



Review

Representation of species mixing in forest growth models. A review and perspective



Hans Pretzsch^{a,*}, David I. Forrester^b, Thomas Rötzer^a

^a Technische Universität München, Chair for Forest Growth and Yield Science, Hans-Carl-von-Carlowitz-Platz 2, D-85354 Freising, Germany

^b University of Freiburg, Chair of Silviculture, Tennenbacherstr. 4, 79108 Freiburg, Germany

ARTICLE INFO

Article history:

Received 9 January 2015

Received in revised form 26 June 2015

Accepted 29 June 2015

Keywords:

Emergent properties

Niche complementarity

Inter-specific interactions

Process based models

Stand-level models

Tree-level models

ABSTRACT

Mixed-species forests can sometimes fulfil forest functions and services better than monocultures and are therefore receiving growing attention in forest science and practice. The productivity of mixtures and the interactions between species are influenced by the availability of different resources and climatic conditions, all of which change spatially and temporally. Models are a valuable tool for understanding and predicting how these interacting factors will influence the growth and other functions and services in mixed-species forests. However, concepts, models and theory are still mainly based on monocultures, which have dominated forest science since its beginnings. Recent empirical works report strong effects of mixing tree species on the environmental conditions within stands (e.g., vertical light profile, rooting space, humus layer), their functioning (e.g., photosynthetic rate, light use, growth), and tree and stand structure (e.g., crown and stem shape, shoot and root morphology). Process-based organ- or tree-level approaches reveal changed resource supply, flows and metabolic rates in high spatial and temporal resolution. Stand-level approaches usually provide predictions with a lower spatial and temporal resolution but can be more accurate in the longer-term. Many studies stress considerable effects of mixing tree species on growth dynamics, yield, resilience and stability, but these effects are still under-represented in existing models. We reviewed 54 forest growth models to show how they incorporate the variability of individual tree or species characteristics that occur in forests and how this variability influences the development and characteristics of the whole stand. While some organ- or tree-level models inherently integrate evident processes, stand-level models do not usually explicitly consider species interactions. Nevertheless, many processes that occur in mixtures can also be modelled at the stand level and are often included in stand-level monospecific models. Stand-level models are likely to offer a simpler alternative model structure for mixtures. We stress how both model approaches can be refined, benefit from mutual adjustment, and can be substantiated by further empirical research into mixed-species forests.

© 2015 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

Contents

1. Introduction	277
2. Overview on empirically revealed mixing effects and their relevance for tree and stand dynamics	278
3. Review of forest growth models and representation of mixing effects	278
3.1. Overview of reviewed models	278
3.2. Essential principles for predicting the stand growth of mixtures	279
3.3. Representation of mixing effects	283
3.3.1. Functioning	283
3.3.2. Structure	286
3.3.3. Environment	286

* Corresponding author. Tel.: +49 8161 714710.

E-mail address: h.pretzsch@lrz.tum.de (H. Pretzsch).

4. Perspectives	287
4.1. Future empirical work: Experiments, monitoring, statistical evaluation	287
4.1.1. Combining data from different spatial and temporal resolutions	287
4.1.2. Incorporation of defoliation effects into models	287
4.1.3. Below-ground processes	287
4.1.4. Responses to climate	287
4.2. Integration at which scale?	287
5. Conclusions	288
Acknowledgements	289
References	289

1. Introduction

Forest growth modelling involves the abstraction of real forest stand dynamics into a conceptual or biometric description. The degree of abstraction depends on existing knowledge about the structure and behaviour of the real system, and also on the reason for developing the model. The systems model can be transferred to a computer programme, creating a simulation model (stand simulator) that allows systems behaviour to be reproduced. In this context, we define simulation as the reproduction of systems behaviour with the aid of a computer. The focus of this review is on models and simulators which may start from the organ- or individual-tree levels, and reach up to the forest stand level, or models that start and finish at the stand level. They should cover the whole lifetime of a stand, but not necessarily stand regeneration. The reviewed models may encompass a broad range of forest functions and services, but mainly aim at modelling tree and stand productivity.

Due to the long lifespan of forest stands and the rarity of experiments covering these lifespans, thoroughly tested models have become indispensable for “fast forward” simulations and analyses in forest research and practice. Beginning with the first experience tables (e.g., Hartig, 1795), yield tables (Schwappach, 1889), mean-tree models (Assmann and Franz, 1965) or diameter distribution models (Gadow, 1987), and more recently, individual-tree simulators (Pretzsch et al., 2002), empirical work and modelling has focused on the productivity of monocultures. The approach was mainly based on the stand-level, i.e., dendrometry variables (e.g., height, volume, site index) were used to describe the growth of trees or whole stands over time. However, transition to individual-tree approaches in silviculture (e.g. crop tree thinning and selection cutting), and interest in disturbance effects (e.g., by air pollution, nutrient export with harvest, climate change) triggered tree-level research into the functions, spatial structures and environmental conditions in order to model yield and productivity (Ulrich, 1990). This development of the classic stand-level concept by tree-level (or organ-level) research and modelling, and especially their combination, paved the way for models that have the potential to represent species mixing effects.

The strong influence of agronomy on forest practice has resulted in extensive forest monocultures, however, mixed-species stands are now receiving more attention (Scherer-Lorenzen et al., 2005) because they have the potential to supply ecological, economic and socio-cultural forest goods and services at similar or even higher levels than monocultures (Hector and Bagchi, 2007; Hooper et al., 2005). While monospecific forestry and science is equipped with a considerable set of models developed and tested over more than 200 years, mixed-species stands have received much less attention.

Some studies model mixtures using monospecific models by artificially separating the species within a given mixed-species stand according to their mixing proportions and growing each species according to the properties of the respective monocultures, or they use parameter sets that apply to whole mixtures (rather than each individual species) (Kramer and Akça, 1995; Nightingale

et al., 2008; Peters et al., 2013). This avoids the need to use a model that considers species interactions but it assumes that stand dynamics of mixed-species forests are the weighted mean of the respective species monocultures or that the species interactions do not change along spatial or temporal gradients in resource availability or climatic conditions.

In reality, many recent studies in theoretical ecology (Hector et al., 2002, 2010; Loreau et al., 2001), growth and yield science (Griess and Knoke, 2011; Pretzsch et al., 2010, 2013a) as well as meta-analyses (Paquette and Messier, 2011; Piotta, 2008; Zhang et al., 2012) show that the productivity of mixed-species stands can exceed the weighted mean productivity by 50% in mixture with nitrogen-fixing species (Forrester et al., 2006b) and by 20–30% in other mixtures (Pretzsch et al., 2013b). This indicates that relying on the weighted mean of monocultures will not enable the simulation of these mixed species dynamics and that closer consideration of mixing effects will be necessary in future models.

The development of such models can be facilitated by many reviews that have examined different types of species interactions and their effects on the growth dynamics of mixed-species forests (Kelty, 1992). These have included reviews or meta-analyses about nutrient-related processes (Richards et al., 2010; Rothe and Binkley, 2001), including nitrogen fixation (Binkley, 1992; Forrester et al., 2006b), water-related processes (Forrester, 2015), inter- and intra-specific variability in crowns (Pretzsch, 2014), which has implications for light-related interactions relating to light absorption and light-use efficiency (Binkley et al., 1992a; Forrester et al., 2012; Forrester and Albrecht, 2014), and modification of yield (Pretzsch, 2010, 2013), carrying capacity (Helms, 1998; Pretzsch, 2013), and resilience to biotic (Jactel et al., 2005; Jactel and Brockerhoff, 2007) or mechanical disturbances (Dhôte, 2005).

A further complexity is that interactions between a given pair of species are not static; they change along spatial and temporal gradients in resource availability and climatic conditions (Forrester, 2014b). For example the facilitative effect of nitrogen-fixing species on the growth of non-nitrogen-fixing species increases as nitrogen availability decreases. However, this also depends on the availability of other resources because if water availability is low, then water could limit growth and prevent the trees from making use of the fixed nitrogen. It is difficult to control for these interacting resources or climatic factors using experiments and mixed-species models are likely to be a valuable tool for determining how these interacting factors combine to influence forest growth. So far, we could not find any models that have been tested for their ability to reproduce these spatial and temporal dynamics.

Existing organ- or tree-level process-based approaches (e.g., Kimmins and Scoullar, 1989; Rötzer et al., 2009, 2010) may inherently represent some species interactions, but have rarely been evaluated because the necessary state variables from long-term observation of mixed stands are rare. Stand-level empirical approaches (Hasenauer, 1994; Pukkala, 1987; Pretzsch et al., 2002) fitted using long-term experimental or inventory data may reflect

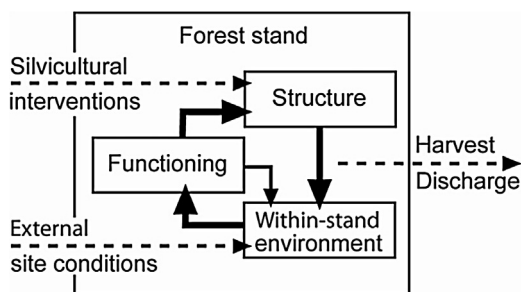


Fig. 1. Schematic representation of the connection between environment, functioning and structure. The species within the stand can modify their environment slowly via structure (solid feedback circle) or quickly via functioning (thin line). External factors, such as silviculture and site conditions can modify the internal environment and silviculture can also modify the structure (modified after Hari, 1985).

part of the mixing effects, however, as long as they don't consider their causes and dependencies on site conditions they cannot be relied upon for site-specific forest planning. As a way out of this lack of both dendrometric data and mechanistic knowledge on mixed-species versus monospecific stands, hybrid models try to combine stand-level bioassay (Kimmins et al., 1990a,b, 1999) with organ- or tree-level mechanisms (Grote and Pretzsch, 2002).

A pivotal question that influences the attractiveness of mixtures to foresters is how their productivity compares with monocultures. To remove some of the uncertainty about the growth dynamics of mixtures and to make more use of their potential improvements in ecosystem services (compared with monocultures), it will be necessary to develop sound knowledge and reliable models for the assessment of their dynamics, productivity and stability compared with monocultures. Many forest growth models have been developed but there is considerable variability in their structure, the processes that are represented, temporal and spatial scales, and the species or locations where they have been tested. This can make it difficult to interpret results, compare different models and to select the models that are most appropriate for specific needs.

This review aims to provide a basis for the selection of appropriate models and to suggest which processes are most important and when. The review focuses on the effect of tree species mixing on the three main interacting units of forest stand dynamics: the functioning of trees and stands, the stand and tree structure and the environmental conditions within the stand, which can influence the functioning of the trees and is itself influenced by the structure (Fig. 1). First we give an overview of mixing effects that can emerge in mixed-species stands at different spatial and temporal scales. We further characterise possible approaches for their reproduction in growth models. We describe effects that result from instantaneous phenomenon at a point level (e.g., occurrence of hydraulic redistribution) to long-term effects at the ecosystem level (e.g., improvement of site resource supply within a stand's life). Then we review whether forest growth models consider mixing effects and how the effects are biometrically integrated and evaluated. Finally we discuss how tree- and stand-level model approaches can be refined, benefit from mutual adjustment, and substantiated by further empirical research into mixed-species forests.

2. Overview on empirically revealed mixing effects and their relevance for tree and stand dynamics

As illustrated in Fig. 1 forest stand dynamics can be conceptualized as an interaction between the environmental conditions within the stand (e.g., light profile, moisture content in humus, temperature in the canopy), the functioning of the system elements (e.g., transpiration, photosynthesis, growth), and the generated structures (e.g., stem, root, crown structure). There is a strong

feedback between all three units: canopy structure for instance determines the light conditions within the stand, the light supply drives photosynthesis, and growth, allocation and the standing biomass results in tree and stand.

The effects of mixing tree species on environment, functioning, and structure can be studied and modelled at different spatial and temporal scales. High resolution studies measure or model the environmental conditions, functioning, and structural changes at the tree, organ or cell levels and in time steps of minutes and hours. These are sometimes also referred to as "bottom-up" approaches. They integrate the effects of species interactions with high spatial and temporal resolution but sometimes produce questionable output when scaled up (e.g. from the tree to the stand level). Lower resolution or stand-level approaches may summarise stand dynamics in monthly-, annual- or even five-year-steps. Models using this approach, also referred to as "top down" models, attempt to reflect the effects of species interactions without the same spatial or temporal resolution for causal drivers. While organ- and tree-level approaches often integrate known processes in a more realistic way, stand-level approaches reveal whether the processes have significant effects on the long-term system dynamics. In the following we classify species interactions and their effects on forest growth using different spatial scales (point, part of the stand, tree versus whole stand and ecosystem) and temporal scales (minute, hour, day versus year decade, lifetime of a tree) and the system components environment, functioning, and structure (Table 1).

An overview of frequently reported processes or stand attributes that can be influenced by mixing tree species is shown in Table 2. These are defined in terms of their temporal and spatial resolution as well as their effects on the stand environment, functioning, and structure. In addition the requirements and approaches that can be used to reproduce these mechanisms in growth models are discussed. For example, to simulate the water translocation in the soil by a deep-rooted species (or tree) to a shallow-rooted species (or tree) the soil layers have to be linked and in the case of tree-to-tree translocation there might also need to be quantification of horizontal differences in soil water availability as effected by different individual trees. This requires a sophisticated water balance module with a low spatial scale (tree) and a short temporal scale (day) to be able to simulate the processes at the scales on which they occur.

To mechanistically reproduce species mixing effects in growth models it is necessary to describe the respective processes and cycles, such as the distribution of light or the water cycle. For the reproduction of some mixing effects (e.g., light flecks, crown plasticity) growth models based on tree individuals are required. However, the effects of mixing tree species on the environment, function or structure cannot be grouped in terms of a specific cycle or process chain. For example, within the water cycle mixing effects at fine spatial scales (organ or tree level) affect the stand environment at coarser spatial scales (e.g. stand precipitation, interception) and also affect the functioning (e.g. hydraulic redistribution or water uptake during drought). Furthermore, at coarse temporal scales of several years, species mixing might be able to change the soil water holding capacity.

