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# Modelling mixed forest growth: a review of models for forest management

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## Abstract

Most forests today are multi-specific and heterogeneous forests ('mixed forests'). However, forest modelling has been focusing on mono-specific stands for a long time, only recently have models been developed for mixed forests. Previous reviews of mixed forest modelling were restricted to certain categories of models only and were generally not considering application and suitability. The purpose of this paper is to give an overview of the models designed for or applied to modelling mixed forest growth and dynamics and to review the suitability of the different model types according to their intended purposes. The first part of the paper gives an overview of previous classifications, after which a new and overall classification scheme is presented. Next, the characteristics of the six modelling approaches that were distinguished are described: distance-dependent stand models, distribution models, average tree models, distance-dependent tree models, distance-independent tree models and gap models. All, except gap models, are close to mono-specific stands modelling approaches. The second part of the paper describes the main applications of these modelling approaches and presents a critical analysis of their suitability. Applications can be separated between growth and yield studies and forest dynamics simulation studies. Attention must be paid to recruitment sub-models, which appear to be inadequate in many models, but which highly influence the simulation outcome. All types of model were used as management tools. Stand level simulations fit the yield data better than tree level simulations, as a result of cumulated model errors from tree to stand level. However, tree level approaches seem most appropriate to understand stand growth as affected by competition between individuals of different species. Forest dynamics were mostly modelled using distribution models, gap models and distance-dependent tree models. The latter appeared to be less suitable because of the difficulties in modelling 3D stand structure over large periods and areas. Gap models could be applied to larger areas and time periods than distribution models, especially when they included detailed descriptions of the ecological functioning of the ecosystem. In sum the empirical models appeared more accurate in their predictions than mechanistic models, but they are highly dependent on the data used for parameterisation. That makes them unsuitable for extrapolation to other systems or conditions. Although mechanistic models can also be misused, adding mechanistic approaches to empirical observations is necessary to model the growth and dynamics of complex forest systems. © 2002 Elsevier Science B.V. All rights reserved.

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## 1. Introduction

### 1.1. Trends in modelling mixed forest growth

Models of forest growth, from the initial sketched diagrams to sophisticated computer models, have been and still are important forest management tools. Four major developments affected the forest growth modelling in the past century: (1) the silvicultural focus moving from even-aged monospecific stands towards mixed-species stands; (2) the growing interest in incorporating causal relationships in models; (3) the changing goals of forest management (not only focussing on growth and yield); and (4) the increasing availability of computers. The history of forest growth modelling hence cannot be characterised simply by a continuous development of improved models. Instead, different model types with diverse objectives and concepts have been developed over the past decades simultaneously. In this section, a brief history of forest growth modelling with emphasis on mixed forest stands is presented.

With a history of over 250 years, yield tables for pure stands are the oldest models in forestry science and forest management (e.g. Paulsen, 1795; Cotta, 1821). As a result of their broad application, yield tables were continuously evolving. Pretzsch (1999) distinguishes four generations of yield tables, from the early elementary ones that used restricted data sets, to the so-called stand growth simulators which rely heavily on the use of fast computers. Despite a number of drawbacks yield tables still form the backbone of sustainable management particularly for plantation forestry. The development of models for mixed stands started somewhere in the first half of the 20th century, initially also in the form of yield tables. In 1949, e.g. Wiedemann produced a yield table for even-aged spruce–beech mixtures. Not many attempts were made, however, due to the large variety of possible stand dynamics and (thus) the lack of data and the restricted applicability. Even when only a two-species mixture is considered, the number of possible stand compositions is huge: apart from the species involved, stands may differ in terms of the species contributions to the mixture, the stand origin (planted or natural regeneration), the planting pattern, and the site conditions (affecting inter-specific relations), resulting in different types of interaction (Holmes and Reed, 1991; Larson, 1992; Bartelink, 1999). Nevertheless, the demand for models of mixed species forest rapidly increased, especially after the 1970s (Pretzsch, 1999). For mixed species forest stands, this resulted in two main developmental trajectories: new empirical growth and yield models; and mechanistic growth models. The latter are models that estimate growth based on growing conditions and species requirements (Jarvis and Leverenz, 1983; Landsberg, 1986), using causal relationships rather than empirical descriptions. Besides this distinction, models can be characterised in terms of spatial resolution: a commonly applied criterion to characterise the modelling approach is whether the model focuses on the stand level or whether it keeps track of individual tree growth.

#### 1.1.1. Empirical versus mechanistic approaches in mixed forest modelling

The first modellers facing the challenge to simulate mixed forest growth took the traditional and empirical yield table as a starting point (Wiedemann, 1949). Also more recently empirical approaches were chosen to model mixed stands (Alimi and Barrett, 1977; Deusen and Biging, 1985). Meanwhile, partly due to the increased availability of computers, the spatial resolution of the models increased: empirical growth and yield models developed recently are mostly tree-level (i.e. based on the individual tree: see below), describing growth in terms of diameter increment (Biging and Dobbertin, 1995).

The major drawback of the empirical approach, where tree or stand growth is estimated using descriptive relationships, is the restricted applicability of the models due to the limited validity of the empirical relationships.

In the 1980s, mechanistic models to simulate forest growth based on species requirements and growing conditions began to be developed, initially for monospecific stands only. For example, Mohren (1987) developed a stand-level model for even-aged Douglas-fir stands, Mäkelä and Hari (1986) and Nikinmaa (1992) applied a stand-level approach in Scots pine, Bossel and Krieger (1994) did likewise for Norway spruce, and Ludlow et al. (1990) for Sitka spruce. Only recently have attempts been made to apply the mechanistic stand approach in mixed forests. Kramer (1995) developed a general carbon-balance model for mixed forest in a study on the role of phenology in competition between tree species. This model was developed primarily to study the climate change aspects. The models by Szwagrzyk (1997) and Bartelink (1998) focused more towards forest management issues. These models do contain mechanistic relationships, but also draw heavily on tree allometry; they combine functional relationships with a tree-based simulation approach. The major drawback here is the large amount of (detailed, eco-physiological) data needed: as a consequence, many causal relationships in such models are still descriptive. These models are in most cases primarily used as research tools rather than applied by forest management.

#### *1.1.2. Stand versus tree level approaches*

Apart from the difference between empirical and mechanistic models, a distinction can be made with respect to spatial resolution, i.e. between stand-level and tree-level approaches. In the stand-level approach, no individual trees are described and the canopy is represented by horizontally homogeneous leaf layers. Most stand-level models are empirical models, such as the yield tables. Stand-level models are by their very nature unable to represent different planting patterns in mixtures, or to take account of spatially non-systematic thinning measures. Neither can they take crown dynamics into account. In contrast, some of the more recently developed growth and yield models are tree-level, modelling individual trees either empirically (Leersnijder, 1992; Pretzsch, 1992) or more mechanistically (Szwagrzyk, 1997; Bartelink, 1998).

One of the first modelling attempts aiming specifically at simulating mixed forest growth was the development of the ‘gap-models’, which started with the work of Botkin et al. (1972). Gap-models can be classified as a special category of tree-level modelling, as they define and keep track of individual trees competing and growing in a restricted area, the gap (Botkin et al., 1972; Shugart, 1984). Many gap-models have been developed, e.g. for central Europe (FORECE: Kienast and Kuhn, 1989b), to simulate old pine stands in Sweden (FORSKA: Leemans, 1992), to estimate effects of climate change (Fischlin et al., 1995), or to determine the effects of ungulates on spontaneous forest development (Jorritsma et al., 1999).

Gap models and tree-level models are more flexible than stand-level models, but generally rely heavily on descriptive relationships. Models that include biological processes and are suitable to support taking decisions about forest management would constitute a great advantage, but unfortunately are still scarce (Mohren et al., 1991). On the other hand, though mechanistic approaches do relate growth to growing conditions, these are in general too theoretical or require too many data to be of much value for forest managers.

### *1.2. Aims of the review*

This study focused on forest growth models that have been developed to support forest management decision taking in mixed or heterogeneous forests. The aims of the study were: (1) to give an overview of the state-of-the-art in the field of modelling mixed forest dynamics; and (2) to give a review of the suitability of modelling approaches regarding the underlying purposes. It is noteworthy that generic forest models that could of course be applied to mixed stands are not included in this study.

### *1.3. Methods*

The search for articles was conducted according to Fig. 1. The search consisted of a combination of the key words of box A till C, so that at least one word out of each of these first three boxes should appear in either the title or the abstract of the paper. Next, one keyword out of either box D and/or box E was added to all combinations ABC, to focus the search. The search-engine 'Webspirs' was used to explore the databases TREECD, TROPAG and RURAL, BIOLOGICAL abstracts, and CAB abstracts. This literature search resulted in about 700 papers. After cleaning up 199 papers remained, which form the basis of this review. To indicate the increasing attention for forest growth modelling over the past decades, in Fig. 2 the amount of publications on this topic per year are presented.

