatures below 18°C significantly increase the fraction of roots at the expense of stems and leaves (Poorter et al. 2011). Way and Oren (2010) revealed that the increasing temperature stimulated height growth more than growth of stem diameter, although evergreen species showed to have a more conservative response to changes in temperature than deciduous species. Faster decomposition at higher temperatures releases more nutrients from the soil organic nitrogen pool, which could in turn result in an increase of gross primary productivity caused by higher needle biomass production (Pumpanen et al. 2012).

Increased nutrient availability leads to increased partitioning to aboveground parts of the tree and decreased partitioning to belowground tree parts (Friedlingstein et al. 1999, Litton et al. 2007, Repola 2008, Poorter et al. 2011), whereas reduced nutrient availability or drought generally favour carbon allocation to the root system (Friedlingstein et al. 1999, Hommel et al. 2016), or to specific parts of the root system growing in wetter soil horizons (Konôpka and Lukac 2012). Waterlogging also affects biomass fractions of leaves and roots, though in the opposite direction as the lack of water, i.e. by favouring leaves (Poorter et al. 2011).

Ericsson (1995) revealed different carbon allocation patterns in tree seedlings limited by different nutrients, e.g. magnesium deficiency was found to reduce allocation to roots, while phosphorus limitation favoured carbon allocation to roots (Ericsson 1995) or to mycorrhizal symbionts (Ekblad et al. 1995). Potassium fertilisation had a significant effect on carbon allocation favouring aboveground tree parts (Epron et al. 2011), and adding calcium resulted in higher carbon allocation to radial growth and reproductive processes (Halman et al. 2013). Water and nutrient demands are closely connected with elevated $CO_{2,}$ because increased photosynthetic rates in response to elevated CO_2 do not not always enhance stem growth (Fatichi et al. 2013), but rather increase fruit production, carbon release into the soil or the amount of non-structural carbohydrates (de Kauwe et al. 2014). An increase in biomass accumulation as a result of higher atmospheric CO_2 was observed only when sufficient nutrients were supplied (Murray et al. 2000, Franklin et al. 2012). The process of downward regulation may be accompanied by higher C sequestration into structural and conducting tissues as well as by proportionally higher reduction of photosynthetically active tissues (Murray et al. 2000, Rolo et al. 2015). Rolo et al. (2015) observed that European beech and Norway spruce show lower values of specific leaf areas when growing under enhanced levels of CO_2.

III. Approaches and examples to overcome the gap

To overcome misleading or unrealistic outcomes from models, the user should be first familiar with the modelling principles/types (Table 2) and relationships the model is established on. Empirical approaches based on fixed ratios or allometric relationships as well as a general pipe model theory assume that partitioning is in a steady state, thus they lack responses to environmental changes (Bugmann 1994, Franklin et al. 2012) and can be used only for a limited range of conditions (Lacointe 2000). However, in some applications of the pipe model theory allocation is responsive to environmental conditions, albeit just those caused by competition / stand density. This is because increased competition accelerates crown rise, so there is more allocation to stem growth relative to the crown than in trees growing in sparse stands (e.g. Valentine and Mäkelä 2005, Mäkelä et al. 2016). According to de Kauwe et al. (2014) and Franklin et al. (2012), approaches constructed on functional relationships, functional balance and eco-evolutionarily principle, as well as models that use source-sink, optimal response, game-theoretic optimisation and maximum entropy (Lacointe 2000, Fabrika and Pretzsch 2011, Franklin et al. 2012, de Kauwe et al. 2014) should be principally sensitive to environmental conditions (Table 2). In the models that rely on functional balance principles, availability of soil nutrients and primarily nitrogen (included in 12 models, 38.7%) can be used as a main driver for distributing carbon into below- or above-ground compartments. Functional balance and sink-source based approaches calculate carbon allocation from the actual biomass of a specific compartment. Since its size is influenced by senescence (13 models, 42%), all environmental conditions that influence this process also affect allocation.

The highest number of factors affecting modelled carbon allocation (11 factors, i.e. 65% of all identified ones) was included in 3D-CMCC-FEM. In this model carbon partitioning is based on coefficients that are controlled by soil water content and light competition which strongly vary according to the phenological stage, e.g. budburst, leaffall (Arora and Boer 2005). Allocation into tree compartments is based on the Frankfurt biosphere model approaches (Lüdeke et al. 1994, Friedlingstein et al. 1999).

GO+ was the only model that accounted for the impact of all identified climatic conditions, i.e. carbon dioxide, light availability (photoperiod), air temperature and precipitation, on carbon allocation. Six models included three of the climatic conditions (ANAFORE, 3D-CMCC-FEM, BASFOR, iLand, 3PG, and ForGEM). However, since allocation in process-based models (25 models in our database) is always driven by assimilated carbon, the intensity of the process depends on environmental conditions that drive photosynthesis (i.e. light, CO_2, temperature, nutrient availability, stress abundance). Overall, there might be few environmental conditions that directly drive allocation but a number of indirect influences. A common approach how to include direct effects is to modify allocation coefficients with regard to simulated resources, most commonly water (ANAFORE) and light (3D-CMCC FEM) and nitrogen (ORCHIDEE-CAN, Xia et al. 2017) following e.g. the work by Friedlingstein et al. (1999). Indirectly, environmental conditions can influence carbon allocation through leaf phenology. Most models use only temperature, but few also include photoperiod (e.g. (Migliavacca et al. 2012, Way and Montgomery 2014, Delpierre et al. 2015) or drought stress (e.g. (Delpierre et al. 2015, Xie et al. 2018) as determinants of phenological development.

Implementing specific nutrient dynamics in models may be important for future projections of the carbon cycle in regions where the particular nutrient is limited (Zaehle 2013). It was shown that the outputs from models simulating only carbon dynamics in ecosystems differ from those that include C-N interactions (Wårlind et al. 2014) and have less well performed in ensemble evaluations (de Kauwe et al. 2014). Since all but one model in our database were derived to simulate temperate and boreal forests, which are considered predominantly nitrogen limited, including nitrogen dynamics and carbon-nitrogen interactions would be beneficial if biogeochemical–climate interactions are to be studied (Zaehle 2013). Almost 40% of the investigated models account for the impact of nitrogen and can serve as an example of its implementations. The influence of other nutrients on carbon allocation is included in only two (i.e. 6%) models (ANAFORE and Heterofor). Both models simulate the impact of magnesium, phosphorus, and potassium on carbon allocation, while calcium is included only in Heterofor.

3.2.3. Impact of disturbances

I. Identification of the gap

Out of the 31 models, 15 (i.e. 48%) included the influence of one or several disturbances on carbon allocation (excluding management as a disturbance). The most commonly included disturbance effect was drought, covered by 13 out of 15 models followed by fire (6 models), wind (6 models) and insects (5 models). Two models also included “generic” disturbance not associated to any specific disturbance agent (LPJ-GUESS, TreeMig). Most of the models (10 out of 15) included one or two disturbances but only 5 models included three or four different disturbance types (Figure 6). While this possibly reflects the dominance of individual disturbance agents in the different regions and forest types the models have been designed for (c.f. Reyer et al. 2017), there is increasing evidence that the interactions of disturbances are actually crucial to assess disturbance impacts under climate change (Seidl et al. 2017). Interestingly, there seems to be no model covering the effects of other regionally important disturbances such as ice-storms and pathogens, which in general seem to be less prominent amongst forest models (Seidl et al. 2011).

It should be noted that many models explored here consider the effect of disturbances only indirectly, i.e., as responses of carbon allocation to disturbance-induced changes in light, nutrient, and water availability. However, there is evidence of additional effects of drought, insect and wind damage on allocation which are not covered by models yet. This includes a reduced hydraulic conductivity that may persist throughout years or a change in root to shoot ratios (e.g. Bansal et al. 2013). In general, even though forest models are increasingly including disturbances, these are often represented by descriptive, statistical modelling approaches (Seidl et al. 2011), which complicates their integration into complex process-based models that explicitly deal with allocation.

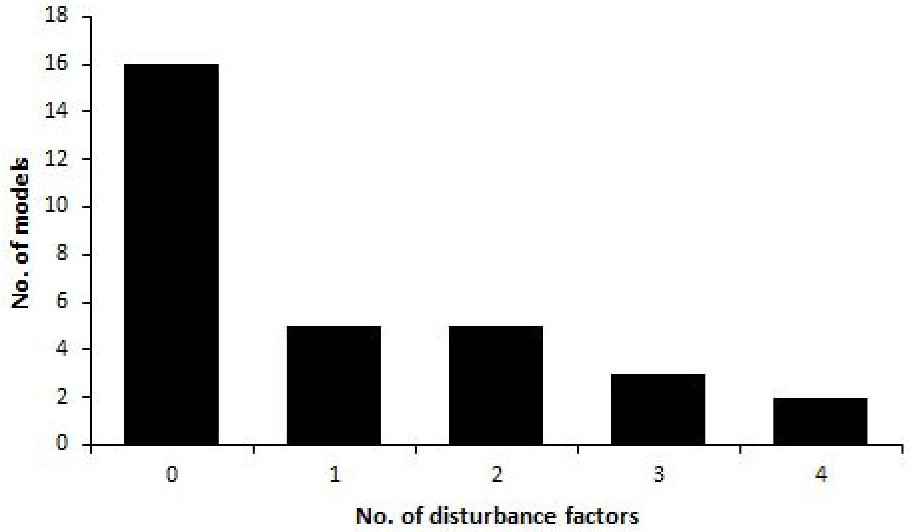


Figure 6. Number of natural disturbance factors (drought, fire, insects, wind, or generic disturbance) affecting carbon allocation in examined models.