3. Review of forest growth models and representation of mixing effects

3.1. Overview of reviewed models

The selection of growth models was based on the review of Fontes et al. (2010) who described existing process-based growth models for Europe. This list was enlarged by adding growth models described in Pretzsch et al. (2008) or Burkhardt and Tomé (2012) or

Table 1

Effects/symptoms of species mixing effects with respect to the inner stand environment (E), functioning (F), and structure (S), occurring at different spatial and temporal scales.

Spatial scale	Temporal scale	
	Short-term (minute, hour, day)	Long-term (year, decade, lifetime)
Point, parts of stand, tree	E: light flecks, wind speed reduction F: photosynthesis, hydraulic redistribution S: cell structure, tree ring development	E: root channels, root layers F: tree mortality, leaf turnover S: tree crown plasticity
Whole stand, ecosystem	E: canopy climate (CO ₂ and H ₂ O exchange) F: allelopathy, water translocation S: current height growth	E: soil fertility, nutrient supply F: gap dynamic, regeneration S: standing stock, potential stand density

found by reviewing the literature. The resulting 54 forest growth models form the basis of our study (Table 3). The aim is not to produce an exhaustive list of models but to include a wide range of different models. We did not include models with temporal scales that exceeded a stand's lifetime, and the models did not need to include stand regeneration.

The growth models listed in Table 3 are classified according to their approach for modelling forest dynamics; process-based, empirical and hybrid, and in terms of their spatial and temporal resolutions.

Process-based models basically simulate physiological processes that influence growth and how these processes are influenced by the environment (Pretzsch et al., 2008; Fontes et al., 2010). These models can potentially account for species interactions that influence any of the processes and environmental conditions considered in the model. *Empirical growth and yield models* are usually based on inventory data or tree ring records. Interactions are included empirically using correction factors and competition indices. Like process-based models these empirical models can be tree-level models or stand-level models. *Hybrid models* couple empirical and mechanistic elements. Two types of hybrid models exist: One type combines process-based and empirical models (Baldwin et al., 2001) by generating signal-transfer environment productivity functions (e.g. Luxmoore et al., 2002), the other has a causal structure comprising both empirical and mechanistic components (Pretzsch, 2009).

Most of the models (38) listed in Table 3 are process based; only some of them are defined as hybrid (10) or empirical models (8). The time steps of the calculations range from less than hourly to periods of 5 years. Time steps of empirical models are often 1-year or 5-year periods, while most of the hybrid models operate on annual time steps. The time step of the process-based models vary from 1/50 h (EMILION) to years (e.g. FORMIND or TRAGIC). Most process-based models, however, simulate at daily time steps. The shortest time steps are mainly used to simulate resource distributions such as water availability, while growth and productivity are often calculated over longer time steps. In BALANCE, for instance, the water balance and micro-climate for each individual tree are simulated on a daily step, while tree growth is calculated for a period of 10 days (Rötzer et al., 2013).

Process-based and empirical models often assume that the species compositions are relatively constant, but these can change, especially over long time scales in response to changes in climatic conditions and stand disturbances (Medlyn et al., 2011). Gap models attempt to capture these changes in species composition and generally simulate establishment, growth and mortality (see review by Taylor et al., 2009 or Shugart and Smith, 1996). A forest is then divided into gaps that may or may not interact with each other.

The basic spatial unit of all reviewed empirical models is the individual tree, with the exception of the model CO2FIX V.2 which operates at a cohort level. The spatial unit of the process-based models is divided evenly between individual, cohort and stand scales. Cohort- and stand-levels are the same

except that cohort models can deal with more than one species. Hybrid models operate either on an individual tree or stand level.

The topic of this review is how growth models can simulate mixing effects and therefore the models should be able to simulate more than one species simultaneously, or have the capacity to do so without significant modification. They must also include a broad range of forest functions and services, and aim to model tree and stand productivity. It must, however, be noted that establishment phases of forest stands are not considered in this review.

3.2. Essential principles for predicting the stand growth of mixtures

Four main algorithms are commonly applied to predict the stand growth of mixtures (Fig. 2). If no information is available, mixed-species stand development is simply assumed to be the weighted mean of the monocultures' productivity (Fig. 2a). This is done by first, choosing appropriate monospecific stand models (e.g., yield tables or diameter distribution models) for the respective species. Second, sub-models for the respective site index and thinning are chosen. Then the species-specific time series of growth and yield characteristics (e.g., productivities $p_1, p_2 \dots p_n$) are read out of the monospecific stand models, and used to calculate the weighted mean based on the proportion of the stand that each species contributes. In this way, mixing proportions ($m_1, m_2 \dots m_n$) in the mixtures are used to calculate their expected performance as a weighted mean of the monoculture productivity (e.g., $p = p_1 \times m_1 + p_2 \times m_2 + \dots + p_n \times m_n$). Other stand growth characteristics such as tree number, basal area, standing volume, or basal area growth are derived analogously. Fig. 2a illustrates the simple linear and sequential procedure; i.e., this approach does not consider any interactions between species, even though these interactions can determine their long-term development. This concept is represented in the yield tables for monospecific forest stands by Assmann and Franz (1965) and Schwappach (1889), and the yield tables for mixed-species stands of *Picea abies* and *Fagus sylvatica* by Wiedemann.

Most models abstract forest stands by their vertical layering. The three-dimensional structure is more detailed in tree-level models and is typically defined using variables such as tree height, height to crown base, crown width and tree coordinates. In empirical models, the 2D or 3D structure is the basis for calculating competition indices for every tree as a proxy for the availability of resources. These competition indices are used to regulate the individual trees' growth and the probability of survival in the subsequent period. The size of all trees and structure of the whole stand can then be updated using the estimates of individual growth rates and survival/dropout. Stand growth and species-specific growth rates are then calculated from the sum of individual-tree growth (Fig. 2b). The updated stand structure is the basis for the next prognosis cycle with typical time steps of 1 or 5 years. Due to the feedback between stand structure and tree growth via the competition indices, species interactions can significantly affect stand development, e.g., by

Table 2
Potential changes in stand structure, functioning and with-stand environment that can result from mixing tree species in forests. The factors are listed starting from high resolution to low resolution as well as their classification and prerequisites for their mechanistic reproduction in individual-tree and cohort models. The cycles and processes that have to be simulated are also indicated (l: light; n: nutrient cycle; p: phenology; s: spatial structure; w: water cycle; o: other). Please notice that regeneration dynamics are excluded.

Temporal scale	Spatial scale	Effect on	Factor influenced by the mixing of species	Prerequisites and possible mechanistic reproduction		Required description
				Individual tree models	Cohort (stand) models	
Short (hour, day, month)	High (organ, tree)	Environment	Light flecks	Highly resolved spatial structure of the model	Not possible	l
			Wind speed reduction	Change of wind speed for calculation of transpiration, leaf temperature	Change of wind speed for calculation of transpiration, leaf temperature	o
			Water balance	Individual tree transpiration, soil water availability, canopy rainfall interception by each tree	Transpiration by each cohort, soil water availability, canopy rainfall interception by each cohort	w
Short (hour, day, month)	High (organ, tree)	Functioning	Light absorption and photosynthesis	Light gradient for individual tree influenced by neighbouring trees, and changes in inter-tree shading due to changes in stand density	Light availability reduction based on competing cohorts, and changes in inter-tree shading due to changes in stand density	l
			Hydraulic lift	Linked soil layers for individual trees	Linked water availability for each cohort	w
			Water uptake and drought stress	Exchange of water in the rooting zone, linked soil layers for individual trees, within canopy climatic gradients	Drought index, linked water availability for different cohorts, within canopy climatic gradients	w
Short (hour, day, month)	High (organ, tree)	Structure	Cell structure	Highly spatially resolved models	Cohort based predictions	s
			Ratio of early to late wood	Highly spatially resolved models	Cohort based predictions	s
			Phenology (temporal partitioning of growing space)	Species-specific simulation of bud burst, leaf fall and length of growing season	Cohort-specific simulation of phenology	p
Short (hour, day, month)	Low (tree, cohort)	Environment	Matter balance and partitioning	Different matter balances (C, N, H ₂ O) have to be predicted for each individual tree	Different matter balances (C, N, H ₂ O) have to be predicted for each cohort	n
Short (hour, day, month)	Low (tree, cohort)	Functioning	Allelopathy	Inhibition of germination and growth through chemicals, simulation of allelochemicals or carbohydrates	Simulation of allelochemicals or carbohydrates	o
			Water translocation from species to species	Linked soil layers for individual trees	Linked water availability for cohorts	w
Short (hour, day, month)	Low (tree, cohort)	Structure	Current height growth	Simulated on tree basis	Influence of neighbouring cohorts on height growth	s
Long (≥year)	High (organ, tree)	Environment	Root channels	Linked root sections for individual trees, change of soil characteristics	Change of soil characteristics depending on species	s
			Root layers and zones	Partitioning of root space, linked root sections for individual trees	Root space for different species, link between cohorts	s
Long (≥year)	High (organ, tree)	Functioning	Tree mortality	Species-specific simulation of mortality depending on neighbouring trees	Species-specific simulation of mortality depending on neighbouring cohorts	s
			Leaf turnover (dependent on nutrient cycle, water balance, light)	Simulation of nutrient and water cycles with linkages between trees	Simulation of nutrient and water cycles with linkages between trees between cohorts	n
Long (≥year)	High (organ, tree)	Structure	Tree crown and root plasticity	Crown and root architecture of each tree must be known	Mean crown and root architecture of each species must be known	s
Long (≥year)	Low (tree, cohort)	Environment	Soil fertility	Nutrient cycle has to be considered	Nutrient supply of the cohorts must be considered	n
			Soil water capacity	Change of soil characteristics must be possible	Change of soil characteristics must be possible	w
			N- fixation	Nitrogen cycle has to be regarded, N-fixing tree species parameterized	Nitrogen supply of the cohorts has to be simulated, N-fixing tree species parameterized	n

Table 2 (Continued)

Temporal scale	Spatial scale	Effect on	Factor influenced by the mixing of species	Prerequisites and possible mechanistic reproduction		Required description
				Individual tree models	Cohort (stand) models	
Long (\geq year)	Low (tree, cohort)	Functioning	Barrier effects against pests Gap dynamic (tree establishment and disturbances)	Pests have to be considered Simulated on individual tree basis	Pests have to be considered Not possible	o s
Long (\geq year)	Low (tree, cohort)	Structure	Standing stock, carbon partitioning	Initial spatial structure and biomass distribution of the trees must be known Competition for space or resources between individual trees	Initial biomass distribution of cohorts must be known Competition between cohorts for space or resources, allometric adjustment	s s
			Size growth and ontogeny (species with different life cycles, feedback tree size -resource acquisition) Wood quality	Quality parameters as stem straightness, branchiness or knot distribution have to be simulated Simulation of soil vegetation, resource uptake by individual trees	Quality parameters as stem straightness, branchiness or knot distribution have to be simulated Cohorts for soil vegetation, resource uptake by each cohort	o o
			Third party trade-offs (1. species inhibits soil vegetation -> reduced resource consumption -> increase of growth for 2. species)	Stability parameters have to be simulated	Stability parameters have to be simulated	s
			Stability and protection (against extremes such as wind throw, snow load, frost winter drought)	Module for these processes is needed, dependent on wind speed	Module for these processes is needed, dependent on wind speed	s
			Mechanistic branch abrasion and crown shyness			

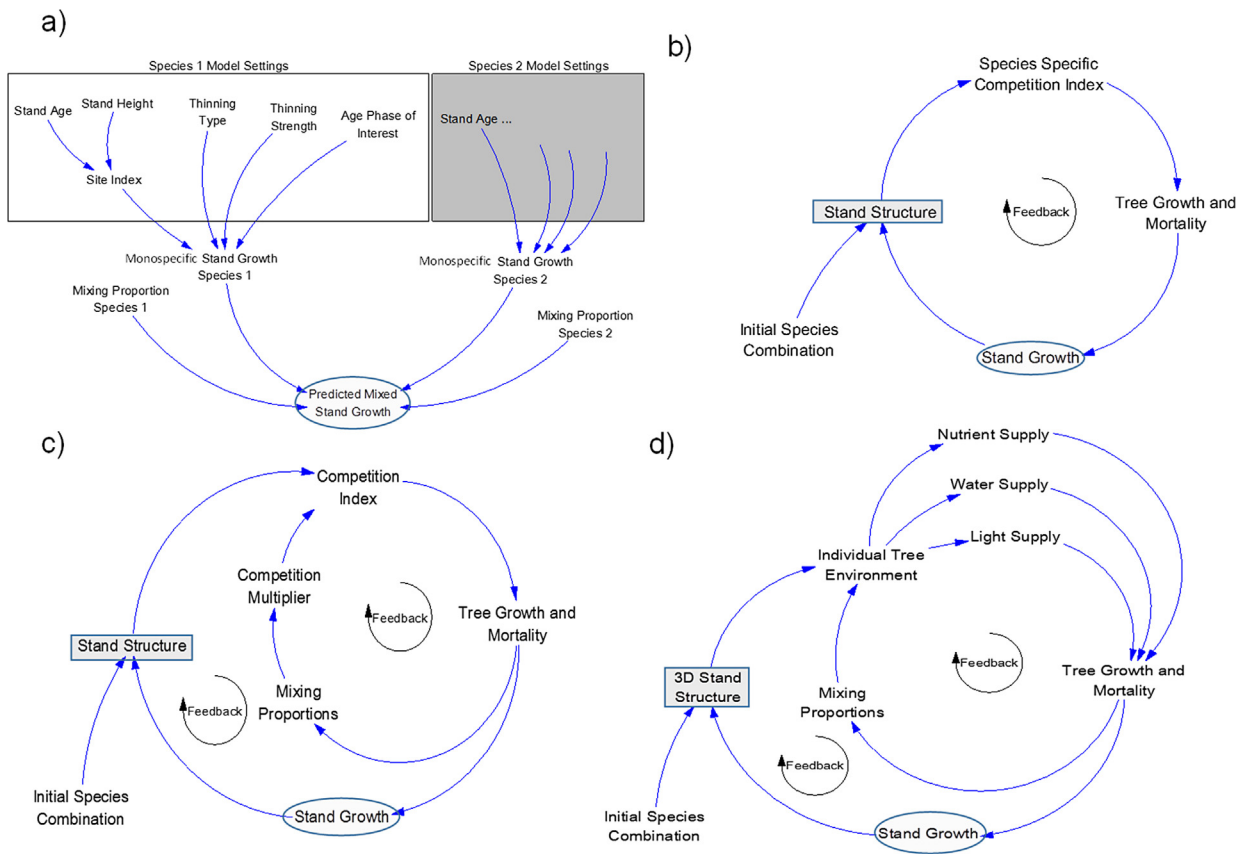


Fig. 2. Main principles for deriving and predicting mixed-species growth by models. (a) Deriving the growth of mixed-species stands as a weighted mean of monocultures using models of the respective species. (b) Indirect incorporation of mixing effects in individual-tree growth models by integration of species-specific growing space competition indices. (c) Direct incorporation of mixing effects using multipliers affecting growth rates and stand density. (d) Process-based representation of mixing effects by incorporating within-stand environmental conditions, species-specific structures, and resource uptake and availability.