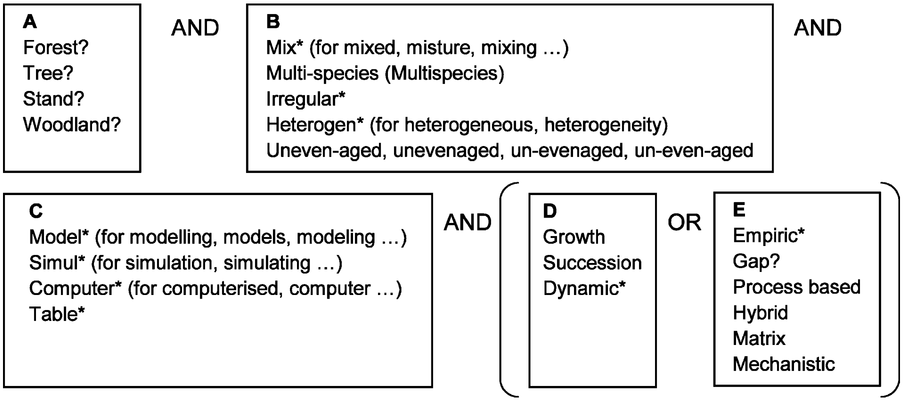

Fig. 1. Keywords used to find relevant publications. Keywords inside the boxes were combined with operator OR and boxes were combined with operator AND. Truncature symbols are: ? for a letter; and * for a group of letters.

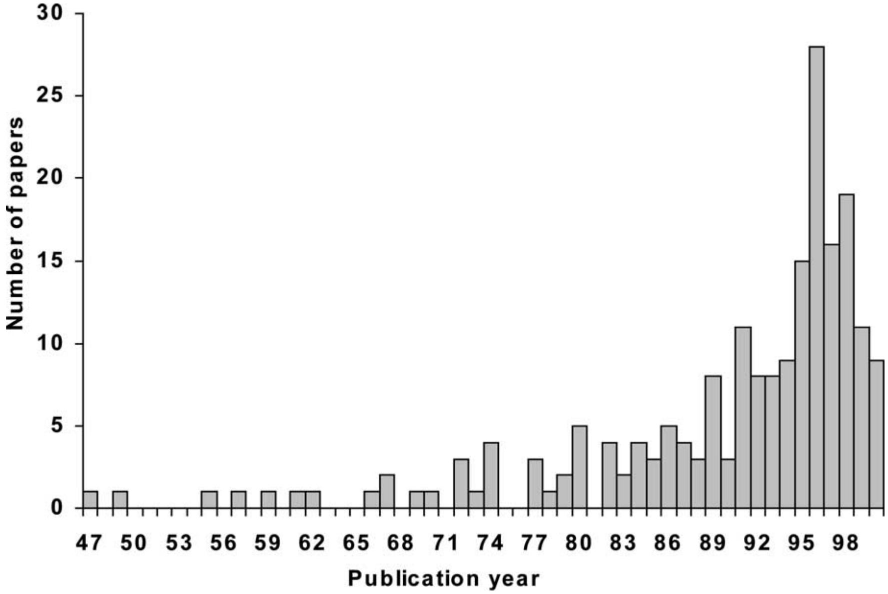

Fig. 2. Number of publications on forest growth modelling over the past decades.

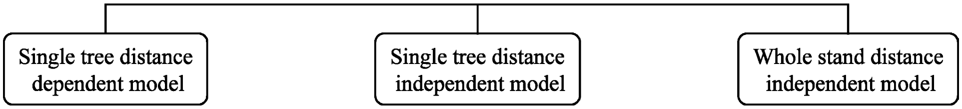

Fig. 3. Classification of forest growth models according to Munro (1974).

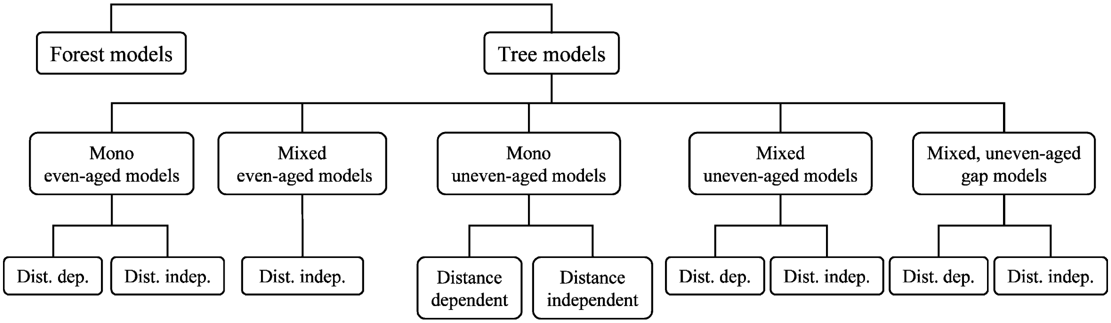

Fig. 4. Classification of forest growth models according to Shugart (1984).

## 2. Model classifications

### 2.1. Present classifications

To get an overview of the state-of-the-art in the field of modelling mixed forest dynamics, a classification of the existing models forms a helpful tool. In the literature, however, several, generally contradicting classification schemes were found. We hence first summarise the main existing classification schemes here.

Only few papers deal explicitly with the classification of mixed forest growth models and, moreover, most of them are restricted to the study of one or a few specific kinds of models such as gap models (Shugart, 1984; Bugmann et al., 1996b; Shugart and Smith, 1996), individual tree models (Liu and Ashton, 1995), stand density management diagrams (Newton, 1997) or models for growth and yield predictions (Vanclay, 1994, 1995). The classification by Munro (1974) appears to be the basis of many of the classifications encountered. This classification was proposed for both mono-specific and mixed stands: it consisted of discriminating the models according to the primary unit that was used to describe the forest (single tree or whole stand) and to the use of inter-tree dependency (Fig. 3). The three resulting categories can still be traced in most classifications: (1) single tree distance-dependent models; (2) single tree distance-independent models; and (3) whole stand distance-independent models.

More recently, classifications that aimed at covering all the existing model types were proposed (Shugart, 1984; Shugart et al., 1988; Houllier, 1995; Loffeier and Favrichon, 1996; Pretzsch, 1999). One way or the other, they all took into account Munro's primary unit description and space dependency to build their classification. However, each author also based the classification on its own purposes.

Shugart (1984), e.g. made a first distinction based on the unit level modelled, i.e. either whole forest growth or tree growth. The second step separated even-aged from uneven-aged forest. The last step in Shugart's classification dealt with spatial relationships within the forest (Fig. 4).

Another example involves the classification of Liu and Ashton (1995), who defined two alternative categories (Fig. 5), namely stand models and individual-based models. 'The stand models are mainly designed for timber projection and have serious drawbacks for species diversity studies as most stand models tend to focus on timber species alone, rather than all species' (Liu and Ashton, 1998). They did not sub-divide stand models any further in their classification. The second class, the individual-based models, simulate establish-

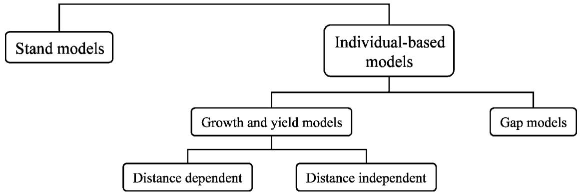

Fig. 5. Classification of tree level forest growth models according to Liu and Ashton (1995).

ment, growth and death of each individual tree, keeping the information for each tree until the individual dies. One way to sub-divide the individual-based models is to distinguish growth and yield models versus gap models. The first one 'provides managers with information about growth and yield dynamics of timber trees, while gap models are mainly used to understand the forest successional patterns and processes in a canopy gap area created by tree falling' (Liu and Ashton, 1995, 1998). Finally, distance-dependency was used as a discriminating characteristic in the growth and yield models (Fig. 5).

Franc et al. (2000) distinguished the three types of models in their classification (Fig. 6): population models; demographic/distribution models; and individual-based models. Population models are characterised by the global variables that are used to model forest stands, e.g. stand basal area or total standing volume. In demographic or distribution models the variables refer to particular species or particular classes of trees within the forest. In contrast, Liu and Ashton (1995) did not make an additional class in which time is the dominant factor to classify models: Franc et al. (2000) sub-divided the distribution models into the following: (a) succession models; (b) mosaic models; (c) continuous time models; and (d) discrete time and state models. In succession models the forest is treated as a group of plots instead as of a group of individuals. Continuous time models describe dynamics according to a continuous time scale. Discrete time and state models on the other hand, depend on probability and state. Individual-based models, finally, are sub-divided in distance-dependent and distance-independent models (gap models). Liu and Ashton (1995) also assign distance dependency as a property to their sub-division of the individual-based models.