II. Evidence to prove the gap

Drought, insect and wind damage have direct effects on carbon allocation in trees. Although the reactions may be species-specific, a recent meta-analysis of plant biomass allocation during drought stress performed by Eziz et al. (2017) revealed that under drought conditions the fraction of plant root mass generally increased, while the fraction of stem, leaf, and reproductive biomass decreased. The process is enhanced by increasing fine root mortality under dry conditions although at a certain threshold, fine root production decreases again (Meier and Leuschner 2008, Nikolova et al. 2010). According to Galvez et al. (2011), severe drought stress promotes the accumulation of carbohydrate reserves in roots at the expense of growth. Similarly, Liu et al. (2017) indicated an accumulation of non-structural carbohydrates (NSC, i.e. labile carbon) in leaves and reduced shoot and stem growth under severe summer drought conditions. However, as Hartmann and Trumbore (2016) pointed out, the accumulation of NSC occurs only in the case of short-term drought events. After drought, plants favour root growth as a recovery strategy in order to restore root functions (Hagedorn et al. 2016). Seidl and Blennow (2012) hypothesized that post-storm stem growth reductions of remaining trees in Sweden might be caused by allocation changes to repair root damages and produce insect defense compounds. The former mechanism has been found both in tree-pulling experiments (Nielsen and Knudsen 2004) and field data analysis (Vargas et al. 2009). Also analyses on seedlings have shown that mechanical stimuli mimicking natural wind sways increase biomass allocation to roots (Coutand et al. 2008). Investment in insect defense compounds has been shown for mildly drought-affected trees (McDowell 2011). Defoliation is also known to cause shifts in carbon allocation towards new leaf production (Mayfield III et al. 2005, Eyles et al. 2009, Pinkard et al. 2011, Jacquet et al. 2012), and accumulation of reserves at the expense of stem growth (Wiley et al. 2013, Piper et al. 2015). Saffell et al. (2014) showed that trees suffering from chronic fungal disease of leaves changed their carbon allocation in favour of NSCs in crowns to maintain foliage growth and shoot extension in the spring. Browsing was also found to have an effect on carbon allocation in trees, particularly in the short term (Palacio et al. 2008, 2011, Endrulat et al. 2016).

III. Approaches to overcome the gaps

The first step to improve modelling of disturbance effects on allocation would be to actually include disturbances and their impacts into existing models (see Seidl et al. 2011). Subsequently, the disturbances can be linked to those processes in the model governing allocation. For drought, progress has already been made. Since drought is an environmental condition that is expected to occur more frequently in the future due to predicted climate change, it is widely investigated and incorporated in the majority of ecosystem models (Fontes et al. 2010). Hence, including drought disturbance effects on allocation via altered respiration needs of each organ, altered order of preference for allocation, changed allocation ratios and/or applying the pipe-model theory is fairly common (Grote and Pretzsch 2002, Lasch et al. 2005, Van Oijen et al. 2005, Deckmyn et al. 2008, Rötzer et al. 2010, Jansson 2012). Farrior et al. (2013, 2015) applied an evolutionarily stable strategy to simulate the influence of water limitation on the carbon allocation of individual trees in a closed-canopy equilibrium forest. The impact of drought can also be simulated by a model based on optimal partitioning theory since it can dynamically change carbon allocation with regard to the limiting source, e.g. in water limiting conditions more carbon is allocated to roots (Pezzatti 2011). Most models follow this theory and increase carbon allocation to roots under drought conditions (Ostle et al. 2009).

Direct effects of other disturbances are fairly seldom covered by existing models. In general we can say that if a model is able to simulate particular disturbances and includes a carbon allocation modifier that responds to light availability or competition (e.g. 3D-CMCC FEM, ORCHIDEE-CAN, Xia et al. 2017), it also accounts for the impact of tree mortality as triggered by windstorms, insect outbreaks, or fire (e.g. iLand). Recently, frameworks on how to model insect and pathogen damage to affect allocation, especially NSC, have been published (Dietze and Matthes 2014). Together with the representation of NSC as suggested by Liu et al. (2011), the next model generation may be able to account for allocation shifts originating from the reduction of different carbon pools. Moreover, also mechanistic models of dynamic biomass partitioning that capture the effects of disturbance-induced changes in the ratio of above- to belowground biomass have been developed (Pezzatti 2011).

3.2.4. Missing pools and repair functions

I. Identification of the gap

The analysis of the questionnaire results showed that on average the models allocate carbon to 6 (calculated mean of 5.8) different biomass compartments. Two models (TreeMig and FORMIND) distinguish only 2 compartments, while a maximum of 9 different compartments of biomass was defined also in two models (CoupModel and 3D-CMCC FEM). The leaf compartment was included in all but one model (97%) followed by fine roots used in 22 models (71%) and sapwood used in 19 models (61%, Figure 7). Although the average number of compartments coincides with the number of main plant parts according to Cannell and Dewar (1994), reproductive and storage sinks are not frequently represented in the models (Figure 7).

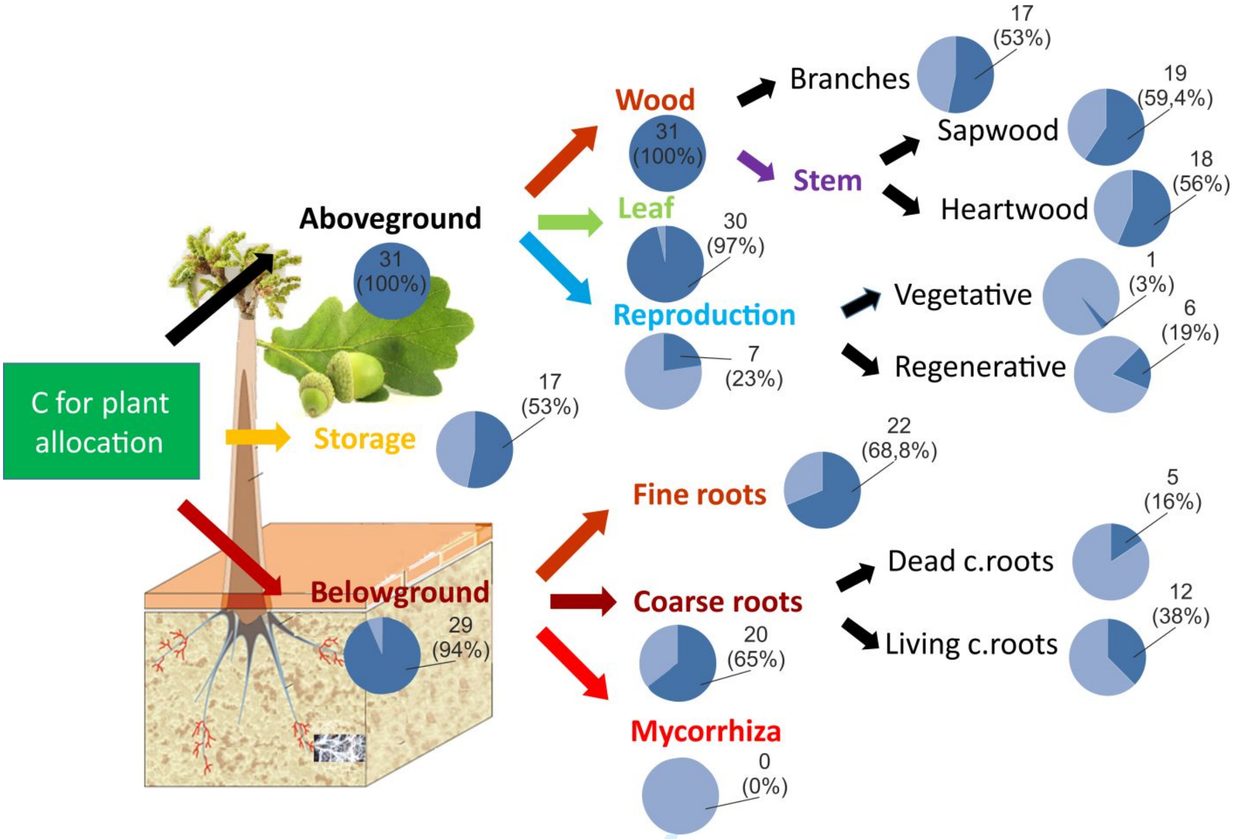


Figure 7. Frequency of tree compartments used in models.