Table 3
Forest growth models considered within this review and their spatial and temporal structure (¹ basic spatial unit; ² shortest time step of calculations).

No	Name	Author(s)	Type	Spatial structure ¹	Temporal structure ²
1	3-PG	Landsberg and Waring (1997), Forrester and Tang (in press)	Process based	Stand or cohort	Month
2	4C	Lasch et al. (2005), pers. comm (2014)	Process based	Cohort	Day
3	AMORPHYS (PIPESTEM)	Valentine et al. (2000), Valentine et al. (1997)	Hybrid	Individual	Year
4	ANAFOR	Deckmyn et al. (2008)	Process based	Cohort	Hour
5	BALANCE	Grote and Pretzsch (2002), Rötzer et al. (2010)	Process based	Individual	Day
6	BIOME-BGC	Pietsch et al. (2003)	Process based	Stand	Day
7	BWIN PRO, TreeGroSS	Albrecht et al. (2011), Hansen and Nagel (2014)	Empirical	Individual	5 Year
8	CABALA	Battaglia et al. (2004)	Process based	Cohort	Day
9	CASTANEA	Dufrene et al. (2005)	Process based	Stand	Hour
10	CO2FIX V.2	Masera et al. (2003)	Empirical	Cohort	Year
11	COMMIX	Bartelink (2000)	Process based	Individual	Year
12	DF.HGS	Weiskittel et al. (2010)	Hybrid	Individual	Day
13	EFIMOD	Chertov et al. (1999)	Hybrid	Individual	Year
14	EMILION	Bosc (2000)	Process based	Individual	1/50 Day
15	FINNFOR	Kellomäki and Vaisanen (1997), Kramer et al. (2002)	Process based	Cohort	Hour
16	FORCLIM	Bugmann (1996)	Process based	Cohort	Month
17	FORCYTE	Kimmins and Scoullar (1989), Kimmins et al. (1990b)	Hybrid	Stand	Year
18	FORCYTE 11	Kimmins et al. (1990a)	Hybrid	Stand	Year
19	FORECAST	Kimmins et al. (1999)	Hybrid	Individual	Year
20	FOREST v5.1	Schwalm and Ek (2004)	Process based	Individual	Day
21	FOREST-BGC	Running and Coughlan (1988), Running and Gower (1991)	Process based	Stand	Day
22	FORGEM	Kramer et al. (2008)	Process based	Individual	Day
23	FORGRO (-SWIF)	Van der Voet and Mohren (1994), Van Wijk et al. (2001)	Process based	Stand	Hour
24	FORMIND	Köhler and Huth (1998), Bohn et al. (2014)	Process based	Individual	Year
25	FORMIX	Bossel and Krieger (1994)	Process based	Cohort	Day
26	FORSKA	Prentice et al. (1993)	Process based	Cohort	Day
27	FORSPACE	Kramer et al. (2003)	Process based	Cohort	Day
28	FORUG	Verbeeck et al. (2006), Verbeeck et al. (2008)	Process based	Cohort	hour
29	FULCAM	Waterworth et al. (2007)	Hybrid	Stand	Year
30	FVS	Wykoff (1990), Crookston and Dixon (2005)	Empirical	Individual	5 Year
31	G-DAY	Comins and McMurtrie (1993), Eliasson et al. (2005)	Process based	Stand	Week
32	GOTILWA+	Gracia et al. (2002), Kramer et al. (2002)	Process based	Individual	Hour
33	Hybrid	Friend et al. (1997)	Process based	Individual	Day
34	LIGNUM	Perttunen et al. (1998)	Process based	Individual	Year
35	MAESTRO/MAESPA	Wang and Jarvis (1990), Baldwin et al. (2001), Duursma and Medlyn (2012)	Process based	Individual	hour
36	MGM	Bokalo et al., 2013, UA (2014)	Empirical	Individual	Year
37	MOSES	Hasenauer (1994)	Empirical	Individual	5 Year
38	N.N.	Palahí et al. (2008)	Empirical	Individual	Year
39	N.N.	Pukkala et al. (2009)	Empirical	Individual	5 Year
40	N.N.	Monserud and Sterba (1996)	Empirical	Individual	5 Year
41	PICUS v1.3	Seidl et al. (2005)	Hybrid	Individual	Month
42	PIPEQUAL	Mäkelä and Makinen (2003)	Process based	Individual	Day
43	PNET (-CN, -DAY)	Aber and Federer (1992), Aber et al. (1997)	Process based	Stand	Month/Day
44	SECRETS	Sampson et al. (2001), Sampson et al. (2007)	Process based	Stand	Hour
45	SILVA	Pretzsch et al. (2002)	Hybrid	Individual	5 Year
46	SIMWAL	Balandier et al. (2000)	Process based	Individual	Hour
47	SORTIE/BC	Coates et al. (2003)	Process based	Individual	5 Year
48	TRAGIC	Hauhs et al. (1995)	Process based	Individual	Year
49	TREE-BGC	Korol et al. (1995)	Process based	Individual	Day
50	TREEDYN3	Bossel (1996), Kramer et al. (2002)	Process based	Stand	Day
51	TREEMIG	Lischke et al. (2006)	Process based	Cohort	Year
52	TRIPLEX	Peng et al. (2002)	Hybrid	Stand	Month
53	WOODPAM	Peringer et al. (2013)	Process based	Stand	Month
54	YIELD-SAFE	Van der Werf et al. (2007)	Process based	Individual	Day

species-specific space occupation in different layers of the canopy, increasing stand density compared with monocultures, or by one species completely outcompeting another. In these empirical tree-level models, the species' competition for resources is modelled by their competition for different spaces within the stand rather than in terms of actual resources. For example, tree heights and crown sizes might be used to calculate indices for competition for light, while tree diameters, root mass or rooting depths might be used to calculate indices of competition for soil resources. When this kind of model is parameterized using data from monocultures, the directly integrated mixing effect is mainly the species-specific growing area requirement and the response to competition. If such models are parameterized using data from mixtures as well as monocultures, various effects of competition and facilitation might be indirectly represented via the estimated parameters. Examples of this approach are the models by Hasenauer (1994), Köhler and Huth (1998), Pretzsch et al. (2002) and Pukkala et al. (2009).

Another approach, Fig. 2c, is a model structure where mixing effects are directly integrated using multipliers. This can be done when the deviation of growth and stand density in mixtures compared with monocultures is known. This is an extension of the classical individual-tree growth models that modify the relationship between competition and growth and the maximum stand density in terms of the self-thinning line. The modifier approach has also been applied to statistically model the effects of site conditions, insect calamities, or fertilizing effects, even when the underlying mechanisms are not yet understood (Wykoff et al., 1982; Komarov et al., 2003; Monserud and Sterba, 1996).

In contrast to empirical models, process-based models consider the actual resources rather than using proxies such as competition indices. Competition for resources is simulated for each individual tree or cohort (Fig. 2d). Consequently, the influence of species interactions on growth is predicted by feedbacks between species-specific spatial structures and tree growth as well as between a tree's individual environment in terms of the resource supply, and its growth and mortality (Fig. 2d). The light distribution within the stand or the light availability for an individual tree, and the uptake and consumption of water and nutrients, all depend on species mixing and determine the growth of trees, cohorts and entire stands. Examples of this approach are the works by Grote and Pretzsch (2002), Kellomäki and Vaisanen (1997), Kimmins et al. (1990a,b, 1999), Rötzer et al. (2009) and Forrester and Tang (in press).

3.3. Representation of mixing effects

It is obvious that the use of empirical expansion factors (multipliers, e.g. Fig. 2c) will enable the simulation of mixing effects in any growth model. The prerequisites are that the compartment that the mixing effect influences is simulated and that the level of the effect is known. In this case, empirical models are likely to be relatively accurate within the parameter space used to fit them. However, there are an infinite number of combinations of soil, climate, species, structure characteristics and interactions between these variables and empirical models that use expansion factors are restricted to the specific combination of factors used to fit or parameterise them.

On the other hand, a process-based approach (Fig. 2d) can potentially provide robust extrapolations to untested conditions, silvicultural regimes (Weiskittel et al., 2010), species combinations and proportions, depending on the relevant prerequisites listed in Table 2. The functions, environmental conditions and structural attributes in Table 2 that are most important to include in models will be those that have the largest effects on growth or any other variables of interest, particularly in the long term. The frequency with which they are included in models is indicated in Fig. 3, while Table 4 shows which models incorporate each effect. The following

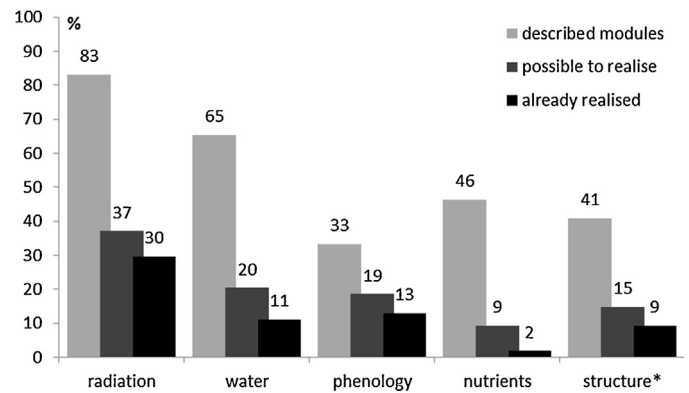


Fig. 3. The percentage of models that contain a given type of module or procedure (described modules), the percentage of models that could potentially model mixing effects for the given process without substantial modification (possible to realise) and the percentage of models that already model the given process in mixtures (already realised) (*: spatial horizontal structure).

discussion puts these into context with regards to their importance when modelling mixed-species forests (Fig. 1) with reference to the temporal and spatial scales at which they are usually included in models.

3.3.1. Functioning

3.3.1.1. Light and phenology. Light absorption is relatively easy to predict for homogeneous, closed canopies, such as even-aged monocultures. However, mixtures often have vertically and horizontally heterogeneous canopies, which make predictions of light absorption much more difficult (Forrester, 2014a). Of all of the functions considered in Fig. 3, light (radiation) was the most commonly considered, and 30% of the models are already capable of modelling light absorption in mixed-forests. About 37% of all models could possibly simulate the effects of species mixing on radiation distribution, and 83% of all analysed models included a description of light absorption by trees or cohorts in different vertical layers (even if it was only for monospecific stands). Several process-based tree-level models predict individual crown light absorption using information about tree positions, crown dimensions and leaf optical properties, and these have performed well against empirical data (le Maire et al., 2013; Charbonnier et al., 2013; Ligot et al., 2014). There are also empirical tree-level models that use similar or simplified crown descriptions (SORTIE; Canham et al., 1999) or competition indices (SILVA; Pretzsch et al., 2002) to quantify light competition. Predictions of light absorption in stand-level models are also often based on mean crown sizes for a given species, however, unlike tree-level models, the predictions of light absorption by stand-level models is rarely compared with empirical data, nor are the predictions compared with those of tree-level models that have performed well against empirical data (Forrester, 2014a; Forrester et al., 2014). Given the large variability in crown structures for which light absorption models are expected to work, and the importance of light absorption predictions in many process-based models, it is surprising that predictions of light absorption for different species in mixtures by stand-level models are rarely tested. The accurate prediction of growth is not an indication that light absorption has been accurately predicted, because accurate growth predictions are easily obtained if the models have been “tuned” to fit.

In addition to the effects of spatial structure on light absorption, the seasonality of leaf area needs to be accounted for (e.g. Baldocchi et al., 1984; Hertel et al., 2012). This partitioning of light over time is mainly a question of the phenological phases such as bud break and leaf fall. Only 33% of the growth models reviewed (Fig. 3) simulate seasonal changes within the canopy by considering the

Table 4
Forest growth models and mixing effects: The number of species for which growth can be simulated simultaneously, description of the modules and processes needed to simulate mixing effects and whether a model could possibly simulate the process (because it already estimates resource availability and the respective processes within the model) or whether the model already simulates the mixing effects (abbreviations: aa: *Abies alba*, b: *Betulus*, df: *Pseudotsuga menziesii*, e: *Eucalyptus*, fs: *Fagus sylvatica*, j: *Juglans*, o: *Quercus*, pa: *Picea abies*, pm: *Picea mariana*, pp: *Pinus pinaster*, ps: *Pinus sylvestris*, po: *Populus*; m() = mixing effect calculated using a multiplier; p() = process-based modeling of mixing effects possible).