Houllier (1995) used classification principles comparable with those of Franc et al. (2000) but on the first level he additionally distinguished mosaic models and gap models (Fig. 7). The population models or distribution models are subdivided into (a) matrix models, and (b) continuous models, which are a sub-class of the demographic/distribution models in the classification of Franc et al. (2000).

Vanclay (1994), lastly, made the most detailed classification: it contains elements of almost all previously described classifications (Fig. 8). Several model types that fit into one class in the other classifications are mentioned here separately, e.g. the growth and yield tables and the growth and yield equations. The drawback of such a detailed approach is that models might belong to more than one class at the same time.

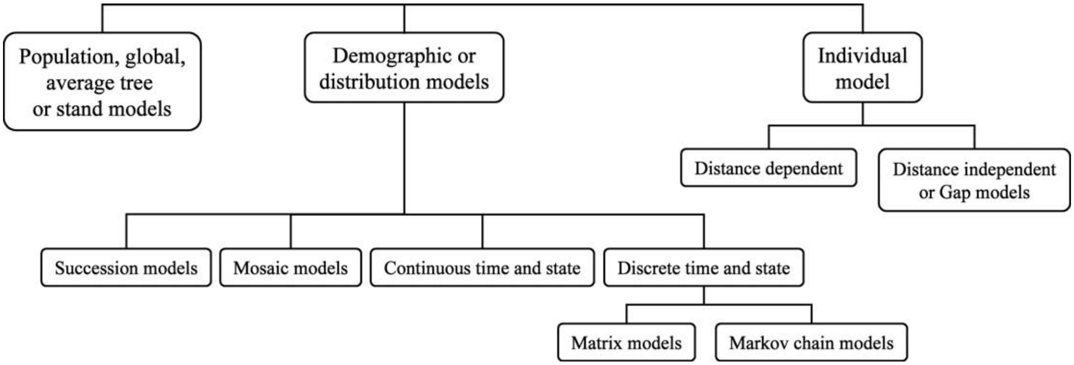

Fig. 6. Classification of forest growth models according to Franc et al. (2000).

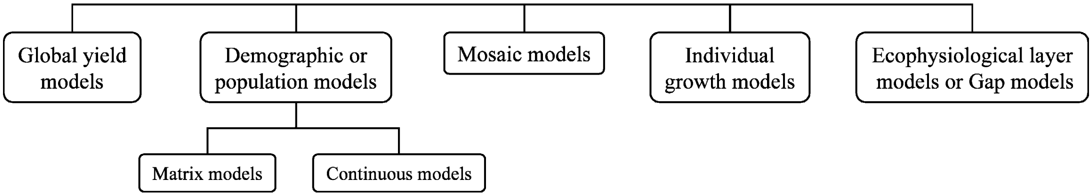

Fig. 7. Classification of forest growth models according to Houllier (1995).

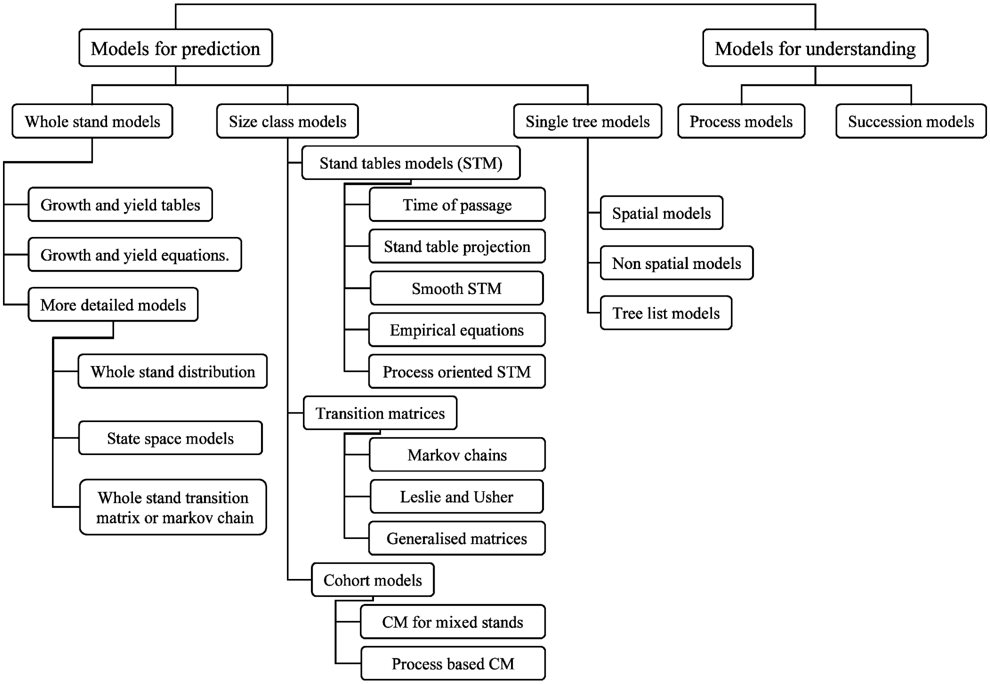

Fig. 8. Classification of forest growth models according to Vanclay (1994).

Summarising the present classifications, it appears that generally a first distinction is made with respect to the spatial level at which the forest is modelled, i.e. stand or global models and individual-based models or individual growth models, except for Shugart (1984) who only distinguishes tree and gap models, and Vanclay (1994), who distinguishes between 'prediction' and 'understanding'. In addition, differences arise because authors use their specific research aims as driving principles for designing the classification scheme. These resulted partly in similar model groups, but partly also in the creation or suppression of some others. Franc et al. (2000) developed a mathematically based discrimination using the concepts of continuous and discrete coding of state and time. Vanclay (1994), in turn, used a crossed criteria based on the same mathematical concepts and on the distinction between empirical and process-based models. Both classifications presented numerous groups of models. On the contrary, some classifications were merging or skipping model groups: Shugart (1984) based its classification on the description of the stand in terms of structure (stand or tree, space or not) and heterogeneity (even or uneven-aged, pure or mixed), building a simple and repetitive sub-division system. Houllier (1995) used a unique complex of criteria based on the level of description and space description to obtain five groups of models.

Looking at the diversity that exists among the few existing classifications, and the confusion that is brought by these different approaches, there appears to be a need for an overall classification that includes all existing model types and that is based on clear objective classification arguments.

### 2.2. Proposal for a new classification

In order to develop a suitable overall classification, clear objective classification arguments are needed. From the previous section it appears that various criteria have been used to classify the models, including:

- Size of the organisational level (Munro's 'primary unit': tree, stand).
- Heterogeneity of the object.
- Distance dependency.
- Spatial explicitness.
- Size of regeneration units.
- Use of size classes.
- Deterministic or stochastic.

Since forest dynamics are strongly related to forest structure (Buongiorno and Michie, 1980; Shugart, 1984), a logical way of discriminating between forest growth models is to look at the description of the stand structure. We hence decided to base our classification on three criteria: the first corresponds to the smallest unit identified (i.e. a branch, a tree, a stand) in the model; the second criterion is spatial dependence (i.e. diameter, whether these units have specific spatial locations or not); and the third criterion describes whether or not forest heterogeneity is taken into account. Applying the first criterion resulted in two groups of models: 'stand models' where the stand constitutes the smallest unit of modelling, and 'tree models' where the single tree represents the most detailed level of modelling. The second criterion divided each of these two groups in 'distance-dependent' and 'distance-independent' stand or tree models. Distance dependence is a commonly used criterion to distinguish subgroups of models (Munro, 1974; Shugart, 1984; Vanclay, 1994; Liu and Ashton, 1995; Pretzsch, 1999). Fig. 9 presents the overall classification based on the criteria described above. The few levels and categories should make it more clear and general, but we must point out that its construction was still influenced by our own point of view and that slightly different classifications could be presented that would also be suitable.