What has obviously been overlooked or oversimplified by forest models is allocation into reproduction. Indeed, out of the 31 simulators presented in the questionnaire, only six (19%) include a carbon pool for sexual reproduction and one model (LPJ-Guess) for vegetative reproduction (Figure 7). Of these, three activate such a pool only for crops (CoupModel, CLM 4.5, Biome-BGCMuSo), while three use fixed allocation fractions for fruit production during defined periods (ANAFORE, ORCHIDEE-CAN, 3D-CMCC FEM).

Two more deficits regarding allocation pools were identified: Carbon available for defense and repair and carbon that is provided to symbionts, i.e. mycorrhiza. Defense and repair processes are important under stressful conditions and are particularly relevant for determining tree mortality. Carbon allocated to mycorrhiza might be seen as a part of the investment into resource acquisition by roots and are thus implicitly considered in root turnover and specific uptake parameters. However, this implicit consideration assumes that the relationship between plant and symbiont stays constant, which is not the case in a changing environment (Vargas 2009). As presented in Figure 7, none of the models explicitly accounted either for mycorrhiza compartment or for defense and repair processes.

II. *Evidence to prove the gap*

One could argue that by assuming the fruit and seed biomass to have a negligible biomass relative to the other pools, or employing a fixed yearly rate of allocation of carbon to fruits and seeds, a model would be kept simple without losing much accuracy. However, seed production can consume between 3 and 20% of annual GPP (Schaefer et al. 2008), depending on species and on interannual variability in reproductive output. In tree species with irregular fruiting patterns, peak seed years ("masting": Ascoli et al. 2017) may result in reductions of 40% in woody growth (Holmsgaard 1956, Eis et al. 1965, Selås et al. 2002, Monks and Kelly 2006, Drobyshev et al. 2010). This indicates that large resources are invested into the reproductive pool, governed by resource accumulation and depletion mechanisms and growth-reproduction trade-offs (Hacket-Pain et al. 2015). Moreover, although masting can synchronize over large areas in response to weather-related drivers (Vacchiano et al. 2017), a huge variability in seed output and its response to the environment exist at the individual tree level (van der Meer et al. 2002, Vilà-Cabrera et al. 2014). In general, results indicate that resource accumulation in cooler years trigger larger fruiting/masting events later on, with later warm temperatures inducing mast flowering (Sala, Hopping, et al. 2012, Müller-Haubold et al. 2015, Monks et al. 2016, Abe et al. 2016, Pearse et al. 2016). Interestingly, it is nevertheless not the stored carbon but the newly produced carbon that is actually used for fruits and seeds (Hoch et al. 2003, 2013), which is corroborated by a frequent decline of wood growth in a masting year (e.g., Drobyshev et al. 2010, Martín et al. 2015). This indicates that full resource pools are a trigger for allocation changes rather than the source of masting. In addition, stress has been suggested to trigger seed production based on the theory that mortality-inducing events create favorable conditions for regeneration (Piovesan and Adams 2001, 2005) which, however, has not always been supported by measurements (Müller-Haubold et al. 2015).

In contrast to the reproductive pool that is separated from other tissues and develops under specific environmental conditions, pools for defense and repair are constitutively present and therefore need to be an integrated part of other biomass fractions (Dietze et al. 2014). As already pointed out, defense and repair processes are important under stressful conditions and are particularly relevant for determining tree mortality. For example, the immediate cause of death due to drought stress might be hydraulic failure (i.e. xylem cavitation) but the ability to postpone this failure may depend on the ability of the tree stabilize water conductivity, repair previous damages or build on new vessels that all depend on carbon supply (Sala, Woodruff, et al. 2012). Failure to represent this process leads to over- or underestimation of mortality and carry-over effects of decreased growth long after the stress has ceased will be missed (Thomas et al. 2009). Similarly, air pollution leads to considerable higher damages if the constitutive defenses of a leaf are exhausted (Wieser and Matyssek 2007).

Similarly to seed production, plants can invest up to 22% of their GPP to their fungal symbionts (Vargas 2009). The differentiation of carbon allocated to mycorrhiza is mainly required under changing environmental conditions (Hasselquist et al. 2015). In particular, nitrogen addition, but also higher temperatures that lead to higher decomposition rates, require a differentiation between roots and fungal biomass. The storage/reserve pool plays an important role in buffering effect of developmental changes on growth as it serves as a source of assimilates for new spring growth (Wardlaw 1990), but it is also an important pool that facilitates recovery processes (Hartmann 2015) after environmental disturbances (e.g. drought, fire, pathogen attacks, defoliation by insect). Nevertheless, this pool needs to be dynamic and may change size based on short term stress occurrence (induced defenses) or long term stress intensity (acclimation) (Hartmann and Trumbore 2016).

III. Approaches and examples to overcome the gap

To overcome the gap in considering reproduction, algorithms have been 'borrowed' from crop simulators (e.g., Pavlick et al. 2013). The onset and/or relative magnitude of allocation to fruits have been related to temperature, growing degree days, heat thresholds or day length (Oleson et al. 2013, Hidy et al. 2016) and additional impacts of available water (Berg et al. 2010) and nitrogen (Hidy et al. 2016) have been considered. These models work for regularly fruiting trees or if only average allocation values throughout longer than annual time scales are required. Some examples also exist for introducing labile or non-structural carbon pools that distribute over other compartments in highly process-oriented forest growth models (Grote 1998, Deckmyn et al. 2008, Collalti et al. 2016).

The difficulty is to consider highly variable reproduction events (masting) that might only occur in intervals of several years. This question is especially addressed by the so-called Resource Budget Models (RBMs), which assume that (i) the tree does not reproduce unless it accumulates enough reserves; (ii) once its reserves exceed a given threshold the tree allocates all its excess reserves to flowers; (iii) female flowers are fertilised by outcross pollen, with a success rate that is positively related to the amount of pollen produced by the neighbouring trees (outcross pollination); (iv) pollinated flowers then develop into mature fruits and incur resource depletion whose severity is governed by a fruiting-to-flowering cost ratio (Isagi et al. 1997, Crone and Rapp 2014). In RBMs, fruiting fluctuates from one year to the next when the tree produces seeds that subsequently deplete resource reserves. Pollination is considered as a limiting factor that may lead to fruiting failure and resource savings, which may be invested in flowering the following year (Satake and Iwasa 2000, Venner et al. 2016). Abe et al. (2016) extended RBMs by introducing environmental stochasticity, i.e. the inhibition of flowering in response to weather conditions of the same year.

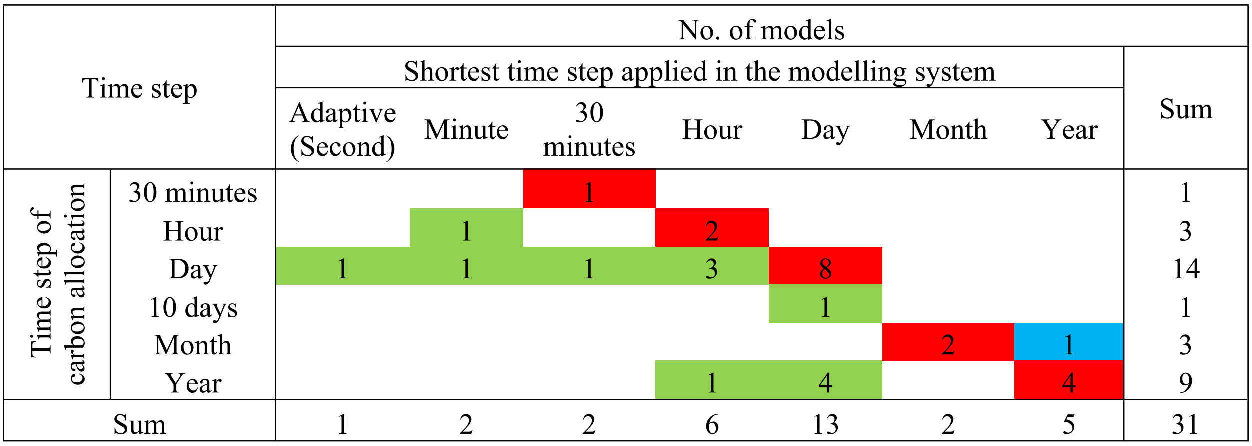
Regarding other carbon pools considered for allocation, some specific approaches have been suggested that might be further elaborated or simplified. Models considering mycorrhiza have been reviewed by Deckmyn et al. (2014) and He et al. (2016), demonstrating the importance of considering plant-fungi feedback relations. An explicit dependence on root growth and soil nitrogen availability has been presented by Ruotsalainen et al. (2002) and Meyer et al. (2009, 2012). Moore et al. (2015) also included a dynamic switch of the role from plant symbiont to decomposer. Damage repair mechanisms have been considered in models describing the impact of air pollution (Van Oijen et al. 2005, Deckmyn et al. 2007), requiring a dynamic pool of carbon that might be linked to a general pool of free available carbon. The latter being considered yet only in few process-oriented forest models (Grote 1998, Deckmyn et al. 2008, Collalti et al. 2016, 2018).