No	Model name	No of species	Description of modules/processes for					Species mixing effects are	
			Radiation [R]	Water [W]	Phenology [P]	Nutrients [N]	Spatial structure [S]	Possible to be simulated	Already realized
1	3-PG	several	x	x	x	x	–	p(R, W, P)	p(R, W, P)
2	4C	7 (pa, ps, o, df, fs, po, b)	x	x	x	x	–	p(R, W, P)	p(R, W, P)
3	AMORPHYS (PIPESTEM)	1 (conifers)	x	x	–	–	x	–	–
4	ANAFOR	4 (po, ps, o, fs)	x	x	x	x	–	p(R, W, P, N)	p(R, W, P)
5	BALANCE	5 (fs, df, o, ps, pa)	x	x	x	x	x	p(R, W, P, N, S)	p(R, W, P, S)
6	BIOME-BGC	1 (o)	x	x	–	x	–	–	–
7	BWIN PRO, TreeGrOSS	several	x	x	x	x	x	m(R, S)	–
8	CABALA	1 (e)	x	x	–	x	x	–	–
9	CASTANEA	1 (fs)	x	x	x	–	–	–	–
10	CO2FIX V.2	several	–	–	–	–	–	–	–
11	COMMIX	2 (fs, df)	x	–	–	–	x	p(R, S)	p(R, S)
12	DF.HGS	1 (d)	x	x	x	x	–	–	–
13	EFIMOD	3 (ps, pa, b)	x	x	–	x	x	m(R, W, N)	R
14	EMILION	1 (pp)	x	x	x	–	x	–	–
15	FINNFOR	3 (ps, pa, b)	x	x	–	x	–	p(R, W, N)	R
16	FORCLIM	30	x	x	–	x	–	–	–
17	FORCYTE	coniferous	–	–	–	x	–	–	–
18	FORCYTE 11	several	x	x	–	x	–	–	–
19	FORECAST	several	x	x	–	x	–	–	–
20	FOREST v5.1	several	x	x	x	x	–	p(R, W, P)	p(R, W, P)
21	FOREST-BGC	several	x	x	–	x	–	–	–
22	FORGEM	1 (fs)	x	–	–	–	x	–	–
23	FORGRO (-SWIF)	1(df)	x	x	–	–	–	–	–
24	FORMIND	several	x	–	–	–	x	p(R, S)	p(R, S)
25	FORMIX	5 species groups	x	–	–	–	x	p(R, S)	p(R, S)
26	FORSKA	several	x	x	–	–	–	m(R, W)	–
27	FORSPACE	4 (fs, ps, o, b)	x	–	–	–	–	p(R)	R
28	FORUG	4 (fs, ps, o, pa)	x	x	–	–	–	–	–
29	FULCAM	13	–	–	–	–	–	–	–
30	FVS	several	–	–	–	–	–	–	–
31	G-DAY	1 (pa)	x	–	–	x	–	–	–
32	GOTILWA+	several	x	x	x	–	–	–	–
33	HYBRID	several	x	x	x	x	–	p(R)	p(R, P)
34	LIGNUM	1 (ps)	x	–	–	–	x	–	–
35	MAESTRO/MAESPA	several	x	x	x	–	x	p(R, W, S)	p(R, W, S)
36	MGM	4 (pa, ps, po, pm)	–	–	–	–	–	R	R
37	MOSES	4 (pa, ps, fs, aa)	–	–	–	–	x	m(R, S)	–
38	N.N.	2 (ps, o)	–	–	–	–	–	–	–
39	N.N.	3 (pa, ps, b)	–	–	–	–	–	–	–
40	N.N.	several	–	x	–	–	x	S	S
41	PICUS v1.3	several	x	x	–	x	–	R	–
42	PIPEQUAL	1 (ps)	x	–	–	–	x	–	–
43	PNET (-CN, -DAY)	several	x	x	–	x	–	–	–
44	SECRETS	several	x	x	x	x	x	p(R, W)	p(R, W)
45	SILVA	5 (pa, ps, fs, o, d)	x	x	x	x	x	m(R, W, N, S)	–
46	SIMWAL	1 (j)	x	–	x	–	x	–	–
47	SORTIE/BC	several	x	–	–	–	x	p(R, S)	p(R, S)
48	TRAGIC	1 (pa)	x	x	–	x	x	–	–
49	TREE-BGC	1 (df)	x	x	–	–	–	–	–
50	TREEDYN3	several	x	–	x	x	–	–	–
51	TREEMIG	30	x	–	–	–	–	–	–
52	TRIPLEX	1	x	x	–	x	x	–	–
53	WOODPAM	13 + shrubs + herbs	–	x	x	–	x	–	–
54	YIELD-SAFE	1 (po) + crops	x	x	x	–	–	–	–

effects of structure on environmental conditions within the stand. About 19% of the models could potentially simulate mixture effects on phenology and only 13% of the models can already simulate mixing effects on phenology in mixtures. For example, the process-based model BALANCE calculates bud break for each species and leaf senescence for each individual tree (Rötzer et al., 2004, 2010). However, most models do not differentiate between species other than whether they are evergreen and deciduous and/or use long-term means for the start and end of the growing season. Only one empirical model (TreeGrOSS) is able to simulate the seasonality of

a given tree species. On the other hand, 9 out of 36 process-based models are capable of considering phenology when calculating tree growth. Only five growth models (4C, ANAFOR, BALANCE, HYBRID, FORESTv5.1) take account of species specific start (bud break), change (sprout) and end (leaf fall) times of the growing season when simulating tree and stand growth.

3.3.1.2. Water balance. The water balance is another component of forest functioning that is likely to be critical in process-based mixed-species models because even in moist stands there can

be periodic droughts that significantly influence growth or survival. Mixing effects on transpiration and water-use efficiency have been reviewed by Forrester (2015). Models can incorporate water-related interactions between species by modelling the soil water balance and species-specific fluxes such as canopy interception and transpiration. It may also be necessary to consider the vertical distribution of each species, above- and below-ground, which will influence the vertical profiles of vapour pressure deficit, radiation and soil moisture, and where in the soil profile each species is competing for water. The response of each species to prevailing climatic conditions may be incorporated by defining their physiology, such as the relationship between vapour pressure deficit and stomatal conductance. Many models (65%) include several of these processes, 20% of models could reproduce mixing effects without major modification, but only 11% can already model mixing effects in relation to the water balance.

Other water-related processes that could be important in mixtures are hydraulic redistribution, phenology and mycorrhizal symbioses. Phenology will also influence light and is often included in models by preventing any transpiration (light absorption etc.) during the leafless periods. There appears to be very little information about whether differences in mycorrhizal communities or mycorrhizal connections between differing tree species have a significant impact on transpiration, and this was also not included in any of the models (Simard et al., 2012).

Many studies have examined hydraulic redistribution, and have shown that this can amount to 0.1 to 1 mm per day in forest ecosystems (Neumann and Cardon, 2012). However, very few studies have been done in mixed-species forests. In one study *Quercus petraea* was found to lift water in mixtures with *F. sylvatica*, however, there was no evidence that *F. sylvatica* used any of the water (Zapater et al., 2011).

3.3.1.3. Nutrients. In comparison to light and water, which can both be modelled in the same way in different forest types, nutrients are more complex. Only a small number of models are general enough to apply to a wide range of soil and forest types, and most nutrient models are relatively complex and cannot be simplified like light and water models. Another problem is that different nutrients are important in different regions or even on different sites within a given region, which means that several different nutrients may need to be included in the model. For example, models such as ANAFORE, BALANCE, EFIMOD and FINNFOR (Table 4) simulate nutrient cycles, however in most cases only nitrogen is regarded and, few models consider other nutrients such as P or K or interactions between different nutrients (Table 4), which are important in many tropical ecosystems (Laclau et al., 2013). While about 46% of all models reviewed include a description of the nutrient cycle, only 2% actually simulated mixing effects resulting from nutrients. In acknowledgement of the difficulty to model nutrients, several models do not calculate nutrient availability or nutrient use dynamically and instead ignore nutrients or use very simplified or empirical approaches (e.g. MAESPA, 3-PG) or are coupled with other models that consider nutrients (Xenakis et al., 2008). To simulate nutrient cycling (but also the water cycle) a detailed description of root biomass and its distribution in the different soil layers is required as in the models ANAFORE and BALANCE.

The lack of models that consider nitrogen fixation in mixed-species stands results from a lack of knowledge about the dynamics of nitrogen fixation in forests or plantations, let alone how these dynamics are influenced by species interactions. Several studies have examined nitrogen fixation in mixtures at a few points in time (Binkley et al., 1992b; Forrester et al., 2007; Bouillet et al., 2008), but there is little information about how the rates of nitrogen fixation and the proportion of nitrogen derived from the atmosphere are influenced by inter-specific competition (Van Kessel et al., 1994).

Filling these knowledge gaps with empirical data and new models could allow for a significant improvement in forest growth models that consider nitrogen-fixing species.

Rates of litter decomposition have been found to be greater in mixtures than expected based on monocultures in about 50% of cases, with no significant effect or antagonistic effects in the other cases (Rothe and Binkley, 2001; Gartner and Cardon, 2004). Some of the forest growth models vary nutrient cycling and hence nutrient availability in relation to litter chemical and physical properties and forest floor microclimate. Most models consider nutrition using a stand-level approach such that soil properties are assumed to be uniform throughout the stand (even in tree-level models). However, we found no model which varies the soil nutrient properties with the spatial distribution of species and litterfall (Table 4).

3.3.1.4. Mortality. The mortality functions in most models are empirical. In many cases the mortality functions that are used were developed using monocultures, or from mixtures where there was no consideration about whether inter-specific competition could have a different effect to intra-specific competition. The empirical nature of most mortality functions results from the fact that the processes driving mortality are still not so well understood, and it also takes time before the tree actually dies. This makes it difficult to develop mortality functions that link different causes including drought, density dependent mortality, pests and diseases (McDowell et al., 2011). Models by Monserud and Sterba (1999), Pukkala et al. (1998), Yao et al. (2001) and Zhao et al. (2004) include algorithms for the intra- and inter-specific competition effect on tree mortality, however, the recently revealed increase of canopy packing density (Pretzsch, 2014) and stand density (Pretzsch et al., 2015) by mixing complementary species needs improved consideration in mortality models.

3.3.1.5. Carbon partitioning. Carbon partitioning and tree allometry influence the trees' ability to acquire and compete for resources and therefore to persist under prevailing or future environmental conditions (see Table 2 for the effects on environment, functioning and structure). Tree allometry also influences the stand structure, but it is discussed here due to its relationship with carbon partitioning. Both depend on the environmental conditions such as soil and climatic characteristics and how these are influenced by the neighbouring plants. Several studies have shown that carbon partitioning can vary significantly between mixed and monospecific stands (Forrester et al., 2006a; Epron et al., 2013), and many studies in monocultures have shown that carbon partitioning can change in response to resource availability (Litton et al., 2007). Most of the models allow partitioning and allometry to change in relation to soil water and nutrient availability and some also allow for changes in terms of stand density. Assuming that these factors can be influenced by the species within the mixture, this should enable species interactions to influence partitioning.

An example of the importance of including mixing effects on carbon partitioning and allometry in models can be shown by considering light absorption. A common requirement of many light models is information about crown sizes e.g. leaf area, crown diameter, crown length. Crown sizes in growth models are often calculated using allometric equations, and these equations can vary in response to inter-specific competition (Pretzsch, 2014; Forrester and Albrecht, 2014) and hence the environment within the forest. For example, Pretzsch (2014) showed that the relationship between crown projection area and stem diameter for *F. sylvatica* varied depending on whether *F. sylvatica* was growing in monospecific or in mixed-species stands with *P. abies*, *Larix decidua*, *Fraxinus excelsior*, and *Q. petraea*. For a given stem diameter the crown projection areas, heights, and heights to the crown base could vary between

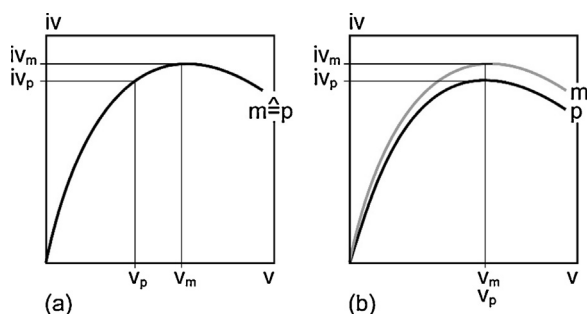


Fig. 4. Differences in individual tree volume increment, iv , in mixed versus monospecific stands (m and p , respectively) may (a) result only from their different sizes because they have the same size-growth relationship in mixtures and monocultures, or (b) from different size-growth relationships in mixtures compared with monocultures. (a) The volume of the individual tree in the mixed stand, v_m , is simply ahead of the tree in the monoculture, v_p , but developing along the same trajectory. (b) The volume growth of trees of equal size is higher in mixed than in monospecific stands and indicates a higher growth efficiency of trees in inter- versus intra-specific neighbourhoods.

0% to more than 100%, depending on the diameter (Pretzsch, 2014). Such changes could have a significant effect on the amount of light absorbed by individual crowns (Forrester and Albrecht, 2014), and it is probably important to include these effects in growth models. Despite this, growth models generally don't allow for intra-specific changes in allometry in response to inter-specific competition.

Another example of the relevance of allometry is shown in Fig. 4. Differences in tree volume growth, iv_m , in mixed-species stands versus the growth in monocultures, iv_p , in a given survey period can result simply from differences in their current size, v_m and v_p , even though their growth rates move along the same $iv-v$ trajectory (Fig. 4a). In contrast, Fig. 4b represents a change in allometry where trees in mixed and monocultures follow different $iv-v$ trajectories, m and p , respectively. Tree species mixing may also cause a combination of both, first, a higher growth efficiency which accelerates size growth, and lead to an advanced size development and hence to a size effect. In such cases the elimination of the size effect by application of general allometric relationships (see Pretzsch, 2010, pp. 347–348) can reveal whether there is a true mixing effect behind any differences between tree behaviour or just a tree size effect. The fact that size rather than age is suitable for prediction of tree growth is considered by model approaches that use the potential modifier principle or difference equations with size growth on the left and size on the right side of the equals sign.

3.3.2. Structure

Stand structure is quantified vertically, horizontally and in terms of inter-tree variability, such as by using diameter distributions. Tree-level models automatically take these structural attributes into account whether they are empirical or process-based. Empirical tree-level models consider the local structure when calculating competition indices (SILVA by Pretzsch et al., 2002; BWIN PRO by Albrecht et al., 2011) and process-based models consider the local environment and structure when modelling different leaf- or tree-level processes and interactions. Tree-level models also keep track of individual tree positions and diameter or height distributions, and therefore consider the horizontal structure of the forest.