#### 2.2.1. The group of stand models

In 'distance-dependent stand models', the stand is described as a mosaic of forest patches. Each patch is characterised by its location in the stand and has its own dynamics, which is interacting with the dynamics of the neighbour patches. On the contrary, 'distance-independent stand models' consider the forest as one unit, without any within-spatial organisation. In 'distance-independent stand models', we can distinguish between models that do and those that do not describe the heterogeneity of the stand: the stand can be described either as the sum of $N$ average (identical) trees (no heterogeneity) or is divided into size-classes ($i$), each class consisting of $N_i$ average trees. This third criterion resulted in two groups of models, being 'average tree models' and 'distribution models'. 'Average tree models' describe the stand using stand level variables such as the num-

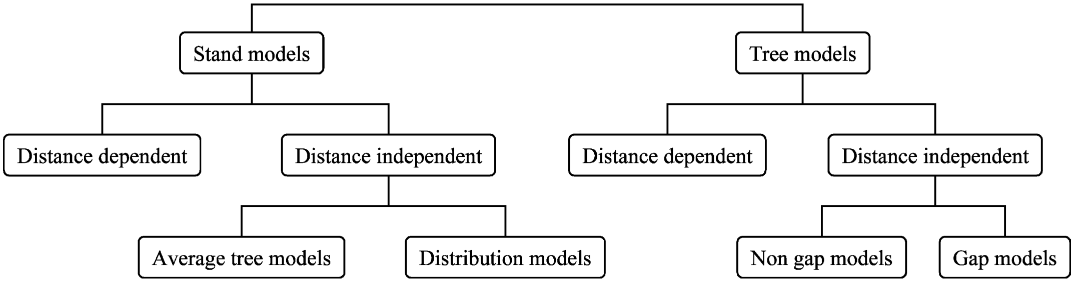

Fig. 9. A new classification of forest growth models (this study).

ber of stems, average tree dimensions height), stand dimensions (volume, basal area, etc.). For mixed forest modelling, the only modification lies in providing output values per species. In the previous classifications, this group was often encountered, although under different and sometimes misleading names like 'global or average tree models' (Pretzsch, 1999), 'global yield models' (Houllier, 1995), 'forest models' (Shugart, 1984), or 'whole stand models' (Vanclay, 1994). 'distribution models' also model the average and total dimensions of the stand per tree species, but they differ from the previous group by partly integrating the natural variability among the trees in a stand. Each modelled characteristic of the stand is then described by a distribution function, either continuous or discrete (dimension classes) hence implicitly defining different size classes. These models were also called 'demographic models' by Houllier (1995) and Franc et al. (2000) or 'size-class models' by Vanclay (1994). Shugart (1984) made no distinction between individual tree models and distribution tree models, which were both part of his 'tree models' group. Not one sub-division seems to prevail (Vanclay, 1994; Houllier, 1995; Pretzsch, 1999). Moreover, there is a recurrent and confusing classification of matrix models and Markov chain models (both presently indicated as distribution models) in the literature. Several researchers (Buongiorno and Michie, 1980; Solomon et al., 1986; Buongiorno et al., 1995; Ingram and Buongiorno, 1996; Lin and Buongiorno, 1997; Favrichon, 1998; Kolbe et al., 1999) use the word matrix model to indicate those models that basically describe the distribution of all trees of a stand over different (diameter-) classes and the fractions of tree numbers per class that will grow up to the next class within one time step. These fractions, often referred to as probabilities, are summarised in a matrix. Matrix models are deterministic models because repeated experiments (i.e. model runs) will result in identical outcomes. Markov chain models, on the other hand, are generally presented as stochastic models (Waggoner and Stephens, 1970; Usher, 1979; Binkley, 1980). The change from one state of the forest to another during a given time is not modelled using a constant fraction, but is a probability (with the fraction as expected outcome). This method permits including variability in the prediction meaning that when coming from a state $j$, the estimated growth can differ from the expected growth. Nevertheless, Markov models used in forest dynamics modelling use fractions rather than probabilities (Bruner and Moser, 1973; Miles et al., 1985; Hinssen, 1994; Acevedo et al., 1996). The confusion becomes only larger when one realises that several other names are found in the literature, like the population model (Batista et al., 1998), demographic model (Houllier, 1995; Franc et al., 2000), transition model (Miles et al., 1985; Nakashizuka, 1991; Kolstrom, 1993; de Azevedo et al., 1994; Acevedo et al., 1996; Sanquetta et al., 1996), Usher matrix (Buongiorno and Michie, 1980; Favrichon, 1998), Lefkovitch (Buongiorno and Michie, 1980; Geldenhuys et al., 1997) or Leslie matrix (Buongiorno and Michie, 1980). The overall conclusion is that these models all basically rely on the same principle, being a list of fractions or probabilities indicating the rate of change of the distribution of the individuals over the size classes. We hence decided to use the term 'distribution models' in our classification scheme to cover all the previous model names, and (in accordance with our classification criteria) not to create any sub-groups within the class of distribution models.

### 2.2.2. The group of tree models

Characteristic for 'tree models' is that these models describe and keep track of each individual tree in the stand. This group of models has also been referred to as 'individual models' (Liu and Ashton, 1995; Franc et al., 2000) or 'single-tree models' (Vanclay, 1994); Shugart (1984), however, did not distinguish this category at all. The spatial location of trees constitutes the second discriminating criterion in our classification, separating 'distance-dependent tree models' where the tree location is known from 'distance-independent tree models' where the tree location is unspecified.

An additional discussion point here is where to put the 'gap models'. Except for Houllier (1995) who considered gap models as a separate category, all authors consider gap models to belong to the category of the 'tree models'. The classification of gap models sometimes raises problems because of their intermediate position: gap models deal with individual trees which do not have specific spatial coordinates, but in the mean time most gap models also describe the forest as a mosaic of these gaps. As a consequence, gap models are either considered as 'distance-independent tree models' (Franc et al., 2000) or as a distinct group additional to the 'distance-dependent' or 'distance-independent' tree models (Shugart, 1984; Liu and Ashton, 1995). Considering that in 'tree models', the unit of interest is the tree, not the cell or the stand, we considered gap models to be part of the 'distance-independent tree models'.

Appendix A presents all models found in the literature with the methods described in Section 1.3. The complete list of references on models and model applications can be found in the literature list.

### 2.3. Terminology

Apart from the discussion around distribution models, there are a few other situations where confusing terminology arises from the papers reviewed. Bossel and Krieger (1991), e.g. distinguished 'descriptive' from 'explanatory' forest dynamics models. The first one refers to empirical models, containing relationships statistically fitted on data. The second group aims at explaining growth using the biological, physical and chemicals processes involved (Mohren and Burkhart, 1994). Multiple expressions have been used to indicate the 'explanatory' character of models: mechanistic models (Mohren and Burkhart, 1994; Pacala et al., 1996; Chave, 1999), process-based models (Bartelink, 2000a,b; Franc et al., 2000) or biologically based process models (Mohren and Burkhart, 1994). In the following text, we will use the words 'empirical' and 'mechanistic' to qualify models mostly based on a descriptive and an explanatory approach, respectively.

Also expressions related to regeneration arose discussion, either by referring to different phenomena using the same terminology, or by using different expressions to name the same event. The definitions between inverted commas are issued from Helms (1998). Regeneration is defined as 'the established progeny from a parent' or 'the seedlings or saplings existing in a stand'. Its synonym 'recruitment' was mostly used in the literature reviewed on distribution models (Vanclay, 1989; Nakashizuka, 1991; Kohyama, 1993; Alder, 1997; Osho, 1997) and distance-dependent tree models (Busing, 1991; Pacala et al., 1996; Moravie et al., 1997; Liu and Ashton, 1998; Chave, 1999). Establishment is the result of the regeneration process, i.e. the 'initiated tree cover'. The expression was only sometimes used alone (Williams, 1996) or jointly to the word recruitment (Shugart and West, 1977; Chave, 1999) or regeneration itself (Leemans and Prentice, 1987; van Daalen and Shugart, 1989; Mohren et al., 1991; Shao et al., 1994). Ingrowth corresponds to the amount of trees (in number, volume or basal area) 'that were smaller than a minimum diameter or height limit at the beginning of any growth period and that, during this period, attained the prescribed size'. However, ingrowth was often restricted to refer to regeneration, but only in matrix-based distribution models (Ek, 1974; Hann, 1980; Solomon et al., 1986; Buongiorno et al., 1995; Ingram and Buongiorno, 1996; Favrichon, 1998). Consequently, 'recruitment' appeared more adequate to refer to the process of installation of new seedlings and it will hence be used from now on.

## 3. Description of the forest growth model types

### 3.1. Distance-dependent stand models

Distance-dependent stand models present the forest as a distance-dependent mosaic of sub-forests. Theoretically, the dynamics of each sub-forest are then described using an average tree model or a distribution model, the respective location of the patches permitting to include interactions between adjacent cells (Franc et al., 2000). There are only few models of this type applied to mixed forest growth modelling: all used a distribution model to represent the dynamics of the cells. In the most common approach (Wissel, 1992; Croc, 1994; Franc et al., 1995; Riéra et al., 1998), each sub-forest is defined by a discrete state (species composition, tree age, stage in the forest succession, etc.): the transition from one state to the other is estimated using probabilities depending on the state of the neighbouring cells. However, the growth of the trees inside the cell is not modelled explicitly. Another approach consists of modelling the diameter distribution inside each cell (Bossel and Krieger, 1991, 1994; Frelich et al., 1993). The model FORMIX 2 (Bossel and Krieger, 1991, 1994) represents the vertical and horizontal structure of the stand: in each cell, growth is modelled using transition probabilities from one canopy class to the other. Mortality and recruitment are affected by the dynamics of the adjacent cells: tree fall in a cell results in damages and higher mortality rates in other plots, recruitment in a cell depends on seed production inside the plot and outside the plot depending on the maximum dispersal distances.