3.2.5. Time step

I. Identification of the gap

The results of the questionnaire revealed that carbon allocation models in our database worked with six different time intervals, where a year was the largest time step, and 30 minutes was the smallest time step used (Figure 8). A day was found to be the most frequent time step used in almost a half of the models (45.2%) followed by a year applied in one third of the models (29%, Figure 8). The smallest time step of 30 minutes was used in one model (CLM 4.5). Similarly, carbon allocation of one model (BALANCE) operated at a time step of ten days (Figure 8). The time steps of a month and an hour were used by three (9.7%) models each (Figure 8). If we compared the time step of the whole modelling system with the time step of the carbon allocation module, we found that 17 models (54.8%) used the same time steps at both modelling levels, while in 13 models (41.9%) the allocation module operated at a larger time step than the whole modelling system, and only in 1 model (3.2%) it was the other way round (Figure 8).

The respondents identified that a step of one year (used in 29% of models) was too large and caused problems in modelling carbon allocation. Models with an annual timescale do not explicitly handle seasonal changes in carbon allocation due to intra-annual variations of phenology and environmental conditions, which can can lead to poorly simulated fluxes also at an inter-annual scale (Vermeulen et al. 2015). In addition, most models (87 % of the models from our database) currently do not include seasonal changes in carbon allocation, although the majority considers on/off of leaves for deciduous tree species. Those models that do include seasonality suffer from our general gaps of understanding of carbon allocation, also related to the role of carbon allocation to NSC and how this regulates the carbon balance in the longer term.



Time step		No. of models							
		Shortest time step applied in the modelling system							Sum
		Adaptive (Second)	Minute	30 minutes	Hour	Day	Month	Year	
Time step of carbon allocation	30 minutes			🟥 1					1
	Hour		🟩 1		🟥 2				3
	Day	🟩 1	🟩 1	🟩 1	🟩 3	🟥 8			14
	10 days					🟩 1			1
	Month						🟥 2	🟦 1	3
	Year				🟩 1	🟩 4		🟥 4	9
Sum		1	2	2	6	13	2	5	31

Figure 8. Comparison of time step of the allocation model and the whole modelling system. Numbers indicate the number of models with the respective combination of time steps. Red colour indicates the same time step at both modelling levels, green colour indicates that the carbon allocation module operates at coarser temporal resolution than the whole modelling system, while blue colour indicates the opposite.

II. Evidence to prove the gap

The questionnaire results reflect our current state of knowledge. For more than a century, growth and biomass production have been the processes of the primary interest of foresters, while modellers have only considered growth as a result of carbon acquisition and allocation since 1970s, and particularly the allocation component has not yet been thoroughly understood from physiological principles. This may be the reason why more than one third of the models in this study use a so called 'top-down approach when simulating carbon allocation in ecosystems. Models operating at coarser time scales are either based on empirical relationships or use an 'average day' approximation (Hastings and Gross 2012). Such an approach is suitable for modelling stable systems, where slow processes at a lower temporal resolution regulate processes at higher scales (Pretzsch 2009).

However, changing environmental conditions cause system instability (Scheffer et al. 2001), due to which signals from faster processes varying at higher temporal scales may become dominant and force slow processes to change (Robinson and Ek 2000, Pretzsch 2009). Models working at an annual temporal resolution often fail to capture these changes caused by novel environmental conditions (Hastings and Gross 2012). Finer temporal resolution enables us to examine the impact of the particular change on the analysed system (Pretzsch et al. 2015). As has already been shown above, carbon allocation depends on the instantaneous values of the environmental variables and their combinations (Da Silva et al. 2011). Hence, mechanistics models operating at shorter time scales are able to provide more robust extrapolation of system behaviour under climate change (Hastings and Gross 2012). They usually include the impact of atmospheric and hydrological conditions, which are most frequently readily available at a daily resolution (Gea-Izquierdo et al. 2015). Models with seasonality often assume that growth of a certain component is completed when its potential demand has been satisfied (Running and Gower 1991, Drouet and Pagès 2007, Gayler et al. 2007, Schippers et al. 2015), and if anything is left over, that is allocated to NSC and can be used for growth in consecutive years. However, this approach is sensitive to how the demand is determined, and assumes that NSC is a passive pool, although several recent studies showed that in some cases the accumulation of NSC competes with growth (McDowell 2011, Sala, Woodruff, et al. 2012, Saffell et al. 2014). We still do not understand the interactions between timing of growth, predetermined "growth potential", and the environment, in order to solve these questions strictly on a physiological basis.

III. Approaches and examples to overcome the gap

The choice of time resolution in carbon allocation is largely related to the principle of allocation applied in the model. If allocation coefficients are constant, time resolution is irrelevant and would naturally follow that of the other components of the model. In models that utilise allometric relationships (whether empirical or derived from optimisation principles) an annual time resolution would be the most logical, as allometric relationships cannot be determined at a shorter time resolution by any reasonable accuracy. If a shorter time step is applied with allometric allocation, it should be regarded as technical rather than trying to realistically mimic intra-annual carbon allocation patterns ("average-day approximation", Hastings and Gross 2012). Similarly, models that derive empirically-induced variations in allocation from annually integrated weather variables, such as mean or extreme temperatures, cumulative rainfall of particular months, etc., follow an annual resolution of allocation, even if the calculation step was sub-annual.

At the sub-annual scale, growth and hence carbon allocation to different tissues varies following a seasonal pattern where the growth of different organs adheres to a species-specific sequence. For example, in oak species cambial growth starts before the growth of foliage and primary wood, whereas in many conifers it is the other way round (Michelot et al. 2012, Schiestl-Aalto and Mäkelä 2016, Gričar et al. 2017). The treatment of allocation can only be genuinely regarded as sub-annual if this seasonal rhythm is considered. Furthermore, probably no sub-seasonal environmental control of allocation is physiologically justified without seasonality.

Including seasonality in models of carbon allocation has been suggested as a means of making the models more environmentally sensitive, i.e. making them capable of reflecting inter-annual environmental changes (Pretzsch 2009). The timing of weather changes would affect the allocation of carbon to different organs in a different way, depending on the timing of respective growth. It has also been argued that including seasonality would reflect the sink-dependence of both growth and growth allocation more faithfully than an annually-based model. For example, different organs may follow the environment in different ways, resulting in contrasting allocation patterns between years (Schiestl-Aalto et al. 2015).

The response of carbon allocation to various environmental factors incorporated using principles and/or types sensitive to environmental conditions (see Table 2) may be interpreted as a representation of seasonality in models. Another option is to define seasons a priori. As the few examples of the models from our database showed, two to three seasons are usually differentiated to account for the changes in carbon allocation within a year, although some models distinguish up to 6 phenological stages (e.g. Campioli et al. 2008). At the beginning of the growing season all of them prioritise leaves, while at the end or after the growing season, carbon is primarily allocated to reserves, which is in accordance with experimental results (Michelot et al. 2012). The biggest differences in carbon allocation were found for the summer period, in which some models, e.g. ANAFORE, allocate carbon to fruit, while other models prioritise wood (e.g. CASTANEA), and some others reserves (e.g. 3D-CMCC FEM). The seasonality in 3D-CMCC FEM v.5.x model follows the latest findings, which showed that reserve is an active pool (Martinez-Vilalta 2014). Hence, at the beginning of the year NSC are moved from a reserve pool to leaves and fine roots until maximum expected LAI is reached. Then the reserve pool is refilled, and only after its saturation the model allocates remaining assimilated carbon to structural pools (stems, branches, coarse roots). When the leaf fall phase starts, carbon is allocated to reserve and fruit pools.

3.2.6. Lack of data for calibration

I. Identification of the gap

Arguably, the biggest challenge for modelling carbon allocation in forest ecosystems is data acquisition and availability. Direct measurements for the allocation of carbon to the various tree compartments is typically resource intensive and hard to acquire (Franklin et al. 2012). To overcome this issue, modelling studies rely on indirect measurements of carbon allocation with the help of allometric relationships (e.g. Wolf et al. 2011). Despite data scarcity regarding the allocation of carbon in forest ecosystems, 24 out of the 31 models (i.e. 77%) reported in our questionnaire that their allocation modules were tested against some data. The data source used to parametrise allocation modules, however, was often not well suited to describe the underlying processes and carbon pools (Figure 9).

The use of allometric relationships between tree compartments is dominant for modelling carbon allocation, especially for the stem and root pools (Figure 9). Other direct measurements of the allocation mechanism, e.g. the samples of root cores for defining fine root biomass, were reported just in two studies out of the 24 models, indicating the need of data sources that provide a better description of below ground biomass. The accurate evaluation of the fine root compartment is critical, especially when considering the functional balance between leaves and fine roots. Moreover, only few studies reported that the derivation of allometric relationships between tree compartments was carried out at the same sites used for calibrating and validating the carbon allocation models (biomass on site), whereas for the majority of studies the sources of the allometric relationships were unclear.