In stand-level models, the vertical structure in terms of cohort height is generally considered in all mixed-species models, whether they are process-based or empirical (Table 4). Accounting for vertical heterogeneity, in terms of the height and the height to the crown base, can be particularly important with regards to competition for light (Forrester, 2014a; Forrester et al., 2014). Some gap models and other stand-level models simplify canopy structure such that all of the leaf area is positioned at the top of the crown,

rather than distributed between the top and bottom of the crown (Bugmann, 2001). However, this will lead to biased estimates such that the taller species gain an unrealistic competitive advantage, and this will be exacerbated as the stand develops (Forrester et al., 2014). Models that assume all leaf area is at the top of a crown may be unlikely to reproduce actual mixing effects even if all other processes are predicted accurately. Other simplifications that are used in stand-level models include dividing the crowns and canopy into vertical layers and allocating a given portion of the leaf area into that layer assuming a uniform vertical distribution of leaf area within the crown.

Accounting for horizontal heterogeneity is important when modelling the effects of stand density and is critical for modelling natural disturbances or silvicultural treatments such as thinning (Forrester, 2014a). Tree-level models such as BALANCE or MAESTRO consider the horizontal structure of a stand (Fig. 3). In contrast to this model type, stand-level models are restricted in their ability to account for horizontal structure, and need to assume that the horizontal heterogeneity is homogeneous (e.g., FORMIX, FORMIND, 3-PG). That is, stand-level models can account for horizontal heterogeneity by changing stand density (leaf area, trees per ha, basal area etc.) but they cannot account for heterogeneous horizontal stand structures such as clumps of trees, row-by-row mixtures and gaps where a given cohort or species develops from seedlings under the influence of an older and taller cohort that surrounds them. Gap models attempt to account for this horizontal heterogeneity but if they are stand-level models the horizontal heterogeneity within a gap still needs to be assumed to be homogeneous, and the horizontal heterogeneity is incorporated by having different gaps.

Below-ground stand structure is much harder to measure than above-ground structure. There is a lot of information about how tree allometry or above-ground stand structure varies between mixtures and monocultures (Bauhus et al., 2004; Forrester and Albrecht, 2014; Pretzsch, 2014), however, there is far less about how species interactions influence below-ground structure (Schume et al., 2004; Laclau et al., 2013). This makes it difficult to model below-ground functions and environmental conditions.

3.3.3. Environment

Consideration of the environmental conditions within a stand and how these are influenced by different species is a critical characteristic of process-based models for mixed-species forests. In general, if the processes (Section 3.3.1) and structures (Section 3.3.2) are modelled realistically, then it follows that the environmental conditions within the stand have probably also been accounted for. For example, the water balance is strongly determined by structural and functional aspects of the stand, and the light availability within the stand is strongly influenced by the vertical and horizontal distributions of leaves (Table 2).

In contrast to process-based models, empirical tree-level models often summarize the whole environment using competition indices. This can result in accurate predictions of mixing effects on growth (e.g. BWIN PRO by Nagel, 1999) for the environmental conditions and stand structures that existed in the forests where the empirical data used to build the models was collected. However, they are unlikely to provide reliable predictions of mixing effects for other environmental conditions that result from changes in climate, management or disturbance regimes. Similarly, empirical models may not be sensitive to inter-annual variability in environmental conditions that can have a dramatic effect on forest productivity, especially in short rotations (Stape et al., 2004).

As indicated in Tables 2 and 3, environmental conditions are considered at a range of temporal scales, from hours to months, in both tree- and stand-level process-based models. The temporal and spatial resolution required to reproduce mixing effects will clearly vary depending on the functions being considered, and which

functions have the largest effects on mixing effects. Given that the ability of models to reproduce mixing effects have rarely been tested, it is not possible to know the temporal or spatial resolution that environmental conditions need to be used.

4. Perspectives

4.1. Future empirical work: Experiments, monitoring, statistical evaluation

4.1.1. Combining data from different spatial and temporal resolutions

Measurement of mixing effects and understanding their relevance for the forest ecosystem as a whole requires investigations at multiple temporal and spatial scales. For example, when the results from observations at the plant level, P_{obs} , (e.g. increment or mortality of individual trees in relation to growing conditions) are upscaled, they predict certain expected patterns at the stand level, S_{pred} . The upscaling may be carried out through simple addition or multiplication, or by modelling. If measurements at the stand level S_{obs} (e.g. long-term records on the stand development through repeated surveys) are assumed to be accurate but do not match the expected pattern ($S_{obs} \neq S_{pred}$), the tree-level process may not have been adequately quantified (temporally or spatially), they may be of limited relevance when explaining the entire system behaviour, or if they were modelled, there might be a problem with the model.

Obviously, the transition from the tree to the stand level introduces new effects, which cannot be solely deduced from the individual level (e.g. adaptation, facilitation, antagonism, density-dependent mortality). Scale-overlapping research approaches enable the relevance of results at a certain level to be determined in relation to the next higher hierarchical level, and often reveal knowledge gaps.

4.1.2. Incorporation of defoliation effects into models

The effects of insect defoliators can differ between monospecific and mixed-species stands (Jactel and Brockerhoff, 2007). Few forest growth models include the dynamics of pests and whether these vary in mixtures or how climatic conditions influence their life cycles (Pinkard et al., 2011). This is probably due to the complexity of these relationships depending on the identity of the pest and the host plants (Castegneyrol et al., 2014). However, several models consider defoliation and key physiological processes that influence the response of trees to defoliation (Lexer and Hönninger, 1998; Pinkard et al., 2011).

4.1.3. Below-ground processes

More empirical data is required to determine the importance of eco-physiological or physical processes like hydraulic redistribution or the effects of changes in mycorrhizal communities in mixed vs. monocultures. Processes such as these might only be important during droughts or on sites where trees are often water stressed. Models may be able to answer questions about the spatial and temporal importance of these processes, but firstly the processes need to be incorporated into the models and the predictions compared with empirical data.

Comparisons of mixtures versus monocultures with respect to root structure and function are difficult, and the few existing studies suggest that mixing species can change the root structure at least as strongly as it can change the crown structure. For example, interspecific competition can modify the vertical and horizontal reach of roots and the proportions of coarse and fine roots (Laclau et al., 2013). Schmid and Kazda (2001) quantified Wiedemann's observation that in mixture with *F. sylvatica*, coarse roots of *P. abies* were restrained to the upper soil layer, while *F. sylvatica* occupied equally

deep layers in the mixed and monocultures (Wiedemann, 1942). Fine roots of *P. abies* were underrepresented in the mixed stand and those of *F. sylvatica* were overrepresented, especially in deeper layers (Schmid and Kazda, 2002). McKay and Malcolm (1988) and McKay (1988) found a similar restriction of *P. abies* to the upper layer when mixed with *Pinus sylvestris*. Like most studies Brassard et al. (2011) found that the soil space was more fully occupied by fine roots and resources were more fully exploited than in monocultures when species with contrasting rooting traits were mixed in boreal stands. They considered the below-ground niche differentiation of roots as the main cause for the over-yielding of mixed stands. The higher specific root length and soil space filling by roots in mixed than in monocultures (e.g., Hendriks and Bianchi, 1995; McKay and Malcolm, 1988) suggest a more intensive foraging and resource exploitation in the mixtures. These studies show that it is very difficult to predict how the distribution and functioning of roots will change in mixtures compared with monocultures. More empirical work will be required to facilitate the incorporation of these dynamics into process-based models.

4.1.4. Responses to climate

Only a few of the process-based models in Table 3 include the effects of changing CO₂ concentrations on forest growth and there are very few studies that have measured how increased CO₂ concentrations might influence species interactions (Smith et al., 2013). In theory, there could be an interaction between increasing CO₂ and drought, such that plants are less susceptible to drought under elevated CO₂ (Duursma and Medlyn, 2012). While most of the processes can be summarised in stand-level process-based models, it appears that there may still not be a good enough understanding of responses to elevated CO₂ to have confidence in stand-level model outputs and that tree-level models may be useful ways to investigate how changes in CO₂ might influence species interactions.

4.2. Integration at which scale?

An appropriate model scale to integrate a given function or environmental condition depends on the purpose and the scale of the outputs that are required (Battaglia and Sands, 1998) more than on the scale of the function or environmental condition themselves. While many functions in mixed-species forests occur at the leaf or tree levels, they can also usually be summarised at the stand level as discussed above. It is therefore interesting to note that most models (in Table 3) that have been used for mixtures, even if mixing effects were not examined, are tree-level models, and very few are stand-level models (e.g. Härkönen et al., 2010; Forrester and Tang, in press). This bias towards tree-level models may indicate that a first objective of the model developers was to further understand how the properties of individual trees influence forest growth, while the development of a relatively simple management tool was only a secondary objective. This may also reflect the view of Seidl et al. (2005) that '... to include forest management realistically, process-based models must operate at the individual tree level.' We do not necessarily share this view. While we agree that if the type of forest management being referred to influences the horizontal structural heterogeneity, such as gap creation, then spatially explicit tree-level models may be necessary. However, tree-level models are probably not necessary to model many other forest management practices, such as thinning or mixing effects. This is because based on the literature reviewed above, most functions, vertical structural attributes and environmental conditions can be modelled using stand-level approaches and could probably be used to predict responses to mixing species and management.

If the aim of developing the model is to understand how the characteristics of each species (or age-class) influence their interactions and the impact on stand level variables (e.g. production, water use) or the relative dominance of each species, then stand-level models could be used to avoid more complex calculations, tree-level input information and associated scaling problems (Härkönen et al., 2010; Medlyn, 1998). This may often suit forest managers who prefer relatively simple models to parameterise and use.

If more detailed information is required, such as how the diameter distributions develop, stand-level models can predict diameter distributions using empirical equations (e.g. TRIPLEX Wang et al., 2011; 4C Lasch et al., 2005) and hierarchical modelling approaches (e.g. CABALA Battaglia et al., 2015). This empirical stand-level approach is consistent with empirical mortality functions (e.g. the $-3/2$ law) that are often used in hybrid models due to the inadequate process-based understanding of mortality in forests. The same diameter distributions can be used to determine how much biomass (or merchantable volume etc.) is removed from the stand following disturbances, and hence the reduction in growth, light absorption, transpiration, nutrient uptake etc.

In contrast, tree-level models are critical because stand-level models cannot replicate horizontal structural heterogeneity and they cannot fully incorporate the variability of individual tree characteristics that occur in forests. This is important because sometimes an aim of modelling is to understand how this variability influences the development and characteristics of the whole stand (Grimm, 1999). That is, which processes and interactions that occur at the organ- and tree-levels are most relevant for the system behaviour as a whole? Therefore, many mixed-species models start at the level of the tree (Table 3) and work at temporal and spatial resolutions that are closer to the scales on which many processes actually occur. This is also consistent with the fact that many studies about the processes that are affected by species interactions are carried out at the organ- and tree levels. The finer resolution is useful for examining how a change in the characteristics of the individual trees will influence or is influenced by certain processes and the effect this has on stand level patterns.

Individual tree models or process-based models in general can help to determine this when they scale up from high resolution (day-year, organ-tree-patch) to low resolution state variables (year-decade, stand-ecosystem) and include variables like growth, yield and stand density.

Integration of mechanistic findings in models at the tree level enables simulation experiments to examine the effect of individual tree behaviour on stand level patterns (Fig. 5). When the models include state variables at the stand level, the model output might be compared with available knowledge on mixed stand dynamics at stand level. This reference for comparison might include empirical research, proven stand models, or ecosystem theory. Comparison of the stand predicted behaviour by the process-based model with the expected behaviour (indicated by a Δ in Fig. 5) reveals which high-resolution environmental effects, structures and functions are relevant to realistic reproduction of the system.

Repeated working through the cycle of model adjustment \rightarrow simulation experiment \rightarrow comparison between prediction and reference \rightarrow model adjustment (solid black feed-back loop in Fig. 5) helps to distinguish which mixing effects on higher levels of resolution (day, organ-tree-patch) are relevant for mixing effects at the stand level.

5. Conclusions

With very few exceptions (e.g., for radiation in BALANCE; Rötzer et al., 2010, or 3-PG; Forrester and Tang, in press) the evaluation of models for their suitability for mixed-species stands are rare. The scale overarching evaluation introduced in the previous section has great potential to identify the relevance and knowledge gaps of environmental, functional, and structural system and model components. An initial approach would be the comparison of simulation results with empirical findings in mixed-species stands. This could include comparisons of any of the structural, functioning and environmental characteristics listed in Table 2. For practical model applications it will be important that they can predict any over- or under-yielding of mixed-species stands along spatial and temporal gradients (e.g., Forrester, 2014b). The main restriction for such approaches has been the scarcity of empirical data, however, since mixed-species forests are becoming more popular, the quantity of data for model evaluation is improving quickly in the form of forest inventories, newly established long-term experiments and monitoring plots (Burkhardt and Temesgen, 2014).

A second evaluation approach is comparing model behaviour with common rules and laws of tree and stand growth. Simulation of stand development with self-thinning and various thinning intensities can reveal whether a model behaves according the self-thinning rule and common density-growth relationships evident for mixed stands.

In conclusion, there are many forest growth models that work at a range of temporal and spatial scales, however, less than a third of these models can be used to predict mixing effects, in their current form, and we could only find one example where the mixing effects had been compared with empirical data. Despite this, several models have been used to model mixing effects even though they contain modules that do not appear to realistically represent the processes that they are supposed to simulate. It is important to consider that just because a model predicts growth accurately does not mean that it is doing so for the correct physiological reasons. Many models contain parameters that can be “tuned” so that the growth predictions match empirical data even though predictions of light, water, stand structure etc. may not be accurate. This is probably particularly important in mixed-species systems where errors with one species will influence the other species. Therefore it is important to test all components of models and not just the main variables of interest (e.g. growth). When this has been done, forest growth models are likely to be a valuable tool to predict when and where different types of species interactions are most important.