### *3.2. Distance-independent stand models: average tree models*

Most of the papers presenting average tree models designed for mixed or uneven-aged stands were yield tables (Mulloy, 1947; Wiedemann, 1949; MacLeod and Blyth, 1955; Magin, 1957; Matsui and Baba, 1959; Nilsson, 1961; Jonsson, 1962; Andonov, 1967; Kozlovskij and Pavlov, 1967; Cuprov, 1970; Armasescu, 1972; Johnstone, 1977; Beky, 1978; Krastanov, 1979a,b; Bernetti, 1980; Baginskii and Terekhova, 1982; Singh and Sharma, 1982; Prudov, 1984; Payandeh and Field, 1986). Stand basal area and volume were always modelled, sometimes together with the other stand level characteristics such as number of trees, average diameter or height increments (Lynch and Moser, 1986; Payandeh and Wang, 1996). Only few models investigate the other features such as species composition (Jogiste, 1998) or recruitment and mortality (Turner, 1966; Moser and Hall, 1969; Lynch and Moser, 1986; Jogiste, 1998).

To initialise model runs and evaluate model performance, all published models require large data sets of successive measurements carried out on permanent plots or chronosequences. Among these approaches, we can distinguish the size-density diagrams from the other growth and yield functions. These consisted of graphical models based on the theory that stand yield or average size was controlled by the stand density (Newton, 1997). The approach was extended recently to mixtures by Puettmann et al. (1992) and Smith (1996): the simple linear relationship between yield and stand density was modified and made dependent on the species proportions. Most of the average tree models, however, consist of a system of differential equations, permitting to estimate the increment in tree number or basal area as a function of the time elapsed from a reference time $t_0$, and depending on the initial characteristics of the stand at $t_0$ (Moser and Hall, 1969; Moser, 1972; Ung et al., 1982; Lynch and Moser, 1986). The concept of relative time instead of age was an important step, which permitted to adapt average tree models from pure even-aged, stands to uneven-aged and/or mixed (Moser and Hall, 1969). Still, ‘age’ was sometimes conserved as an independent variable by using the age of the mean tree of the stand (Jogiste, 1998).

Stand heterogeneity is seldom represented in average tree models, and when it is it only concerns the species composition. The simplest models were not even providing outputs per species: the mixture was considered only in the data used for fitting which were collected in mixed stands (Moser and Hall, 1969; Moser, 1972). Sometimes, the mixture dynamics were estimated as the sum of the independent dynamics of each species (Ung et al., 1982; Payandeh and Wang, 1996). Only a few models described the forest with the interacting species: e.g. the basal area increment, tree mortality and recruitment of each species was linked to the basal area and number of trees of the other species (Lynch and Moser, 1986). Similarly, Jogiste (1998) and Puettmann et al. (1992) introduced the effect of species proportion on the basal area increment per species.

### *3.3. Distance-independent stand models: distribution models*

Unlike average tree models, this category of distance-independent stand models is characterised by the inclusion of stand heterogeneity in the simulation approach, providing not only average dimensions of the stand but also information on tree dimensions. Apart from yield tables, most of the distance-independent models are distribution models. Most of them were published in the 1980s and 1990s.

All distribution models appeared to be empirical models, quite similar in their outputs and using the same independent variables (stand or class BA or DBH, and tree number or density). Most of the models estimate ingrowth (or recruitment or seedling establishment), mortality, radial growth and the changes in diameter distribution, except for Bruner and Moser (1973) who were dealing with adult trees only, excluding the processes of recruitment. Models generally provide outputs per species or groups of species. Grouping is used when the diversity in species is too large, like in tropical forests (Vanclay, 1989; Alder, 1995; Favrichon, 1998) or in some complex temperate mixtures (Solomon et al., 1986; Kohyama, 1992b). Sometimes no distinction was made between species (Bruner and Moser, 1973; Ek, 1974; Buongiorno and Michie, 1980; Hyink and Moser, 1983; Lin and Buongiorno, 1997): as some average tree models, the distribution model has been applied to mixtures, but it has been frequently used in pure stands as well.

In distribution models, the changes in each process are calculated over discrete time periods. The time steps are often equal to the time (1–9 years) elapsed between two of the field measurements used for fitting (Bruner and Moser, 1973; Ek, 1974; Buongiorno and Michie, 1980; Vanclay, 1989; Hinssen, 1994; Alder, 1995; Lin et al., 1996), to the thinning period (Solomon et al., 1986; Buongiorno et al., 1995; Favrichon, 1998) or to the rotation period (Miles et al., 1985). A high diversity appeared in the approaches used to model the forest dynamics, which can be separated into a discrete matrix approach (Bruner and Moser, 1973; Buongiorno and Michie, 1980; Hann, 1980; Miles et al., 1985; Solomon et al., 1986; Walker et al., 1986; Bowling et al., 1989; Nakashizuka, 1991; Ojo, 1991; Osho, 1991, 1996; Kolstrom, 1993; de Azevedo et al., 1994; Hinssen, 1994; Buongiorno et al., 1995, 1996; Nakashizuka and Kohyama, 1995; Favrichon, 1996, 1998; Ingram and Buongiorno, 1996; Lin et al., 1996, 1998; Sanquetta et al., 1996; Volin and Buongiorno, 1996; Favrichon and Damio, 1997; Geldenhuys et al., 1997; Virgilietti and Buongiorno, 1997; Batista et al., 1998; Schulte and Buongiorno, 1998; Virgilietti, 1998; Yu and Zhou, 1998; Kolbe et al., 1999) and a continuous regression approach (Ek, 1974; Hyink and Moser, 1983; Lynch and Moser, 1986; Vanclay, 1989; Kohyama, 1992b; Alder, 1995, 1997; Osho, 1997; Kohler and Huth, 1998; Alder and Silva, 2000).

### 3.3.1. Recruitment

Regeneration is the result of seed production, germination and seedling establishment. The first process is likely to be favoured by the presence of mature trees, the last features by the occurrence of gaps in the stand, resulting from natural death or silvicultural clearings. This implies a positive relationship between recruitment and tree number, but a negative relationship between recruitment and stand DBH or BA (Moser, 1972; Ek, 1974).

All models treat recruitment at the stand level, i.e. as the number of small trees which appear during one time step per area unit. Recruitment has been modelled using either a constant value per hectare (Nakashizuka, 1991; Kolstrom, 1993; Hinssen, 1994) or a positive relationship with tree number and/or a negative relationship with the stand basal area or the stand density (Ek, 1974; Buongiorno and Michie, 1980; Lynch and Moser, 1986; Solomon et al., 1986; Kolbe et al., 1999). The regressions used differed depending on the available data: most relationships were assumed to be linear (Buongiorno and Michie, 1980; Solomon et al., 1987; Vanclay, 1989; Alder, 1995; Buongiorno et al., 1995; Solomon et al., 1995; Ingram and Buongiorno, 1996; Favrichon, 1998), some were described as exponential regressions (Ek, 1974; Kohyama, 1993; Alder, 1997; Favrichon, 1998). The diameter of the ingrowth tree was always determined empirically, being set equal to the observed average DBH of new trees, per species (e.g. Alder, 1995) or for all species (e.g. Vanclay, 1989).

### 3.3.2. Growth and mortality

Matrix models represent the stand as a discrete distribution of the trees in $N$ classes (Bruner and Moser, 1973; Buongiorno and Michie, 1980; Miles et al., 1985; Buongiorno et al., 1995; Lin et al., 1996; Favrichon, 1998). The number of trees at the next time step $(t+k)$ is calculated as follows:

$$Y_i(t+k) = G(t) \times (Y_i(t) - H(t)) + J \tag{1}$$

where $Y_i(t)$ is the number of trees in class $i$ at the previous time step $t$, $J$ is the vector describing ingrowth, $H$ the vector describing harvesting and $G$ the growth matrix. $G$ contains the transition probabilities that a tree from class $i$ dies ($m_i$), grows into another class $j$ ($a_{ij}$) or remains in the same class ($b_i$). Transition probabilities are derived from field data. The simplest models use constant values corresponding to the average observed percentage of trees which have died (or were cut), stayed within the same size-class, or jumped to the next one. This is the case with all Markov chain models (Bruner and Moser, 1973; Binkley, 1980; Miles et al., 1985; Hinssen, 1994; Acevedo et al., 1996) and some of the matrix models (Buongiorno and Michie, 1980; Miles et al., 1985; Nakashizuka, 1991; Lin and Buongiorno, 1997). Most of the time, the probabilities were calculated per diameter class and per species, using regression on the stand BA and the mean class diameter or class BA (Solomon et al., 1986; Buongiorno et al., 1995; Favrichon, 1998). A site index, such as average or dominant tree height combined with age (Kolstrom, 1993; Kolbe et al., 1999) was sometimes introduced to extend the applicability of the model to other environmental conditions.