The use of allometric relationships based on tree height and diameter at breast height for modelling allocation into non-structural carbon, reproductive structures and foliage biomass, as displayed in our results (Figure 9), may not be particularly appropriate. Traditional forest inventory collecting information on tree height and diameter is usually carried out in one to five years intervals, and thus the data are unable to capture the short-term dynamics of the pools. For such purposes, data sources with a finer temporal scale, such as from experiments using dendrometers and microcores, would be required.

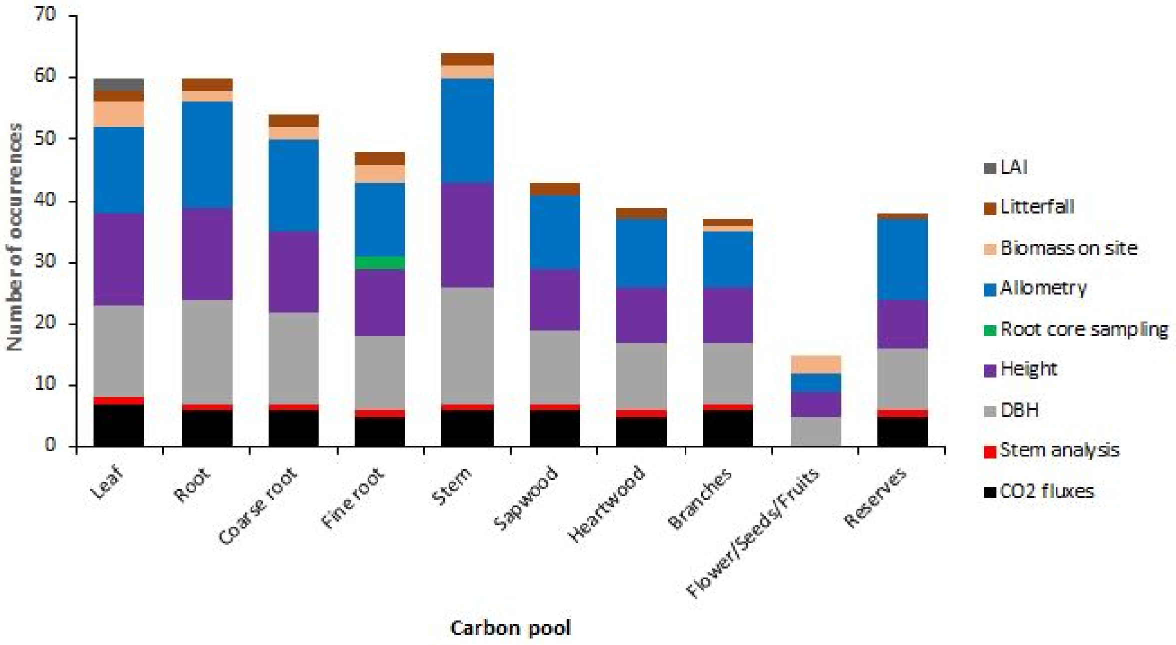


Figure 9. Data sources used to test the carbon allocation submodules in 24 models (for some models more sources of data were used). Legend: LAI is leaf area index, DBH is diameter at breast height.

II. Evidence to prove the gap

The data constraints for modelling carbon allocation have been widely recognised in the literature (e.g. Litton et al. 2007, Franklin et al. 2012, de Kauwe et al. 2014). While the allocation of aboveground carbon is fairly well understood and evaluated with allometric relationships, from which data is readily available, the dynamics of internal carbon allocation and the representation of belowground biomass patterns still demands investigation, as such fluxes require more detailed experiments and resource intensive methods (Warren et al. 2011, Mildner et al. 2014). Similarly, as evidenced in our results, modelling the dynamics of non-structural carbohydrates in reserve pools remains a major challenge. Traditionally, the evaluation of non-structural carbon has been carried out through the analysis of NSC concentration in plant tissues. However, the accurate evaluation of NSC in plant tissues is a difficult task and the uncertainty related to such quantifications may be substantial (Hartmann and Trumbore 2016). The same caveat is highlighted by Fatichi and Leuzinger (2013), recognising the inaccuracy of carbon pools and flux data as a major constraint for selecting suitable carbon allocation schemes, and suggesting that field data collection and laboratory experiments with higher precision are key for improving carbon allocation modelling.

The inconsistency between datasets for evaluating carbon allocation patterns has also been acknowledged as an important limitation of carbon allocation modelling, and the harmonisation of data from various sources, such as eddy covariance and forest growth data, is a key for a comprehensive understanding of carbon allocation processes (Guillemot et al. 2015). Such a link might provide valuable information on the responses of allocation patterns to environmental drivers and improve model performance. Smith et al. (2014) point out that unless the link between growth data and carbon flux data is established, we might be able to test model performance but not to improve the parameterisation of the underlying allocation processes.

Another important issue regarding data availability for carbon allocation modelling refers to the variability of sampling methods, as it induces a large uncertainty of the parameters and forecasts (Reich et al. 2014). Different methods are applied to quantify the amount of biomass and carbon in different pools, thus hindering robust evaluation and comparison of different allocation schemes. For example, Quentin et al. (2015) compared the results of non-structural carbohydrates evaluation performed by 29 laboratories using their specific protocols and found substantial differences in the outcomes, concluding that the results may not be comparable between laboratories.

III. Approaches to overcome the gap

Direct study of carbon allocation is a major challenge and an important limitation for modelling internal carbon dynamics. Sap flow measurements and labelling carbon isotopes appear to be promising methodologies for a better understanding of tree carbon dynamics (e.g. Kuptz et al. 2011, Klein, Siegwolf, et al. 2016, McCarroll et al. 2017). Recent developments in tools to trace carbon isotopes, such as isotope ratio infrared spectroscopy, has contributed to a substantial increase in accuracy for the evaluation of carbon in ephemeral pools and transport rates, providing an important step towards a better understanding of carbon allocation processes (Epron, Bahn, et al. 2012). For the evaluation of non-structural carbohydrates other methods might be required when analysing allocation patterns over long time periods (seasonal, yearly and decadal). Bomb radiocarbon measurements have been proposed for such evaluations (Carbone et al. 2013), as it allows deriving the average time since the NSC was initially assimilated from the atmosphere (Hartmann and Trumbore 2016). Moreover, combining multiple data sources may be a way to overcome limitations on the temporal resolution required for the growth patterns of each carbon pool, e.g. combining eddy covariance flux data, allowing the evaluation of canopy photosynthesis, with dendrochronological data series, evaluating the influences of environmental factors on the pools development may provide a better understanding of the allocation dynamics under environmental pressures (Gea-Izquierdo et al. 2015).

A natural approach for overcoming data limitations for carbon allocation modelling, especially under budget and other resources constraints is the creation of comprehensive databases on carbon fluxes and growth patterns. For example, Luyssaert et al. (2007) created a database from multiple experiments describing carbon budget variables, ecosystem traits, management history and environmental variables, including climate and soil characteristics, that is well suited for modelling purposes. In a similar fashion, Bond-Lamberty and Thomson (2010) compiled a global dataset with soil respiration experiments, providing a basis for a better understanding of soil respiration dynamics, which usually require resource intensive experiments. Such initiatives, however, are still scarce for forest dynamics experiments, but they could contribute greatly to improving the development and evaluation of carbon allocation schemes.

4. Discussion and conclusions

Since the first study about carbon allocation at the end of 19th century (Hartmann and Trumbore 2016), the process of carbon allocation has gained recognition both in experimental as well as in modelling studies (Figure 10). The increasing attention to this process over the last 20 years results from ongoing climate change affecting the functioning of ecosystems (Charru et al. 2017). To synthesise carbon allocation modelling concepts from the reviewed models and literature we analysed approaches with regard to process representation in models along a gradient from fixed ratio to thermodynamic modelling approaches (Franklin et al. 2012), and its integration into ecosystem simulation, including environmental conditions and ecosystem processes that affect carbon allocation in the model. Based on our review and synthesis of experimental knowledge and modelling approaches we suggest that the major challenge is to overcome key limitations in understanding of carbon allocation fundamentals, which can subsequently enhance its description in models. This is in line with several recent works (de Kauwe et al. 2014, Garcia et al. 2016).

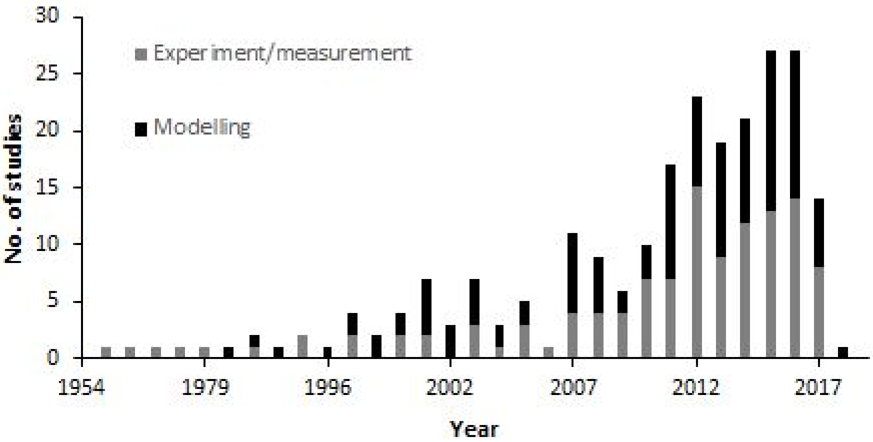


Figure 10. Temporal distribution of reviewed literature sources.