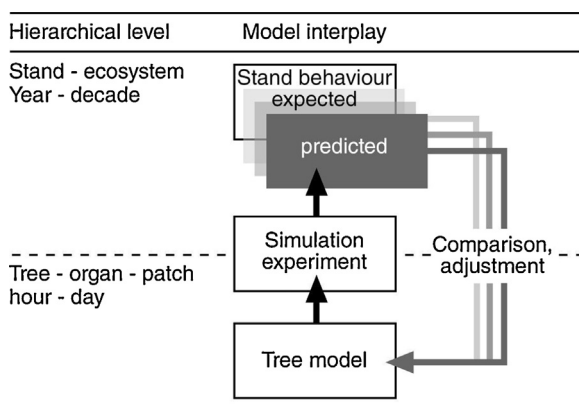


Fig. 5. Comparison between the effects of species interactions found on different levels of system organisation. High-resolution findings of mixing effects are integrated in process-based models, which should include stand variables. Simulation experiments with such models and comparison of their stand-level predictions with empirical observation, stand level models or theory, helps to determine which mixing effects are the most important and the temporal and spatial variability in their effects.

Acknowledgements

Thanks to the German Science Foundation (Deutsche Forschungsgemeinschaft) for providing the funds for the project “Tree and stand-level growth reactions on drought in mixed versus pure forests of Norway spruce and European beech” (project number PR292/12-1). Thanks are also due to the Bavarian State Ministry for Nutrition, Agriculture and Forestry and the Bavarian State Ministry for Environment and Health for generous support of the Forest Roof Experiment (KROOF), a rainfall exclusion approach, for examining the role of water supply in mixed versus monocultures each of Norway spruce and European beech. DF's contribution was funded by the Lin² Value project (project number 033L049) supported by the German Federal Ministry of Education and Research (BMBF, Bundesministerium für Bildung und Forschung). We further thank Peter Biber for pre-review of the manuscript, Ulrich Kern for the graphical artwork, and two anonymous reviewers for their constructive criticism.

References

- Aber, J.D., Federer, C.A., 1992. A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems. *Oecologia* 92/4, 463–474.
- Aber, J.D., Ollinger, S.V., Driscoll, C.T., 1997. Modeling nitrogen saturation in forest ecosystems in response to land use and atmospheric deposition. *Ecol. Modell.* 101/1, 61–78.
- Albrecht, A., Kohnle, U., Nagel, J., 2011. Übertragbarkeit empirischer statistischer Waldwachstumsmodelle: Prüf- und Anpassungsverfahren anhand des Beispiels BWinPro für Baden-Württemberg. *AFZ* 182 (1/2), 11.
- Assmann, E., Franz, F., 1965. Vorläufige Fichten-Ertragstafel für Bayern. *Forstw. Cbl.* 84/1, 13–43.
- Balandier, P., Lacoine, A., Le Roux, X., Sinoquet, H., Cruziat, P., Le Dizès, S., 2000. SIMWAL: a structural-functional model simulating single walnut tree growth in response to climate and pruning. *Ann. For. Sci.* 57/5, 571–585.
- Baldocchi, D.D., Hutchinson, B.A., Matt, D.R., McMillen, R.T., 1984. Seasonal variations in the radiation regime within an oak-hickory forest. *Agric. Forest. Meteorol.* 33, 177–191.
- Baldwin, V.C., Burkhardt, H.E., Westfall, J.A., Peterson, K.D., 2001. Linking growth and yield and process models to estimate impact of environmental changes on growth of loblolly pine. *For. Sci.* 47/1, 77–82.
- Bartelink, H.H., 2000. A growth model for mixed forest stands. *For. Ecol. Manage.* 134/1, 29–43.
- Battaglia, M., Sands, P.J., 1998. Process-based forest productivity models and their application in forest management. *For. Ecol. Manage.* 102, 13–32.
- Battaglia, M., Sands, P., White, D., Mummery, D., 2004. CABALA: a linked carbon, water and nitrogen model of forest growth for silvicultural decision support. *For. Ecol. Manage.* 193 (1), 251–282.
- Battaglia, M., Bruce, J., Latham, R., O'Grady, A., Greenwood, A., 2015. Process-based size-class distribution model of trees within forest plantations: a hierarchical modeling approach. *For. Ecol. Manage.* 344, 63–72.
- Bauhus, J., van Winden, A.P., Nicotra, A.B., 2004. Above-ground interactions and productivity in mixed-species plantations of *Acacia mearnsii* and *Eucalyptus globulus*. *Can. J. For. Res.* 34, 686–694.
- Binkley, D., 1992. Mixtures of nitrogen-fixing and non-nitrogen-fixing tree species. In: Cannell, M.G.R., Malcol, D.C., Robertson, P.A. (Eds.), *The Ecology of Mixed Species Stands of Trees*. Blackwell Scientific, London, pp. 99–123.
- Binkley, D., Dunkin, K.A., DeBell, D., Ryan, M.G., 1992a. Production and nutrient cycling in mixed plantations of *Eucalyptus* and *Albizia* in Hawaii. *For. Sci.* 38, 393–408.
- Binkley, D., Sollins, P., Bell, R., Sachs, D., Myrold, D., 1992b. Biogeochemistry of adjacent conifer and alder-conifer stands. *Ecology* 73, 2022–2033.
- Bohn, F.J., Frank, K., Huth, A., 2014. Of climate and its resulting tree growth: simulating the productivity of temperate forests. *Ecol. Modell.* 278, 9–17.
- Bokalo, M., Stadt, K.J., Comeau, P.G., Titus, S.J., 2013. The validation of the Mixedwood Growth Model (MGM) for use in forest management decision making. *Forests* 4 (1), 1–27.
- Bosc, A., 2000. EMILION, a tree functional-structural model: presentation and first application to the analysis of branch carbon balance. *Ann. For. Sci.* 57/5, 555–569.
- Bossel, H., Krieger, H., 1994. Simulation of multi-species tropical forest dynamics using a vertically and horizontally structured model. *For. Ecol. Manage.* 69/1, 123–144.
- Bossel, H., 1996. TREEDYN3 forest simulation model. *Ecol. Modell.* 90/3, 187–227.
- Bouillet, J.P., Laclau, J.P., Gonçalves, J.L.M., Moreira, M.Z., Trivelin, P.C.O., Jourdan, C., Silva, E.V., Piccolo, M.C., Tsai, S.M., Galiana, A., 2008. Mixed-species plantations of *Acacia mangium* and *Eucalyptus grandis* in Brazil. 2: Nitrogen accumulation in the stands and biological N₂ fixation. *For. Ecol. Manage.* 255, 3918–3930.
- Brassard, B.W., Chen, H.Y.H., Bergeron, Y., Paré, D., 2011. Differences in the fine root productivity between mixed- and single-species stands. *Funct. Ecol.* 25, 238–246.
- Bugmann, H.K.M., 1996. A simplified forest model to study species composition along climate gradients. *Ecology* 77 (7), 2055–2074.
- Bugmann, H., 2001. A review of forest gap models. *Clim. Change* 51, 259–305.
- Burkhardt, H.E., Tomé, M., 2012. *Modeling Forest Trees and Stands*. Springer Science and Business Media, Dordrecht, The Netherlands, pp. 458p.
- Burkhardt, H.E., Temesgen, H., 2014. Forest observational studies: data sources for analysing forest structure and dynamics. *For. Ecol. Manage.* 316, 1–148.
- Canham, C., Coates, K.D., Bartemucci, P., Quaglia, S., 1999. Measurement and modeling of spatially explicit variation in light transmission through interior cedar-hemlock forests of British Columbia. *Can. J. For. Res.* 29, 1775–1783.
- Castegneyrol, B., Jactel, H., Vacher, C., Brockerhoff, E.G., Koricheva, J., 2014. Effects of plant phylogenetic diversity on herbivory depend on herbivore specialization. *J. Appl. Ecol.* 51, 134–141.
- Charbonnier, F., Maire, G.L., Dreyer, E., Casanoves, F., Christina, M., Dauzat, J., Eitel, J.U.H., Vaast, P., Vierling, L.A., Rouspard, O., 2013. Competition for light in heterogeneous canopies: application of MAESTRA to a coffee (*Coffea arabica* L.) agroforestry system. *Agric. Forest. Meteorol.* 181, 152–169.
- Chertov, O.G., Komarov, A.S., Tsiplianovsky, A.M., 1999. A combined simulation model of Scots pine, Norway spruce and Silver birch ecosystems in the European boreal zone. *For. Ecol. Manage.* 116 (1–3), 189–206.
- Coates, K.D., Canham, C.D., Beaudet, M., Sachs, D.L., Messier, C., 2003. Use of a spatially explicit individual-tree model (SORTIE/BC) to explore the implications of patchiness in structurally complex forests. *For. Ecol. Manage.* 186 (1), 297–310.
- Comins, H.N., McMurtrie, R.E., 1993. Long-term response of nutrient-limited forests to CO₂ enrichment—equilibrium behaviour of plant-soil models. *Ecol. Appl.* 3, 666–681.
- Crookston, N.L., Dixon, G.E., 2005. The forest vegetation simulator: a review of its structure, content, and applications. *Comput. Electron. Agric.* 49 (1), 60–80.
- Deckmyn, G., Verbeek, H., De Beeck, M.O., Vansteenkiste, D., Steppe, K., Ceulemans, R., 2008. ANAFORE: a stand-scale process-based forest model that includes wood tissue development and labile carbon storage in trees. *Ecol. Modell.* 215 (4), 345–368.
- Dhôte, J.F., 2005. Implication of forest diversity in resistance to strong winds. In: Scherer-Lorenzen, M., Körner, C., Schulze, E.D. (Eds.), *Forest Diversity and Function*. *Ecol. Studies*, vol. 176. Springer-Verlag, Berlin, pp. 291–307.
- Dufrene, E., Davi, H., Francois, C., Le Mare, G., Le Dantec, V., Granier, A., 2005. Modelling carbon and water cycles in a beech forest Part I: Model description and uncertainty analysis on modelled NEE. *Ecol. Modell.* 185 (2–4), 407–436.
- Duursma, R.A., Medlyn, B.E., 2012. MAESPA: a model to study interactions between water limitation, environmental drivers and vegetation function at tree and stand levels, with an example application to [CO₂] × drought interactions. *Geosci. Model Dev.* 5, 919–940.
- Eliasson, P.E., McMurtrie, R.E., Pepper, D.A., Strömgren, M., Linder, S., Ågren, G.I., 2005. The response of heterotrophic CO₂ flux to soil warming. *Global Change Biol.* 11 (1), 167–181.
- Epron, D., Nouvellon, Y., Mareschal, L., MoreiraeMoreira, R., Koutika, L.-S., Geneste, B., Delgado-Rojas, J.S., Laclau, J.-P., Sola, G., Gonçalves, J.L., Bouillet, d.M.J.P., 2013. Partitioning of net primary production in *Eucalyptus* and *Acacia* stands and in mixed-species plantations: two case-studies in contrasting tropical environments. *For. Ecol. Manage.* 301, 102–111.
- Fontes, L., Bontemps, J.D., Bugmann, H., van Oijen, M., Gracia, C., Kramer, K., Lindner, M., Rötzer, T., Skovsgaard, J.P., 2010. Models for supporting forest management in a changing environment. *For. Syst.* 19, 8–29.
- Forrester, D.I., 2014a. A stand-level light interception model for horizontally and vertically heterogeneous canopies. *Ecol. Modell.* 276, 14–22.
- Forrester, D.I., 2014b. The spatial and temporal dynamics of species interactions in mixed-species forests: from pattern to process. *For. Ecol. Manage.* 312, 282–292.
- Forrester, D.I., 2015. Transpiration and water-use efficiency in mixed-species forests versus monocultures: effects of tree size, stand density and season. *Tree Physiol.* 35, 289–304.
- Forrester, D.I., Bauhus, J., Cowie, A.L., 2006a. Carbon allocation in a mixed-species plantation of *Eucalyptus globulus* and *Acacia mearnsii*. *For. Ecol. Manage.* 233, 275–284.
- Forrester, D.I., Bauhus, J., Cowie, A.L., Vanclay, J.K., 2006b. Mixed-species plantations of *Eucalyptus* with nitrogen-fixing trees: a review. *For. Ecol. Manage.* 233, 211–230.
- Forrester, D.I., Guisasaola, R., Tang, X., Albrecht, A.T., Dong, T.L., le Maire, G., 2014. Using a stand-level model to predict light absorption in stands with vertically and horizontally heterogeneous canopies. *For. Ecosyst.* 1, 17.
- Forrester, D.I., Schortemeyer, M., Stock, W.D., Bauhus, J., Khanna, P.K., Cowie, A.L., 2007. Assessing nitrogen fixation in mixed- and single-species plantations of *Eucalyptus globulus* and *Acacia mearnsii*. *Tree Physiol.* 27, 1319–1328.
- Forrester, D.I., Lancaster, K., Collopy, J.J., Warren, C.R., Tausz, M., 2012. Photosynthetic capacity of *Eucalyptus globulus* is higher when grown in mixture with *Acacia mearnsii*. *Trees* 26, 1203–1213.
- Forrester, D.I., Albrecht, A.T., 2014. Light absorption and light-use efficiency in mixtures of *Abies alba* and *Picea abies* along a productivity gradient. *For. Ecol. Manage.* 328, 94–102.
- Forrester, D.I., Tang, X., 2015. Analysing the spatial and temporal dynamics of species interactions in mixed-species forests and the effects of stand density using the 3-PG model. *Ecol. Modell.* (in press).
- Friend, A.D., Stevens, A.K., Knox, R.G., Cannell, M.G.R., 1997. A process-based, terrestrial biosphere model of ecosystem dynamics (Hybrid v3, 0). *Ecol. Modell.* 95 (2), 249–287.