A few models, here referred to as continuous distribution models, predict radial growth using either regressions fitted on data or classical distributions functions. As for transition probabilities, the regressions were functions of stand BA and tree diameter or tree BA (Ek, 1974; Vanclay, 1989; Alder, 1995). The main difference with discrete matrix models consists of modelling directly the tree increment instead of a probability of moving up from one diameter class to another. However, all trees in a class will have the same annual increment if their individual diameter is represented by the average class diameter (Alder, 1995); but if a uniform distribution of the trees inside the class is assumed, each tree has its own diameter increment (Fulton, 1991). The second type of continuous distribution models assumed that the stand distribution was corresponding either to a Weibull or another two-parameter classic distribution function. The parameters were then derived from stand level variables such as stand ingrowth, density and BA or BA per species (Hyink and Moser, 1983; Lynch and Moser, 1986).

Similarly, tree mortality has been modelled in matrix models using probabilities of dying, differing among diameter classes, which were either constant values (Nakashizuka, 1991; Favrichon, 1998) or functions of stand BA and diameter class (Solomon et al., 1986; Buongiorno et al., 1995). Continuous distribution models use regression on stand BA and tree diameter (Vanclay, 1989; Kohyama, 1993) or constant values per tree categories based on species, canopy class, logging history, etc. (Alder, 1995).

## 3.4. Distance-dependent tree models

Especially since computers started to invade forest research institutes, the development of distance-dependent tree models expanded quickly. Compared with the other types of tree models, this last category of models keep track not only of each individual tree characteristics (growth, mortality) but also of the exact location of a tree in a certain area (e.g. one hectare). Apart from these common features, the distance-dependent tree models are characterised by their diversity in the modelling approaches (empirical, mechanistic), the levels of spatial description (patch, tree) and the purposes (production and management, dynamics). Most of the models include the processes of growth, mortality and recruitment (Ek and Monserud, 1974a,b; Busing, 1991; Pacala et al., 1993, 1996; Williams, 1996; Kellomäki and Väisänen, 1997; Moravie et al., 1997; Liu and Ashton, 1998; Chave, 1999) but recruitment is not always represented (Pretzsch, 1992; Pretzsch and Kahn, 1996b; Kahn and Pretzsch, 1997; Bartelink, 1998, 2000a; Vettenranta, 1999). Sometimes, tree growth is the only process modelled (Pukkala et al., 1994, 1998; Courbaud et al., 1997). Most of the models are empirically based using regressions to represent tree growth (Ek and Monserud, 1974b; Busing, 1991; Pacala et al., 1993; Pretzsch and Kahn, 1996b; Courbaud et al., 1997; Kahn and Pretzsch, 1997; Moravie et al., 1997; Liu and Ashton, 1998; Pukkala et al., 1998; Vettenranta, 1999) and a few use a mechanistic approach of growth modelling based on the description of the processes of primary and secondary production (Williams, 1996; Kellomäki and Väisänen, 1997; Chave, 1999; Bartelink, 2000a). All phenomena are described using a discrete time step varying from 1 to 5 years. Williams (1996), in his model, partitioned a year into three 'seasons' to estimate the net primary production more accurately.

Parameterisation in the models was mostly carried out per species, except for highly diverse tropical forests where species were gathered into functional groups based on light requirements and growth rates (Chave, 1999) or structural groups according to canopy position (Moravie et al., 1997; Liu and Ashton, 1998).

### 3.4.1. Recruitment

In a distance-dependent tree model, recruitment must be modelled not only by the number and dimensions of the seedlings but also by their location. In the first models a rather elementary approach was chosen, not modelling seed production and dispersal per se, whereas more recent models tend to be more mechanistic. Moravie et al. (1997) assumed that the total tree number was in equilibrium and that recruitment was equal to mortality. The location of the seedlings was then selected at random among the open areas of the stand. The approach used in most of the models corresponds to the recruitment model presented in many gap models with the difference that recruitment is estimated at the level of the tree (Ek and Monserud, 1974a; Busing, 1991; Pacala et al., 1993; Williams, 1996; Liu and Ashton, 1998; Chave, 1999). Each tree per species can produce a potential number of seeds (random or function of tree dimension), which will germinate in case of proper environmental conditions (light, temperature, etc.). Seedling position results from the estimation of seed dispersal: seedling density decreases with increasing distance from the parent tree. In all these models, seed dispersal always requires the presence of adult trees nearby. FORMOSAIC (Liu and Ashton, 1998) developed an original multi-scale approach: the target forest is integrated in a landscape of forested and non-forested areas. Recruitment in a cell results not only from the presence of adult trees inside the forest, but also from long distance seed dispersal from adult trees located in the surroundings of the modelled forest. As a consequence, the characteristics of the surrounding areas can influence the number and species of the recruits.

### 3.4.2. Mortality

Tree death was estimated at the tree level using probabilities. Most models include a maximum age limit per species to avoid maintaining impossibly old trees (Busing, 1991; Pretzsch, 1992; Pacala et al., 1993; Liu and Ashton, 1998). Mortality was then either increased by using competition indexes depending on tree density or resource availability (Kahn and Pretzsch, 1997; Liu and Ashton, 1998; Vettenranta, 1999), or submitted to internal limitations such as an insufficient growth rate (Ek and Monserud, 1974b; Busing, 1991; Pacala et al., 1993; Moravie et al., 1997; Bartelink, 1998) or assimilation rate (Williams, 1996; Chave, 1999). Indirect mortality resulting from tree fall was sometimes included in the models. When dying, the falling tree can kill or damage the neighbour trees: this was represented by an increment in the mortality probabilities of the neighbour trees, according to their height, the dimensions of the fallen tree and the distance between the two (Williams, 1996; Liu and Ashton, 1998; Chave, 1999).

### 3.4.3. Growth

The models may require a lot of computation time, especially when detailed physiological processes are simulated, but distance dependency allows the simulation of inter-tree competition and, in principle, a detailed prediction of stand structure, growth and yield and biodiversity. Models focused on estimating DBH increment and other characteristics are estimated from empirical relationships: tree height, for instance, is generally estimated using relationships to DBH and/or age (Busing, 1991; Pacala et al., 1993; Williams, 1996; Pukkala et al., 1998; Chave, 1999; Bartelink, 2000a). Exceptions are SILVA 2 which focus on height increment (Pretzsch, 1992) and the model developed by Moravie et al. (1997) where crown radius increment is represented first and DBH and *H* increments derived from the crown characteristics later. Competition for light is included in all models and most of them represent crowding effects (Ek and Monserud, 1974a; Busing, 1991; Pretzsch, 1992; Kahn and Pretzsch, 1997; Moravie et al., 1997; Liu and Ashton, 1998; Pukkala et al., 1998; Vettenranta, 1999) but FORMOSAIC (Liu and Ashton, 1998) and SILVA 2 (Pretzsch, 1992; Kahn and Pretzsch, 1997) are the only models that consider the competition for other resources (water, nutrients).

The way growth and competition are represented depend on the choice of an empirical or mechanistic approach. Empirical models used either multivariate regressions with characteristics of the target tree and neighbour trees (actual or maximum DBH and height, sometimes tree age) as explanatory variables (Busing, 1991; Pacala et al., 1993; Courbaud et al., 1997; Liu and Ashton, 1998; Pukkala et al., 1998; Vettenranta, 1999) or potential growth rates with reduction factors (Ek and Monserud, 1974b; Pretzsch, 1992; Kahn and Pretzsch, 1997; Moravie et al., 1997). Reduction factors correspond to limitations of growth as a result of limited resources. Light was considered as a limiting factor in all the models but the other ecological factors such as water availability (Pretzsch, 1992; Liu and Ashton, 1998) or nutrition, temperature and $CO_2$ concentration (Pretzsch, 1992) were hardly ever considered.