Due to the incomplete knowledge of allocation within plants, this component has long been considered as a major weakness of simulation models (Le Roux et al. 2001, Richardson et al. 2015). Despite considerable research focused on carbon allocation over the last years (Figure 10), a comprehensive picture of carbon allocation in trees is still missing There are still several methodological issues to be solved, particularly those focusing on measuring carbohydrates in plant tissues and the accurate determination of their absolute concentrations (Quentin et al. 2015), and explaining the role of NSC in plant tissues (Carbone et al. 2013).

For a better understanding and mechanistic description of carbon allocation in models more studies dealing with the effect of changing environmental conditions mostly as the consequences of climate change (Guillemot et al. 2015, Sevanto and Dickman 2015) are required. The accumulation and utilisation of NSC, the impact of disturbances on carbon allocation, and the carbon use by symbionts and/or for defense or repair are the areas of yet limited understanding in this field, which are likely to become more pressing issues with ongoing climate change.

The importance of NSC for plant survival and for post-disturbance regrowth has been documented by several authors, e.g. Barigah et al. (2013). Recently, Klein, Siegwolf, et al. (2016) found that temperate deciduous tree species store a large amount of NSC in their stems, which could be used for stem growth for a period of 7 to 30 years. For modelling purpose, NSC are important as reserves to repair or replace stress-related damages. This is a pre-requisite to mortality estimates and also affects long-term development including delayed recovery, and carry-over effects. The knowledge on the NSC mobilisation for metabolic activities would enhance not only our understanding of tree recovery and resilience adaptation mechanisms but also the estimates of both aboveground and belowground NPP provided by models (Langley et al. 2002).

The size of the NSC pool might also be used to define feedbacks to photosynthesis, decreasing the CO2 effect. Since photosynthesis controls short term carbon fluxes, more accurate representations of canopy layers, leaf temperature, and light intensity can be very important. However, forest growth and development are determined by complex interactions between allometry, competition and environmental conditions and therefore cannot be determined by photosynthesis alone (Dai et al. 2004, Kobayashi et al. 2012). By uncoupling photosynthesis and growth under stress conditions, e.g. drought, a more realistic representation of carry-over effect of stress periods on growth can be obtained due to buffering power of the carbon storage/reserve pool.

From the point of the long-term plant strategy, successful reproduction is the main evolutionary goal dependent on carbon allocation (Agren and Wikstrom 1993). When the conditions are met, the reproductive pool usually takes priority over the other compartments as long as its potential sink strength is not reached. Hence, omitting allocating carbon into reproductive organs, particularly during masting years, may be a cause of low prediction accuracy of forest models (Vacchiano et al. 2018). However, the potential sink strength is difficult to define. It is generally determined from a combination of temperature and growth history (Lescourret et al. 1998). In particular the state of reserves based on previous year growth conditions seems to be triggering fruit production (Piovesan and Adams 2001, Masaka and Maguchi 2001, Müller-Haubold et al. 2015). For example Vacchiano et al. (2017) showed that seed production in beech (Fagus sylvatica L.) responds negatively to temperature in the summer two years prior to masting, and positively to summer temperature one year before masting.

Similarly, simulating forest development under changing conditions may require accounting for the carbon allocation to symbionts (Hasselquist et al. 2015), since Bellgard and Williams (2011) showed that climate changes will significantly modify mycorrhisal diversity, which will subsequently affect plant growth and survival. Symbiotic mycorrhizal fungi are particularly important in nitrogen-limited environments. A recent paper studying carbon and nitrogen fluxes in boreal forests showed that a predictive power of a process-based model can be significantly enhanced by implementing an explicit dynamic model of ectomycorhizal fungi (He et al. 2018).

Increased empirical knowledge about carbon allocation in plants should stimulate the formulation of the carbon allocation pathways in models. This is of particular importance under changing environmental conditions because a realistic representation of processes in models may enhance their applicability in diverse situations (Seidl et al. 2011).

The choice of a model and an adequate principle depends on the hypotheses and scientific questions. We suggest to consider a sufficient number of modelling concepts and principles and to perform ensemble tests on different spatial scales in order to find the best principle in relation to available input data and a sensitivity analysis of the model as Cariboni et al. (2007) and Pianosi et al. (2016) suggested and as is performed in Fischlin et al. (1995), Alvenäs and Jansson (1997), White et al. (2000), Pappas et al. (2013). This will support model usage and provide useful material for users such as correlated variables and processes.

Although several different principles of carbon allocation modelling are available (Franklin et al. 2012), no single best option exists. Several publications (e.g. Lacointe 2000, Franklin et al. 2012, de Kauwe et al. 2014) recommended using the functional balance approach to explore the environmental effects on carbon allocation. However, Chen et al. (2013) pointed out that a bottom-up approach is not able to capture complex allocation patterns controlled by environment and suggested to use a top-down evolutionarily-based principle, which is considered to be the most robust approach for modelling carbon allocation (Drewniak and Gonzalez-Meler 2017). Nevertheless, according to Smith (1982), an evolutionarily stable approach is not the best realisation of carbon allocation in the population because competition among species is an important factor affecting their survival. In addition, due to the dynamic complexity of carbon allocation, integration of such an approach into models may be difficult and its application may be time demanding (Drewniak and Gonzalez-Meler 2017). On the basis of the model-data comparison, de Kauwe et al. (2014) reported that allocation schemes based on functional relationships and optimisation theory are more robust than those based on fixed allocation or resource limitation principles and thus, should be favoured when modelling carbon allocation. Pappas et al. (2013) and Fatichi and Leuzinger (2013) suggested using a more mechanistic representation of carbon allocation and translocation such as a carbon sink driven approach. In general, dynamic carbon allocation schemes responsive to limiting factors aboveground and belowground (Montané et al. 2017) should be favoured because they can at least principally respond to the new combination of environmental conditions expected under climate change (Campioli et al. 2008). In addition, it would be favourable if these schemes are based on physiological traits that are characterised by measurable parameters.

Furthermore, it should be noted that there is no uniform way to implement a dynamic carbon allocation because each single model differs in its internal structure, logic, and scale (temporal and spatial). Direction of the development needs to be model-specific. Process-based models have good representation of biogeochemical processes within the ecosystem, but they often lack the explicitly modelled stand structure and therefore dynamic allocation regarding competition between individuals cannot be simply implemented. On the other hand, hybrid models that have good representation of stand structure often miss the physiological detail such as a full nitrogen balance, needed to describe the sensitivity of allocation to specific environmental impacts. Only one model in our database (BALANCE) was a process-based model working at a single-tree level that can explicitly simulate stand structure and can therefore consider dynamic allocation in response to competition between individuals. This, however, is not only computational demanding but requires detailed knowledge about the tree species considered as well as a realistic representation of tree size and positions.

The applied allocation principle determines the temporal resolution of allocation. If variable allocation across years is aimed for, then the NSC dynamics need to be included in the allocation pattern, and the interaction of inter-annual and intra-annual carbon allocation must be considered. In the longer term, an evolutionary argument implies that certain balance principles must be met (e.g. Franklin et al. 2012, Mäkelä 2012). However, these may be violated at the shorter term due to the fact that environmental drivers during the growing season favour allocation to some parts relative to others (Pretzsch et al. 2015). Therefore models that cover short-term developments need to account for both kinds of allocation mechanisms as well as their interaction. To find a common ground in disputes such as the role of carbon in limiting tree growth, we need to recognise the central importance of time scales in any discussion about carbon allocation (Dietze et al. 2014), and we need to be aware that data interpretation might be complicated by issues of definition.

Data collection is always constrained by budget, equipment, labor availability, among others. Therefore, data collection must be optimised to bring as much information as possible to the understanding of the underlying processes studied. Ideally, we should aim for methods of direct quantification of carbon allocation, such as the use of isotopes enabling to trace the path of carbon from the assimilation to formation of new structures, especially when the allometric relationships have low explanatory power, such as fine roots and non-structural carbon and for studying the impacts of changing environmental conditions. When the use of allometric relationships is necessary, applying site and species-specific biomass measurements is warranted for evaluating and calibrating allocation models.