- Gadow, von K., 1987. Untersuchungen zur Konstruktion von Wachstumsmodellen für schnellwüchsige Plantagenbaumarten. Forstl Forschungsber. München 77, 147p.
- Gartner, T.B., Cardon, Z.G., 2004. Decomposition dynamics in mixed-species leaf litter. *Oikos* 104, 230–246.
- Griess, V.C., Knoke, T., 2011. Growth performance, windthrow, and insects: meta-analyses of parameters influencing performance of mixed-species stands in boreal and northern temperate biomes. *Can. J. For. Res.* 41, 1141–1158.
- Grimm, V., 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future. *Ecol. Modell.* 115, 129–148.
- Gracia, C., Sabate, S., Nadal-Sala, D., Sánchez, A., Pla, E., 2002. <http://www.creaf.uab.es/gotilwa/download.htm>; download 06.September 2014.
- Grote, R., Pretzsch, H., 2002. A model for individual tree development based on physiological processes. *Plant Biol.* 4, 167–180.
- Hansen, J., Nagel, J., 2014. Waldwachstumskundliche Softwaresysteme auf Basis von TreeGross—Anwendung und theoretische Grundlagen. Beiträge der Nordwestdeutschen Forstlichen Versuchsanstalt. Universitätsverlag Göttingen, Göttingen.
- Hari, P., 1985. Theoretical aspects of eco-physiological research. In: Tigerstedt, P.M.A., Puttonen, P., Koski, V. (Eds.), *Crop Physiology of Forest Trees*. Helsinki Univ Press, Helsinki, pp. 21–30 (336 p.).
- Härkönen, S., Pulkkinen, M., Duursma, R., Mäkelä, A., 2010. Estimating annual GPP, NPP and stem growth in Finland using summary models. *For. Ecol. Manage.* 259, 524–533.
- Hartig, G.L., 1975. Anweisung zu Taxation der Forsten oder zur Bestimmung des Holztrages der Wälder. Heyer Verlag, Gießen, pp. 166 p.
- Hasenauer, H., 1994. Ein Einzelbaumwachstumssimulator für ungleichaltrige Kiefern- und Buchen- Fichtenmischbestände. Forstl Schr Univ Bodenkultur, Wien, pp. 152 p.
- Hauhs, M., Kastner-Maresch, A., Rost-Siebert, K., 1995. A model relating forest growth to ecosystem-scale budgets of energy and nutrients. *Ecol. Modell.* 83 (1), 229–243.
- Hector, A., Bazeley-White, E., Loreau, M., Otway, S., Schmid, B., 2002. Overyielding in grassland communities: testing the sampling effect hypothesis with replicated biodiversity experiments. *Ecol. Lett.* 5 (4), 502–511.
- Hector, A., Bagchi, R., 2007. Biodiversity and ecosystem multifunctionality. *Nature* 448, 188–190.
- Hector, A., Hautier, Y., Saner, P., Wacker, L., Bagchi, R., Joshi, J., Scherer-Lorenzen, M., Spehn, E.M.E., Bazeley-White, E., Weilenmann, M., Caldeira, M.C., Dimitrakopoulos, P.G., Finn, J.A., Huss-Danell, K.A., Jumpponen, A., Mulder, C.P.H., Palmberg, C., Pereira, J.S., Siamantziouras, A.S.D., Terry, A.C., Troumbis, A.Y., Schmid, B., Loreau, M., 2010. General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding. *Ecology* 91 (8), 2213–2220.
- Helms, J.A., 1998. *The Dictionary of Forestry*. The Society of American Foresters, Bethesda, MD.
- Hendriks, C.M.A., Bianchi, F.J.J.A., 1995. Root density and root biomass in pure and mixed forest stands of Douglas-fir and beech. *Netherlands J. Agric. Sci.* 43, 321–331.
- Hertel, C., Leuchner, M., Rötzer, T., Menzel, A., 2012. Assessing stand structure of beech and spruce from measured spectral radiation properties and modeled leaf biomass parameters. *Agric. Forest. Meteorol.* 165, 82–91.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.* 75 (1), 3–35.
- Jactel, H., Brockerhoff, E.G., 2007. Tree diversity reduces herbivory by forest insects. *Ecol. Lett.* 10, 835–848.
- Jactel, H., Brockerhoff, E.G., Duelli, P., 2005. A test of the biodiversity-stability theory: meta-analysis of tree species diversity effects on insect pest infestations, and re-examination of responsible factors. In: Scherer-Lorenzen, M., Körner, C., Schulze, E.D. (Eds.), *Forest Diversity and Function*. Ecol. Studies, vol. 176. Springer-Verlag, Berlin, pp. 235–262.
- Kellomäki, S., Vaisanen, H., 1997. Modelling the dynamics of the forest ecosystem for climate change studies in the boreal conditions. *Ecol. Modell.* 97 (1–2), 121–140.
- Kelty, M.J., 1992. Comparative productivity of monocultures and mixed-species stands. In: Kelty, M.J., Larson, B.C., Oliver, C.D. (Eds.), *The Ecology and Silviculture of Mixed-Species Forests*. Kluwer Academic Publishers, Dordrecht, pp. 125–141.
- Kimmins, J.P., Scoullar, K.A., 1989. FORCYTE: A Computer Simulation Approach to Evaluating the Effect of Whole-tree Harvesting on the Nutrient Budget in Northwest Forest. Report to the Canadian Forestry Service, National Forestry Institute, Petawawa, ON.
- Kimmins, J.P., Comeau, P.G., Kurz, W., 1990a. Modelling the interactions between moisture and nutrients in the control of forest growth. *For. Ecol. Manage.* 30 (1), 361–379.
- Kimmins, J.P., Scoullar, K.A., Apps, M.J., Kurz, W.A., 1990b. The FORCYTE experience: a decade of model development. In: Proc. Symp. Forestry Canada Inf. Rep. NOR-X-308, pp. 60–67.
- Kimmins, J.P., Maily, D., Seely, B., 1999. Modelling forest ecosystem net primary production: the hybrid simulation approach used in FORECAST. *Ecol. Modell.* 122, 195–224.
- Köhler, P., Huth, A., 1998. The effects of tree species grouping in tropical rainforest modelling: simulations with the individual-based model FORMIND. *Ecol. Modell.* 109 (3), 301–321.
- Komarov, A., Chertov, O., Zudin, S., Nadporozhskaya, M., Mikhailov, A., Bykhovets, S., Zudina, E., Zoubkova, E., 2003. EFIMOD 2—a model of growth and cycling of elements in boreal forest ecosystems. *Ecol. Modell.* 170 (2), 373–392.
- Korol, R.L., Running, S.W., Milner, K.S., 1995. Incorporating intertree competition into an ecosystem model. *Can. J. For. Res.* 25 (3), 413–424.
- Kramer, H., Akça, A., 1995. *Leitfaden zur Waldmeßlehre*. JD Sauerländer's Verlag, Frankfurt am Main (266 p.).
- Kramer, K., Leinonen, I., Bartelink, H.H., Berbigier, P., Borghetti, M., Bernhofer, C., Cienciala, E., Dolman, A.J., Froer, O., Gracia, C.A., Granier, A., Grünwald, T., Hari, P., Jans, W., Kellomäki, S., Loustau, D., Magnani, F., Markkanen, T., Matteucci, G., Mohren, G.M.J., Moors, E., Nissinen, A., Peltola, H., Sabaté, S., Sanchez, A., Sontag, M., Valentini, R., Vesala, T., 2002. Evaluation of six process-based forest growth models using eddy-covariance measurements of CO₂ and H₂O fluxes at six forest sites in Europe. *Global Change Biol.* 8/3, 213–230.
- Kramer, K., Groen, T.A., Van Wieren, S.E., 2003. The interacting effects of ungulates and fire on forest dynamics: an analysis using the model FORSPACE. *For. Ecol. Manage.* 181 (1–2), 205–222.
- Kramer, K., Buiteveld, D.J., Forstreuter, M., Geburek, T., Leonardi, S., Menozzi, P., Povillon, F., Schellass, M., Du Cros, E.T., Vendramin, G.G., Van der Werf, D.C., 2008. Bridging the gap between ecophysiological and genetic knowledge to assess the adaptive potential of European beech. *Ecol. Modell.* 216 (3–4), 333–353.
- Laclau, J.P., Nouvellon, Y., Reine, C., Gonçalves, J.L.d.M., Krushe, A.V., Jourdan, C., le Maire, G., Bouillet, J.-P., 2013. Mixing *Eucalyptus* and *Acacia* trees leads to fine root over-yielding and vertical segregation between species. *Oecologia* 172, 903–913.
- Landsberg, J.J., Waring, R.H., 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *For. Ecol. Manage.* 95 (3), 209–228.
- Lasch, P., Badeck, F.W., Suckow, F., Lindner, M., Mohr, R.P., 2005. Model-based analysis of management alternatives at stand and regional level in Brandenburg (Germany). *For. Ecol. Manage.* 207 (1–2), 59–74.
- le Maire, G., Nouvellon, Y., Christina, M., Ponzoni, F.J., Gonçalves, J.L.M., Bouillet, J.P., Laclau, J.P., 2013. Tree and stand light use efficiencies over a full rotation of single- and mixed-species *Eucalyptus grandis* and *Acacia mangium* plantations. *For. Ecol. Manage.* 288, 31–42.
- Lexer, M.J., Hönninger, K., 1998. Simulated effects of bark beetle infestations on stand dynamics in *Picea abies* stands: coupling a patch model and a stand risk model. In: Beniston, M., Innes, J.L. (Eds.), *The Impacts of Climate Change on Forests*. Lecture Notes in Earth Sciences. Springer Verlag, Berlin, Heidelberg, pp. 289–308.
- Ligot, G., Balandier, P., Courbaud, B., Claessens, H., 2014. Forest radiative transfer models: which approach for which application? *Can. J. For. Res.* 44, 385–397.
- Lischke, H., Zimmermann, N.E., Bollinger, J., Rickebusch, S., Löffler, R.T.J., 2006. TreeMig: a forest-landscape model for simulating spatio-temporal patterns from stand to landscape scale. *Ecol. Modell.* 199 (4), 409–420.
- Litton, C.M., Raich, J.W., Ryan, M.G., 2007. Carbon allocation in forest ecosystems. *Global Change Biol.* 13, 2089–2109.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D.A., 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294 (5543), 804–808.
- Luxmoore, R.J., Hargrove, E.W.W., Tharp, M.L., Macpost, T.W., Berry, M.W., Minser, K.S., Cropper, W.P., Johnson, D.W., Zeide, B., Amateis, R.L., Burkhardt, H.E., Baldwin, V.C., Peterson, K.D., 2002. Addressing multi-use issues in sustainable forest management with signal-transfer modeling. *For. Ecol. Manage.* 165 (1–3), 295–304.
- Mäkelä, A., Makinen, H., 2003. Generating 3D sawlogs with a process-based growth model. *For. Ecol. Manage.* 184 (1–3), 337–354.
- Masera, O.R., Garza-Caligaris, J.F., Kanninen, M., Karjalainen, T., Liski, J., Nabuurs, G.J., Pussinen, A., de Jong, B.H.J., Mohren, G.M.J., 2003. Modeling carbon sequestration in afforestation, agroforestry and forest management projects: the CO2FIX V.2 approach. *Ecol. Modell.* 164 (2), 177–199.
- McDowell, N.G., Beerling, D.J., Breshears, D.D., Fisher, R.A., Raffa, K.F., Stitt, M., 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends Ecol. Evol.* 26, 523–532.
- McKay, H.M., Malcolm, D.C., 1988. A comparison of the fine root component of a pure and a mixed coniferous stand. *Can. J. For. Res.* 18 (11), 1416–1426.
- McKay, H.M., 1988. The influence of pine on the form of Sitka spruce fine roots. *J. Exp. Bot.* 39 (206), 1263–1266.
- Medlyn, B.E., 1998. Physiological basis of the light use efficiency model. *Tree Physiol.* 18, 167–176.
- Medlyn, B.E., Duursma, R.A., Zeppel, M.J.B., 2011. Forest productivity under climate change: a checklist for evaluating model studies. *Clim. Change* 2, 332–355.
- Monserud, R.A., Sterba, H., 1996. A basal area increment model for individual trees growing in even- and uneven-aged forest stands in Austria. *For. Ecol. Manage.* 80 (1), 57–80.
- Monserud, R.A., Sterba, H., 1999. Modeling individual tree mortality for Austrian forest species. *For. Ecol. Manage.* 113 (2), 109–123.
- Nagel, J., 1999. Konzeptionelle Überlegungen zum schrittweisen Aufbau eines waldwachstumskundlichen Simulationssystems für Nordwestdeutschland. *Schr Forstl Fak Univ Göttingen u Niedersächs Forstl Versuchsanst 128*. JD Sauerländer's Verlag, Frankfurt am Main (122 p.).
- Neumann, R.B., Cardon, Z.G., 2012. The magnitude of hydraulic redistribution by plant roots: a review and synthesis of empirical and modeling studies. *New Phytol.* 194, 337–352.
- Nightingale, J.M., Hill, M.J., Phinn, S.R., Davies, I.D., Held, A.A., Erskine, P.D., 2008. Use of 3-PG and 3-PCS to simulate forest growth dynamics of Australian tropical