Tree location is used to calculate distance-dependent competition indexes. They allow a description of competition between each target tree and its neighbouring trees. Trees located inside a limited area around the target tree are used to estimate a competition index for light (Busing, 1991; Pretzsch, 1992; Pacala et al., 1993; Courbaud et al., 1997; Kahn and Pretzsch, 1997; Moravie et al., 1997; Pukkala et al., 1998; Vettenranta, 1999) or for space (Ek and Monserud, 1974a; Pukkala et al., 1994, 1998; Moravie et al., 1997; Liu and Ashton, 1998; Vettenranta, 1999). Light competition indexes are based either on the characteristics of the target tree (crown radius or shape; Pretzsch, 1992; Pacala et al., 1993; Courbaud et al., 1997; Moravie et al., 1997) to evaluate the capacity of a tree to make use of the intercepted light or on the characteristics of the competitors that can shade the tree (leaf area cover or height of the neighbour trees (Ek and Monserud, 1974a,b; Busing, 1991; Pretzsch, 1992; Pretzsch and Kahn, 1996b; Pukkala et al., 1998; Vettenranta, 1999). As in stand level models and distance-independent models, distance-independent competition indexes are also used in the distance-dependent models: stand BA for instance is used to represent a crowding competition (Pukkala et al., 1998; Vettenranta, 1999).

Mechanistic models introduced a more functional representation of growth and competition. Light competition is the driving force behind individual tree growth in COMMIX (Bartelink, 2000a), ARCADIA (Chave, 1999) and TROLL (Williams, 1996). A 3D representation of the stand including a distribution of leaf area density in space is required to estimate light attenuation using a Lambert–Beer attenuation function. Absorbed light is then converted to net primary production and growth in slightly different ways. COMMIX is based on a concept of radiation use efficiency: intercepted light is directly translated into a dry matter production that is allocated to biomass components and used to estimate the diameter increment. TROLL represents the processes of assimilation and respiration as a function of intercepted light and links the DBH increment to the annual net assimilation rate. ARCADIA integrates more steps and mechanisms: light interception, assimilation rate sensitive to water availability and temperature requirements, growth and maintenance respiration rates per tree compartment, allocation biomass increment per compartment, DBH and *H* increments. FINNFOR (Kellomäki and Väisänen, 1997) is certainly the most complete mechanistic model, integrating very detailed and interacting sub-models of local weather (precipitation, temperature, radiation, clouds, etc.), soil behaviour (moisture, temperature, litter decomposition, nutrient mineralisation) and tree growth and dynamics. Tree growth is described mechanistically including the processes of photosynthesis, stomatal aperture, respiration rates, and allocation, for instance.

### 3.5. Distance-independent tree models: non-gap models

In forest modelling, there are a lot of distance-independent tree models designed for mixed forests, most of them being gap models (see below). Some, however, do not belong to this category (Wykoff et al., 1982; Siekierski, 1991; Poker, 1993; McTague and Stansfield, 1995; Carpentier, 1996; Keane et al., 1996a). This group of what is called here as non-gap models consist of empirical approaches except for FIRE-BGC (Keane et al., 1996a,b) which is derived from the process-based model FOREST-BGC (Running and Gower, 1991; Running and Coughlan, 1998).

#### 3.5.1. Growth

Individual tree growth is modelled empirically as a function of tree and crown dimensions (Carpentier, 1996; Monserud et al., 1997), jointly with time (Siekierski, 1991; McTague and Stansfield, 1995). FIRE-BGC is the only mechanistic distance-independent tree model we found (Keane et al., 1996a,b): this model includes a mechanistic representation of the carbon, water and nitrogen balances. Carbon is fixed by the whole canopy by photosynthesis depending on light, water and nutrient availability. Allocation and growth are more empirical but still based on mechanistic hypothesis: allocation to trees relies on the species potential growth, the tree leaf area and the proportion of light availability at the tree level. Then DBH increment is modelled using an allometric relationship with the stem biomass increment and the previous year stem volume. Its worthwhile noticing that among mixed forest models, FIRE-BGC is the first non-gap model that simulates competition for resources. In most non-gap models, stand structure variables such as BA and crown index of larger trees (Monserud et al., 1997; Sterba and Monserud, 1998) or simply stand BA (Carpentier, 1996) are used to build descriptive rather than explanatory relationships (Keane et al., 1996a).

#### 3.5.2. Recruitment

Recruitment is generally modelled at the stand level. The number of recruits per species is represented as a function of stand variables like BA, density, species proportion (McTague and Stansfield, 1995; Carpentier, 1996; Monserud et al., 1997) and site characteristics such as soil depth, elevation (Keane et al., 1996a; Monserud et al., 1997). Seed dispersal was included by Keane et al. (1996a) at the landscape level to model the specific effects of fire occurrence on regeneration. Mortality is described at the tree level as a probability depending on tree DBH or DBH increment (Siekierski, 1991; McTague and Stansfield, 1995); mortality probability generally increases with increasing competition, represented by stand density or competitors BA (Wykoff et al., 1982; Monserud et al., 1997) or with increasing fire and pathogen occurrence, as, e.g. in FIRE-BGC (Keane et al., 1996a).

### 3.6. Distance-independent tree models: gap models

In gap models, the forest is simulated as a group of patches or gaps, each being characterised by a list of individual trees (Botkin et al., 1972; Shugart, 1984). In the model, the gap size has to be chosen so that the environmental conditions inside the gap can be considered horizontally homogeneous. It often matches the crown size of a dominant tree (Shugart, 1984). Inside each patch, forest dynamics are modelled with a description of recruitment, growth and mortality at the individual tree level. In most gap models, the location of the gaps is not made spatially explicit: as a consequence, gaps behave independently from one another. However, a few exceptions exist. Probably the first gap model with spatial location of the patches within the stand is ZELIG (Smith and Urban, 1988; Urban et al., 1991), which accounts for the shading between trees from neighbouring patches.

The first gap model, JABOWA, was developed by Botkin et al. (1972) to simulate the dynamics of a mixed broadleaved forest. In FORET (Shugart and West, 1977), a major modification consisted of describing the vertical distribution of foliage from treetop to crown base instead of accumulating it at the top of the tree. Until today, the JABOWA and FORET models still form the conceptual basis for new gap models (Shugart and West, 1977; Shugart et al., 1980; Waldrop et al., 1986; Leemans and Prentice, 1987; van Daalen and Shugart, 1989; Kienast and Krauchi, 1991; Mohren et al., 1991; Desanker and Prentice, 1994; Shao et al., 1994; Bugmann, 1996; Jorritsma et al., 1999; Miller and Urban, 1999a). The main differences among gap models are the functions, routines and/or parameters that have to be adapted to specific forests, climates or purposes. Recruitment and mortality are mostly modelled as stochastic processes, over an annual time step. On the contrary, more variation exists regarding the simulation of tree growth: many models use deterministic empirical functions depending on tree dimensions, describing diameter or biomass increment. Some models based tree growth on photosynthesis (e.g. Prentice and Leemans, 1990; Kellomäki et al., 1992, Lindner et al., 2000) or even used a complete carbon-balance (e.g. Post and Pastor, 1996; Jorritsma et al., 1999). In all gap models light availability plays a key role in the regeneration and tree growth processes.

### *3.6.1. Recruitment*

Recruitment in gap models is modelled as a stochastic process, triggered by light availability and (occasionally) other environmental conditions. The regeneration routine determines the species that will reproduce in a gap, the number of new individuals that will appear and their initial dimensions. In almost all gap models, these new individuals are saplings rather than seedlings: seedling establishment is difficult to simulate because the light modelling approach used in gap models underestimates light levels at the forest floor. Generally, all species are supposed to dispose of an infinite seed source on the patch. Whether a species will establish in the plot depends on the environmental conditions as well as on the species' ecological requirements, such as a minimum light intensity at the ground level, a sum of degree-days compatible with their growth requirements and satisfactory soil moisture conditions (Botkin et al., 1972; Shugart and West, 1977; Shugart et al., 1980; Waldrop et al., 1986; Leemans and Prentice, 1987; van Daalen and Shugart, 1989; Prentice and Leemans, 1990; Kienast and Krauchi, 1991; Desanker and Prentice, 1994; Shao, 1996; Kolstrom, 1998). Sometimes additional criteria are added such as the presence or absence of grazers or rodents (Shugart and West, 1977), the requirement for mineral soil or litter (Shugart and West, 1977; Waldrop et al., 1986), for bird presence or wind occurrence to insure dispersal (Shugart et al., 1980; van Daalen and Shugart, 1989). The number of juveniles produced by each eligible species is determined randomly, within a given range (Botkin et al., 1972; Shugart and West, 1977; Shugart et al., 1980; Waldrop et al., 1986; Leemans and Prentice, 1987; van Daalen and Shugart, 1989; Desanker and Prentice, 1994). An alternative way of modelling sapling number consists of setting the number of juveniles to a maximum per species; this number then will decrease due to undesirable environmental conditions such as low light availability, low temperature and low soil moisture, using the so-called limiting functions (Mohren et al., 1991; Jorritsma et al., 1999; Miller and Urban, 1999a) or choosing a random survival rate (Shao et al., 1994). FORCAT is the only gap model found that presents a more mechanistic recruitment model: the availability of seed in a gap depends on seed production inside the gap and seed dispersal originating from outside the gap, using a probability bound to the (previous) presence of an adult tree on the patch, and a probability of seeds entering the gap, which is negatively dependent on seed weight (Waldrop et al., 1986). The size of the saplings is sometimes uniform, e.g. the FORECE (Kienast and Kuhn, 1989a; Kienast and Krauchi, 1991) and FORCLIM models (Bugmann, 1996) where saplings of the same species enter the gap with exactly the same DBH, constituting a cohort. In other gap models DBH's (and/or sapling heights) are picked randomly out of a pre-defined range (Botkin et al., 1972; Shugart and West, 1977; van Daalen and Shugart, 1989; Prentice and Leemans, 1990; Desanker and Prentice, 1994).