During the past years, a substantial improvement in the transparency of experiments in forest dynamics has occurred. The publication of datasets and raw data from experiments is becoming progressively more popular, and is often a mandatory requirement for publication in scientific journals. This increasing availability of published datasets is an important step towards a better understanding of ecological processes and can contribute substantially to carbon allocation modelling. Accordingly, the disclosure of raw data from forest experiments should be further encouraged, and efforts for harmonizing and standardizing these datasets will be crucial for a better description of carbon allocation patterns and reduce uncertainties in the calibration and forecasts provided by allocation models.

Finally, it is highly desirable that the improvement of carbon allocation processes preserves model simplicity (i.e. number of parameters) and model robustness (i.e. applicability) as far as possible. Improved models generally end up with an increased number of parameters which need to be derived from experimental and observational evidence. However, available data are often not sufficient to support and evaluate the processes within the new complex model. Moreover, models with higher spatial resolution need spatially more differentiated inputs that are often not available at a larger scale despite some improvements in the area of remote sensing techniques. As a result, model uncertainty increases causing an undesirable decrease in model applicability. Therefore, model improvements need to be performed with regard to this trade-off between model complexity and model robustness, and conceptually sound, experimentally supported processes that are consistent with the general model structure need to be pursued.

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Supplementary

A. *Questionnaire*

1. General information about the whole modelling system

1.1. Name of the model * (the whole modelling system)

1.1.1. Name of the subsystem / module, which comprises a carbon allocation model you will describe below

If the whole modelling system consists of several different modules used in specific cases, e.g. in different vegetation types, please indicate the name of the subsystem, in which the described carbon allocation model is incorporated.

1.1.2. Ecosystems that can be simulated by the subsystem / module you entered in question 1.1.1. (or the whole modelling system if you did not answer question 1.1.1.) *

- forest
- arable land
- grassland
- shrubland
- wetland
- C3 plants
- C4 plants
- Other:

1.2. Modelling concept of the subsystem / module, which comprises the carbon allocation model you are going to describe below *

Please, tick one or more appropriate options

- hybrid (combination of any below-listed concepts) - please tick the concepts that are used in the model
- empirical (based on statistical relationships derived from empirical data)
- structural (development of tree morphology)
- physiological / process-based (based on mathematical description of processes in ecosystems)
- theoretical (data-free concept based on mathematical or physical theories)

1.2.1. Predominant modelling concept

If your system/subsystem uses a hybrid approach, tick the basic approach the system is built upon

- empirical
- structural
- physiological / process-based
- theoretical

1.3. Modelled object *

The minimum representative level of your modelling system. (= the object that the applied mathematical algorithms and input state variables are related to.)

- ecosystem (e.g.biome)
- population (e.g. forest stand)
- class / cohort (e.g. diameter class)
- organism / individual / tree
- organ (e.g. leaf)

1.4. Modelled spatial scale *

- global
- landscape
- region
- forest stand
- biogroup (a group of trees in a specific developmental phase covering an area of 100 to 1,000 m2. A biogroup can consist of several cohorts or size classes.)
- cohort / size class (a group of trees with identical properties, e.g. size, species)
- modelled object located in 2D space (e.g. tree or organ)
- modelled object located in 3D space
- Other:

1.5. Prevailing spatial unit simulated by the modelling system/subsystem

If you specified more than one spatial scale in the previous question, please indicate the scale for which the model is used most frequently

- global
- landscape
- region
- forest stand
- biogroup
- cohort / size class
- modelled object located in 2D space
- modelled object located in 3D space

1.6. Resolution of minimum spatial unit

Please indicate an area or pixel size (e.g. 100x100m)

1.7. Shortest model time step *

that your modelling system is able to simulate

- millenium
- century
- decade
- 5 years
- year
- month
- day
- hour
- minute
- Other:

1.8. Applicable region *

Please tick all regions for which the model was parameterised

- Boreal
- Temperate
- Mediterranean
- Tropical

1.9. The country of model origin *

1.10. Number of carbon allocation models incorporated in one subsystem / module *

Please specify how many carbon allocation models are incorporated in the subsystem, e.g. if the subsystem uses different carbon allocation models for C3 and C4 plants, the answer is 2

2. Information about carbon allocation modelling

If your modelling system comprises more carbon allocation models used in specific conditions, please fill in this part for each carbon allocation model separately.

2.1. Principles of carbon allocation modelling *

(based on de Kauwe et al. 2014 and Franklin et al. 2012)

- empirical approach (based on statistically described relationships)
- functional relationship (based on the scaling relationships among plant organs)
- functional-balance approach (allocation is controlled to ensure internal balance among organs, e.g. root vs. shoot growth)
- eco-evolutionarily-based approach (allocation is determined by maximising a fitness proxy, e.g. photosynthesis, NPP)
- thermodynamic approach (maximisation of entropy / entropy production)
- Other:

2.2. Type of carbon allocation modelling *

(based on de Kauwe et al. 2014, Franklin et al. 2012, Fabrika and Pretzsch 2011, Lacointe 2000)

- fixed ratios (fixed fractions of assimilated carbon are allocated to individual organs)
- allometry (growth of an organ is related to the growth of the whole organism or its other part)
- teleonomic (functional) balance of root/shoot activities
- resource limitation (allocation depends on the most limiting resource to growth)
- pipe model (based on the balance between foliage and sapwood)
- mechanical constraints (allocation of biomass along the stem ensures mechanical stability of a tree)
- transport-resistance model (allocation is driven by concentration of elements: carbon, nitrogen)
- source-sink model (allocation to individual compartments is controlled by their demands and the availability of assimilates)

- optimal response (maximisation of a fitness proxy, e.g. photosynthesis, with respect to functional traits, e.g. stomatal conductance, subject to environmental and/or physiological constraints, e.g. N balance)
- game-theoretic optimisation (based on the concept of an evolutionary stable strategy, when the success of each individual depends on the competition with other individuals)
- adaptive dynamics (based on the concept of an evolutionary stable strategy, the allocation at the individual level evolves through the effect of selection via explicit modeling of population dynamics)
- maximum entropy production (based on thermodynamics, which identifies the most likely allocation considering the state of population)
- Other:

2.3. Time step of the carbon allocation model *

- minute
- hour
- day
- month
- year
- 5 years
- decade
- century
- millennium
- Other:

2.4. Spatial scale of the carbon allocation model *

Please specify, at what spatial level allocation occurs.

- tree
- cohort
- stand
- region
- biome
- Other:

2.5. Parameters affecting carbon available for allocation *

Please indicate the parameters that modify GPP prior to the allocation itself. Do not indicate the variables driving GPP, but specify what parameters affect the total amount of carbon that is available for the allocation. Use semicolon (;) to separate multiple entries under "Other" option.

- growth respiration
- maintenance respiration
- temperature
- CO2 concentration
- light availability
- nitrogen availability
- water availability
- availability of other nutrients - please specify which nutrients in question 2.5.1.
- disturbance - please specify the type of disturbances in question 2.5.2.
- phenology
- no
- Other:

2.5.1 What nutrients affect carbon available for allocation?

Please indicate the nutrients that modify GPP prior to the allocation itself. Use semicolon (;) to separate multiple entries under "Other" option.

- P (Phosphorus)
- K (Potassium)
- Mg (Magnesium)
- Other:

2.5.2. What disturbances affect carbon available for allocation?

Please indicate the disturbances that modify GPP prior to the allocation itself. Use semicolon (;) to separate multiple entries under "Other" option.

- wind
- fire
- insects
- drought
- Other:

2.6. Individual compartments for carbon allocation *

Please specify the smallest pools your model uses in the allocation algorithm. If your model identifies more detailed or lumped compartments not specified below, e.g. stem+branches+roots, please indicate that under "Other" option. Use semicolon (;) to separate multiple entries under "Other" option.

- leaf
- live stem / sap wood
- dead stem / heart wood
- stem (sap wood + heart wood)
- live coarse roots
- dead coarse root
- coarse root (live + dead coarse root)
- fine root
- root (coarse root + fine root)
- branch
- crown (branch + twig + leaf)
- flower
- pollen
- fruit (including seeds)
- seed
- storage / reserve
- vegetative reproduction
- stem + crown
- stem + branch
- branch + root
- branch + coarse root
- aboveground carbon (leaf + stem + crown)
- belowground carbon (coarse root + fine root)
- tree diameter
- tree height
- tree volume
- diameter increment
- height increment
- volume increment

- Other:

2.7. Constant parameters *

Please specify, which carbon allocation parameters / coefficients are kept constant during a single simulation. Use semicolon (;) to separate multiple entries under "Other" option.

- C:N ratios of individual compartments
- compartment fractions (i.e. parameters specifying the proportion of carbon allocated to each compartment)
- compartment allocation ratios (i.e. ratio of allocated carbon between two compartments, e.g. ratio between carbon allocated to new stem and carbon allocated to new leaf)
- allometric coefficients (i.e. coefficients of allometric relationships)
- fraction of growth respiration
- fraction of maintenance respiration
- growth proportion
- reproduction fraction
- Other:

2.7.1. Can the constant parameters be changed by a model user for different simulations? *

- No, they are defined in the source code
- Yes, they can be changed e.g. in input box, file
- Some parameters can be changed externally - please specify below in question 2.7.2.