- rainforests I. Parameterisation and calibration for old-growth, regenerating and plantation forests. *For. Ecol. Manage.* 254, 107–121.
- Palahi, M., Pukkala, T., Kasimiadis, D., Poirazidis, K., Papageorgiou, A.C., 2008. Modelling site quality and individual-tree growth in pure and mixed *Pinus brutia* stands in north-east Greece. *Ann. For. Sci.* 65 (501), <http://dx.doi.org/10.1051/forest:2008022>
- Paquette, A., Messier, C., 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. *Global Ecol. Biogeogr.* 20 (1), 170–180.
- Peng, C., Liu, J., Dang, Q., Apps, M.J., Jiang, H., 2002. TRIPLEX: a generic hybrid model for predicting forest growth and carbon and nitrogen dynamics. *Ecol. Model.* 153 (1), 109–130.
- Peringer, A., Siehoff, S., Chételat, J., Spiegelberger, T., Buttler, A., Gillet, F., 2013. Past and future landscape dynamics in pasture-woodlands of the Swiss Jura Mountains under climate change. *Ecol. Soc.* 18 (3), <http://dx.doi.org/10.5751/ES-05600-180311>
- Perttunen, J., Sievänen, R., Nikinmaa, E., 1998. LIGNUM: a model combining the structure and the functioning of trees. *Ecol. Modell.* 108 (1), 189–198.
- Peters, E.B., Wythers, K.R., Bradford, J.B., Reich, P.B., 2013. Influence of disturbance on temperate forest productivity. *Ecosystems* 16, 95–110.
- Pietsch, S.A., Hasenauer, H., Kucera, J., Cermak, J., 2003. Modeling effects of hydrological changes on the carbon and nitrogen balance of oak in floodplains. *Tree Physiol.* 23 (11), 735–746.
- Pinkard, E.A., Battaglia, M., Roxburgh, S., O'Grady, A.P., 2011. Estimating forest net primary production under changing climate: adding pests into the equation. *Tree Physiol.* 31, 686–699.
- Piotto, D., 2008. A meta-analysis comparing tree growth in monocultures and mixed plantations. *Forest. Ecol. Manage.* 255, 781–786.
- Prentice, I.C., Sykes, M.T., Cramer, W., 1993. A simulation model for the transient effects of climate change on forest landscapes. *Ecol. Modell.* 65 (1), 51–70.
- Pretzsch, H., 2009. *Forest Dynamics, Growth, and Yield*. Springer, Berlin/Heidelberg, pp. 1–39, 664 p.
- Pretzsch, H., 2010. Re-evaluation of allometry: state-of-the-art and perspective regarding individuals and stands of woody plants. *Prog. Bot.* 71, 339–369.
- Pretzsch, H., 2013. Facilitation and competition in mixed-species forests analysed along an ecological gradient. *Nova Acta Leopoldina* 114 (391), 255–266.
- Pretzsch, H., 2014. Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. *For. Ecol. Manage.* 327, 251–264.
- Pretzsch, H., Biber, P., Ďurský, J., 2002. The single tree based stand simulator SILVA. Construction, application and evaluation. *For. Ecol. Manage.* 162, 3–21.
- Pretzsch, H., Grote, R., Reineking, B., Rötzer, T., Seifert, S., 2008. Models for forest ecosystem management: a European perspective. *Ann. Bot.* 101, 1065–1087.
- Pretzsch, H., Block, J., Dieler, J., Dong, P.H., Kohnle, U., Nagel, J., Spellmann, H., Zingg, A., 2010. Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. *Ann. For. Sci.* 67, 1–12.
- Pretzsch, H., Bielak, K., Block, J., Bruchwald, A., Dieler, J., Ehrhart, H.P., Kohnle, U., Nagel, J., Spellmann, H., Zasada, M., Zingg, A., 2013a. Productivity of pure versus mixed stands of oak (*Quercus petraea* (MATT.) LIEBL. and *Quercus robur* L.) and European beech (*Fagus sylvatica* L.) along an ecological gradient. *Eur. J. For. Res.* 132 (2), 263–280.
- Pretzsch, H., Bielak, K., Bruchwald, A., Dieler, J., Dudzińska, M., Ehrhart, H.P., Jensen, A.M., Johannsen, V.K., Kohnle, U., Nagel, J., Spellmann, H., Zasada, M., Zingg, A., 2013b. Species results from long-term experiments. *AFJZ* 184 (7–8), 177–196.
- Pretzsch, H., del Río, M., Ch., A., Avdagic, A., Barbeito, I., Bielak, K., Brazaitis, G., Coll, L., Dirnberger, G., Drössler, L., Fabrika, M., Forrester, D.I., Heym, M., Hurt, V., Kurylyak, V.M.L., Lombardi, F., Mohren, F., Motta, R., den Ouden, J., Pach, M., Ponette, Q., Schütze, G., Schweig, J., Skrzyszewski, J., Sramek, V., Sterba, H., Stojanović, D., Svoboda, M., Vanhellemont, M., Verheyen, K., Wellhausen, K., Zlatanov, T., Bravo-Oviedo, A., 2015. Growth and yield of mixed versus pure stands of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) along a gradient of productivity through Europe. *Eur. J. For. Res.*, <http://dx.doi.org/10.1007/s10342-015-0900-4>
- Pukkala, T., 1987. Simulation model for natural regeneration of *Pinus sylvestris*, *Picea abies*, *Betula pendula* and *Betula pubescens*. *Silva Fenn.* 21, 37–53.
- Pukkala, T., Miina, J., Kurttila, M., Kolström, T., 1998. A spatial yield model for optimizing the thinning regime of mixed stands of *Pinus sylvestris* and *Picea abies*. *Scand. J. For. Res.* 13 (1–4), 31–42.
- Pukkala, T., Lähde, E., Laiho, O., 2009. Growth and yield models for uneven-sized forest stands in Finland. *For. Ecol. Manage.* 258 (3), 207–216.
- Richards, A.E., Forrester, D.I., Bauhus, J., Scherer-Lorenzen, M., 2010. The influence of mixed tree plantations on the nutrition of individual species: a review. *Tree Physiol.* 30 (9), 1192–1208.
- Rothe, A., Binkley, D., 2001. Nutritional interactions in mixed species forests: a synthesis. *Can. J. For. Res.* 31, 1855–1870.
- Rötzer, T., Grote, R., Pretzsch, H., 2004. The timing of bud burst and its effect on tree growth. *Int. J. Biometeorol.* 48, 109–118.
- Rötzer, T., Seifert, T., Pretzsch, H., 2009. Modelling above and below ground carbon dynamics in a mixed beech and spruce stand influenced by climate. *Eur. J. For. Res.* 128, 171–182.
- Rötzer, T., Leuchner, M., Nunn, A.J., 2010. Simulating stand climate, phenology, and photosynthesis of a forest stand with a process-based growth model. *Int. J. Biometeorol.* 54 (4), 449–464.
- Rötzer, T., Liao, Y., Görden, K., Schüler, G., Pretzsch, H., 2013. Modelling the impact of climate change on the productivity and water-use efficiency of a central European beech forest. *Clim. Res.* 58, 81–95.
- Running, S.W., Coughlan, J.C., 1988. A general model of forest ecosystem processes for regional applications. I. Hydrologic balance, canopy gas exchange and primary production processes. *Ecol. Model.* 42, 125–154.
- Running, S.W., Gower, S.T., 1991. FOREST-BGC, a general model of forest ecosystem processes for regional applications. II. Dynamic carbon allocation and nitrogen budgets. *Tree Physiol.* 9 (1–2), 147–160.
- Sampson, D.A., Janssens, I.A., Ceulemans, R., 2001. Simulated soil CO₂ efflux and net ecosystem exchange in a 70-year-old Belgian Scots pine stand using the process model SECRETS. *Ann. For. Sci.* 58, 31–46.
- Sampson, D.A., Janssens, I.A., Curriel Yuste, J., Ceulemans, R., 2007. Basal rates of soil respiration are correlated with photosynthesis in a mixed temperate forest. *Global Change Biol.* 13 (9), 2008–2017.
- Scherer-Lorenzen, M., Körner, C., Schulze, E.D., 2005. Forest diversity and function. In: *Ecol. Studies* 176. Springer, Berlin, Heidelberg, pp. 399p.
- Schmid, I., Kazda, M., 2001. Vertical and radial growth of coarse roots in pure and mixed stands of *Fagus sylvatica* and *Picea abies*. *Can. J. For. Res.* 31, 539–546.
- Schmid, I., Kazda, M., 2002. Root distribution of Norway spruce in monospecific and mixed stands on different soils. *For. Ecol. Manage.* 159, 37–47.
- Schume, H., Jost, G., Hager, H., 2004. Soil water depletion and recharge patterns in mixed and pure forest stands of European beech and Norway spruce. *J. Hydrol.* 289, 258–274.
- Schwalm, C.R., Ek, A.R., 2004. A process-based model of forest ecosystems driven by meteorology. *Ecol. Modell.* 179 (3), 317–348.
- Schwappach, A., 1889. *Wachstum und Ertrag normaler Kiefernbestände in der norddeutschen Tiefebene*. Verlag Julius Springer, Berlin, pp. 72p.
- Seidl, R., Lexer, M.J., Jager, D., Honninger, K., 2005. Evaluating the accuracy and generality of a hybrid patch model. *Tree Physiol.* 25 (7), 939–951.
- Shugart, H.H., Smith, T.M., 1996. A review of forest patch models and their application to global change research. *Clim. Change* 34, 131–153.
- Simard, S.W., Beiler, K.J., Bingham, M.A., Deslippe, J.R., Philip, L.J., Teste, F.P., 2012. Mycorrhizal networks: mechanisms, ecology and modelling. *Fungal Biol. Rev.* 26, 39–60.
- Smith, A.R., Lukac, M., Hood, R., Healey, J.R., Miglietta, F., Godbold, D.L., 2013. Elevated CO₂ enrichment induces a differential biomass response in a mixed species temperate forest plantation. *New Phytol.* 198, 156–168.
- Stape, J.L., Ryan, M.G., Binkley, D., 2004. Testing the utility of the 3-PG model for growth of *Eucalyptus grandis* × *urophylla* with natural and manipulated supplies of water and nutrients. *For. Ecol. Manage.* 193, 219–234.
- Taylor, A.R., Chen, H.Y.H., VanDamme, L.A., 2009. A review of forest succession models and their suitability for forest management planning. *For. Sci.* 55, 23–36.
- UA, 2014. <http://www.rr.ualberta.ca/en/Research/MixedwoodGrowthModel/TheModel.aspx> down-loaded: Sept.2014.
- Ulrich, B., 1990. Waldsterben: forest decline in West Germany. *Environ. Sci. Technol.* 24 (4), 436–441.
- Valentine, H.T., Gregoire, T.G., Burkhart, H.E., Hollinger, D.Y., 1997. A stand-level model of carbon allocation and growth, calibrated for loblolly pine. *Can. J. For. Res.* 27, 817–830.
- Valentine, H.T., Herman, D.A., Gove, J.H., Hollinger, D.Y., Solomon, D.S., 2000. Initializing a model stand for process-based projection. *Tree Physiol.* 20 (5–6), 393–398.
- Van Kessel, C., Farrell, R.E., Roskoski, J.P., Keane, K.M., 1994. Recycling of the naturally-occurring ¹⁵N in an established stand of *Leucaena leucocephala*. *Soil Biol. Biochem.* 26, 757–762.
- Van der Voet, H., Mohren, G.M.J., 1994. An uncertainty analysis of the process-based growth model FORGRO. *For. Ecol. Manage.* 69 (1), 157–166.
- Van der Werf, W., Keesman, K., Burgess, P., Graves, A., Pilbeam, D., Incoll, L.D., Metselaara, K., Mayusa, M., Stappers, R., van Keulene, H., Palma, J., Dupraz, C., 2007. Yield-SAFE: a parameter-sparse, process-based dynamic model for predicting resource capture, growth, and production in agroforestry systems. *Ecol. Eng.* 29 (4), 419–433.
- Van Wijk, M.T., Dekker, S.C., Bouten, W., Kohsiek, W., Mohren, G.M.J., 2001. Simulation of carbon and water budgets of a Douglas-fir forest. *For. Ecol. Manage.* 145 (3), 229–241.
- Verbeeck, H., Samson, R., Verdonck, F., Lemeur, R., 2006. Uncertainty and parameter sensitivity of the forest carbon flux model FORUG: a Monte Carlo analysis. *Tree Physiol.* 26, 807–817.
- Verbeeck, H., Samson, R., Granier, A., Montpied, P., Lemeur, R., 2008. Multi-year model analysis of GPP in a temperate beech forest in France. *Ecol. Modell.* 210 (1), 85–103.
- Wang, Y.P., Jarvis, P.G., 1990. Description and validation of an array model—MAESTRO. *Agric. Forest. Meteorol.* 51, 257–280.
- Wang, W., Peng, C., Zhang, S.Y., Zhou, X., Larocque, G.R., Kneeshaw, D.D., Lei, X., 2011. Development of TRIPLEX-management model for simulating the response of forest growth to pre-commercial thinning. *Ecol. Modell.* 222, 2249–2261.
- Waterworth, R.M., Richards, G.P., Brack, C.L., Evans, D.M.W., 2007. A generalised hybrid process-empirical model for predicting plantation forest growth. *For. Ecol. Manage.* 238 (1), 231–243.
- Weiskittel, A.R., Maguire, D.A., Monserud, R.A., Johnson, G.P., 2010. A hybrid model for intensively managed Douglas-fir plantations in the Pacific Northwest, USA. *Eur. J. For. Res.* 129 (3), 325–338.
- Wiedemann, E., 1942. Der gleichaltrige Fichten-Buchen-Mischbestand. *Mitt. Forstwirtschaft. Forstwiss* 13, 1–88.

- Wykoff, W.R., 1990. A basal area increment model for individual conifers in the northern Rocky Mountains. *For. Sci.* 36 (4), 1077–1104.
- Wykoff, W.R., Crookston, N.L., Stage, A.R., 1982. User's guide to the stand prognosis model. In: *US Forest Serv, Gen Techn Rep INT-133*. Ogden, UT (112 p.).
- Xenakis, G., Ray, D., Mencuccini, M., 2008. Sensitivity and uncertainty analysis from a coupled 3-PG and soil organic matter decomposition model. *Ecol. Mod.* 219, 1–16.
- Yao, X., Titus, S.J., MacDonald, S.E., 2001. A generalized logistic model of individual tree mortality for aspen, white spruce, and lodgepole pine in Alberta mixedwood forests. *Can. J. For. Res.* 31 (2), 283–291.
- Zapater, M., Hossann, C., Bréda, N., Bréchet, C., Bonal, D., Granier, A., 2011. Evidence of hydraulic lift in a young beech and oak mixed forest using 18O soil water labelling. *Trees* 25, 885–894.
- Zhang, Y., Chen, H.Y., Reich, P.B., 2012. Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. *J. Ecol.* 100 (3), 742–749.
- Zhao, D., Borders, B., Wilson, M., 2004. Individual-tree diameter growth and mortality models for bottomland mixed-species hardwood stands in the lower Mississippi alluvial valley. *For. Ecol. Manage.* 199 (2), 307–322.