2.7.2. Which constant parameters can be changed by a model user for different simulations?

Please answer this question if you selected the last answer on the previous question 2.7.1. Use semicolon (;) to separate multiple entries under "Other" option.

- C:N ratios of individual compartments
- compartment fractions
- compartment allocation ratios
- allometric coefficients
- fraction of growth respiration
- fraction of maintenance respiration
- growth proportion
- reproduction fraction
- Other:

2.8. Priority of carbon allocation to any compartments *

Please specify if carbon is allocated according to any pre-defined priorities.

- No
- Yes, please specify below in questions 2.8.1 to 2.8.3.

2.8.1. If carbon allocation is prioritised to any compartments, please specify the compartment of the 1st priority below

Use semicolon (;) to separate multiple entries under "Other" option.

- leaf
- stem
- root
- fruit
- fine root
- coarse root
- live stem / sapwood
- dead stem / heartwood
- Other:

2.8.2. If carbon allocation is prioritised to any compartments, please specify the compartment of the 2nd priority below

Use semicolon (;) to separate multiple entries under "Other" option.

- leaf
- stem
- root
- fruit
- fine root
- coarse root
- live stem / sapwood
- dead stem / heartwood
- Other:

2.8.3. If carbon allocation is prioritised to any compartments, please specify the compartment of the 3rd priority below

Use semicolon (;) to separate multiple entries under "Other" option.

- leaf
- stem
- root
- fruit
- fine root
- coarse root
- live stem / sap wood
- dead stem / heart wood
- Other:

2.8.4. If carbon allocation is prioritised to compartments depending on the phenological phase, please specify the phase and the compartment(s), which is prioritised in the specific phase

Example: leaf unfolding - leaf; leaf colouring - root. Use semicolon (;) to separate multiple entries.

2.8.5. If carbon allocation is prioritised to specific compartments depending on any other parameter, please specify the parameter and individual states of the parameter (if applicable) and the compartment(s), which is/are prioritised

Example: leaf damage by insects - leaf. Use semicolon (;) to separate multiple entries.

2.9. Sensitivity of the carbon allocation algorithm to *

Please tick what parameters drive carbon allocation (e.g. type of allocation, its parameters, coefficients, equations). This question does not refer to the sensitivity of GPP algorithm. Use semicolon (;) to separate multiple entries under "Other" option.

- air temperature
- precipitation
- CO2 concentration
- light availability
- soil water
- nitrogen
- soil nutrients - please specify them in question 2.9.1.
- competition
- leaf phenology
- size of the modelled object (e.g. tree)
- age of the modelled object (e.g. tree)
- compartment senescence (e.g. fine root mortality)

- tree species (group) / functional type - please specify them in question 2.9.2.
- genetics
- no
- Other:

2.9.1. What soil nutrients is the carbon allocation algorithm sensitive to?
Use semicolon (;) to separate multiple entries under "Other" option.

- P (Phosphorus)
- K (Potassium)
- Mg (Magnesium)
- Other:

2.9.2. If the carbon allocation model is sensitive to tree species / functional types, please specify the particular tree species (groups) or functional types the allocation model is applicable to

2.10. Was the carbon allocation model evaluated on data? *

- No
- Yes - please specify the data set below in question 2.11.

2.11. If the carbon allocation model was evaluated on data, please specify the data set and provide the reference (e.g. ICP Level II plots of Slovakia, Author, Year, Literature source)

2.12. Why was this carbon allocation model chosen? *
Please tick one or more appropriate reasons. Use semicolon (;) to separate multiple entries under "Other" option.

- Literature survey
- Expert opinion
- Model simplicity
- Data availability / requirements
- After the test of multiple carbon allocation models
- Sensitivity to environmental conditions
- I do not know
- Other:

2.13. Have you identified any problems of the implemented carbon allocation model? *

- No
- Yes - please specify them in question 2.13.1.

2.13.1. What problems of the implemented carbon allocation model have you identified?

3. General information

3.1. Reference - forest growth model (modelling system or subsystem) *

3.2. Has the implemented carbon allocation model been published? *

- No - please specify the reason in question 3.2.1.
- Yes - please provide the reference in question 3.2.2.

3.2.1. Why has the carbon allocation model not been published?

- It has not been validated
- It is a modification of another model - please specify it in question 3.2.2.
- Other:

3.2.2. Reference - carbon allocation model *

3.3. Reference - carbon allocation parameters *

3.4. May we contact you for further information if needed? *

- yes - please fill in questions 3.5. and 3.6.
- no

3.5. Your name

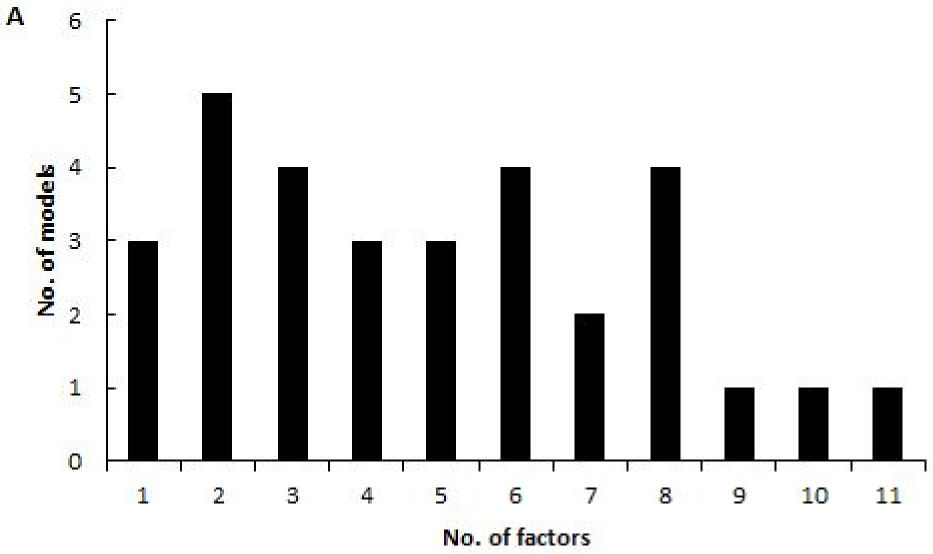
3.6. Your e-mail address
3.7. Please indicate whether you are *

- a model developer
- a model user

3.8. The country in which you are professionally active *
3.9. Comments

B. *Partial results*

A descriptive sensitivity analysis of carbon allocation models identified 17 properties which influence simulated carbon allocation in the examined models. We divided the factors into three main groups representing climatic conditions (4 factors), soil characteristics (4 factors), and plant or stand properties (9 factors). Although all models included at least one factor, none of them accounted for the direct impact of all the identified factors on modelled carbon allocation (Figure S1A). Only the factors from the group of plant characteristics were considered in every model from our database (Figure S1B). Only three models accounted for more than 50% of the factors (i.e. more than 8), while the majority of models (58%) included five or fewer factors and three models included only one factor (Figure S1A).
From plant characteristics, tree species or similar differentiation of vegetation (e.g. biomes, plant functional types, tree species groups) was the most common factor included in 23 models (74%, Figure 5). More than 50% of the models (16 models) accounted for the impact of leaf phenology or the size of the modelled object on the simulated carbon allocation, while wood phenology, genetics and the size of the allocated pool were considered only in one model each (Figure 5).



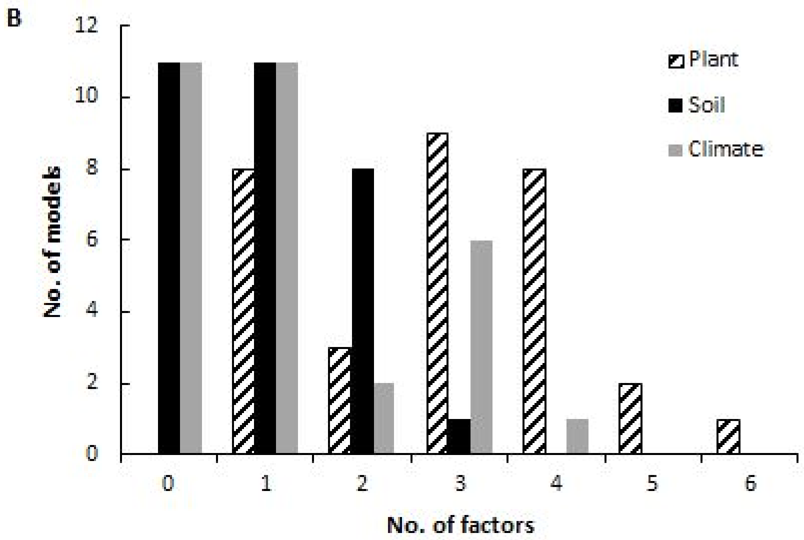


Figure S1. Frequency distribution of models with regard to number of environmental and stand/tree factors directly affecting simulated carbon allocation (A) divided into three main groups representing plant and stand characteristics, soil and climate conditions (B).

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