According to the forest and the species, sprouting sometimes is considered an alternative regeneration strategy (Shugart and West, 1977; Waldrop et al., 1986; Kienast and Kuhn, 1989a; Kolstrom, 1998). The eligible species, the number and dimensions of the sprouts are then estimated in a similar way as for sapling recruitment.

### *3.6.2. Growth*

Growth in most gap models is modelled using deterministic formulas. Again, not many gap models use equations that are really different from the approach proposed in JABOWA (Botkin et al., 1972). In most of these approaches it is assumed that the maximum annual volume increment is proportional to the tree leaf area (LA), diminished by a term depending on the relative tree size (tree size/maximum tree size), see, e.g. Eq. (2):

$$\frac{\mathrm{d}(\mathrm{DBH}^2 \cdot H)_{\max}}{\mathrm{d}t} = R \cdot \mathrm{LA} \cdot \left(1 - \frac{\mathrm{DBH} \cdot H}{\mathrm{DBH}_{\max} H_{\max}}\right) \quad (2)$$

with DBH and $H$ the diameter at breast height and the height of the tree, respectively, $\mathrm{DBH}_{\max}$ and $H_{\max}$ their species-specific maximum values, LA the leaf area and $R$ corresponding to a growth rate parameter. LA and $H$ can be expressed using allometric relationships on DBH: Eq. (2) then reflects the maximum diameter increment as a function of tree DBH, maximum DBH, maximum height and the growth rate parameter. The actual DBH increment is obtained by applying reducing factors on maximum growth. These factors represent the limitations resulting from competition for resources and from environmental conditions. For a tree in a patch, the shading from trees higher results in a reduction of photosynthesis or growth rate of the target tree. Photosynthesis being sensitive to temperature, a decrease is assumed when the sum of degree-days of the growing season deviates from the optimal temperature conditions. The third common reduction factor is based on the ratio between the stand biomass and the maximum stand biomass, to reflect crowding and root competition for nutrient and water. In some gap models, these relationships remained basically unchanged apart from the determination of new parameter values (Botkin et al., 1972; Shugart and West, 1977; Shugart et al., 1980; van Daalen and Shugart, 1989). Most of the models, however, chose the extended approach described in the model LINKAGES (Post and Pastor, 1996) where an index related to water stress is added to better account for soil water availability (Kercher and Axelrod, 1984a; Waldrop et al., 1986; Kienast and Krauchi, 1991; Mohren et al., 1991; Desanker and Prentice, 1994; Shao et al., 1994; Bugmann, 1996; Kolstrom, 1998; Miller and Urban, 1999a).

A few models differ from the consensual approach, by estimating growth mechanistically (Prentice and Leemans, 1990; Kellomäki et al., 1992; Post and Pastor, 1996; Jorritsma et al., 1999, Lindner, 2000; Lindner et al., 2000). For example, Prentice and Leemans (1990) estimate the net assimilation at any level in the canopy as a function of available light, and determine the annual volume increment as its integral over the crown, reduced by a factor representing crowding on the patch (total biomass/total maximum biomass). FORGRA (Jorritsma et al., 1999) estimates biomass increment of a single tree knowing the amount of absorbed light and the radiation use efficiency concept (Monteith, 1977), including the effects of water and nutrient limitations. Biomass is allocated to the tree biomass components and tree diameter increment is derived from stem biomass increment and (imposed) tree height increment. Both approaches do not impose an imperative maximum to tree DBH, but present an asymptotic limit (Leemans and Prentice, 1987).

### *3.6.3. Mortality*

Tree mortality is modelled as a probability. An intrinsic probability of dying is based on the assumption that only a small percentage (1–2%) of the seedlings will reach the maximum tree age. A conditional mortality cause is added: when the tree annual increment is too low, the probability of dying increases, reflecting the low probability of survival of non-vigorous trees (Botkin et al., 1972; Shugart and West, 1977; Shugart et al., 1980; Waldrop et al., 1986; Leemans and Prentice, 1987; Smith and Urban, 1988; van Daalen and Shugart, 1989; Kienast and Krauchi, 1991; Mohren et al., 1991; Shao et al., 1994; Kolstrom, 1998; Jorritsma et al., 1999; Miller and Urban,

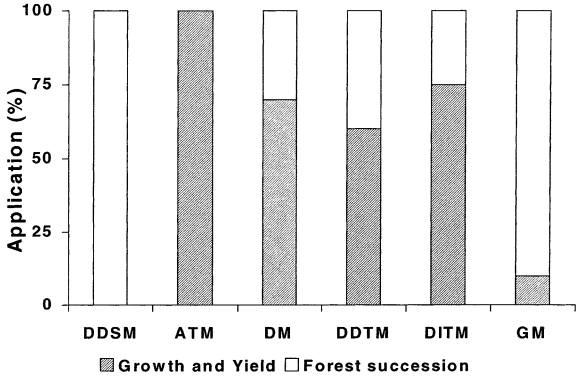

Fig. 10. Application (%) of the different model types. Two main applications were distinguished: growth and yield studies and forest succession studies. DDSM = distance-dependent stand models, ATM = average tree models, DM = distribution models, DDTM = distance-dependent tree models, DITM = distance-independent (non-gap) tree models, GM = gap models.

1999a). In some models tree death may occur as a result of larger scale disturbances, like fire (Kercher and Axelrod, 1984a,b; Bonan, 1989; Kellomäki et al., 1992; Miller and Urban, 1999a,b), insects (Bonan, 1989; Kellomäki et al., 1992), or wind throw (Kellomäki et al., 1992). Finally, a few models include mortality as a consequence of damages following a tree fall (natural death or harvesting): the remaining trees on a patch or on adjacent patches have an increased probability of dying the year after the event (Shugart et al., 1980; van Daalen and Shugart, 1989).

## 4. Model application and suitability

### 4.1. General

Two main applications of the models presented were encountered in the literature. The first one concerns growth and yield estimations including the prediction of the effects of forest management practices, whereas the second one aims at studying forest dynamics and succession including the effects of natural disturbances and stand structure. Not all the model types are applied to both objectives. Fig. 10 presents a rough proportion of the applications for each model type.

Model suitability is highly linked to: (i) the amount of empirism that is found in the modelling; and (ii) the initial objective of the scientist who built the model. In general, an empirical model is more accurate in its predictions, but it is also limited to specific conditions depending on the dataset used for parameter fitting. According to the main objective of model construction, the authors chose not only a specific approach but also selected the steps and processes to be included in the model. As a consequence of these selections, a model will be appropriate for certain purposes but not necessarily accurate for others as well.

This chapter will mainly develop a critical analysis of the applications of the model types, through a detailed presentation of the outputs of specific representative models, with the objective of determining the model type that is best suitable for each application type. We did not run the models by ourselves to make any sensitivity analysis, but based our judgement on the following points:

- What was the model used for: objective, time scale, space scale?
- Is the model accurate: comparison of outputs to measurements and observations?
- Is the model reasonable: confrontation of the limitations resulting from the content of the model to its application?

Difficulties in modelling recruitment are a general characteristic independent of the model types. It will be discussed first, followed by model application for growth and yield prediction, and finally the models simulating forest dynamics and succession will be analysed.

### 4.2. Methodology of model evaluation

According to Shugart (1984), model testing consists of two procedures: model verification, and model validation. Model verification is a qualitative assessment of the consistency of the model outputs when compared with general observations. Model validation is a more quantitative test that directly compares the model outputs to an independent dataset. More often than not, models are tested using at least one of these two procedures.

Model testing is difficult to undertake when model structure is getting more complex, such as in mechanistic and/or tree level approaches and when model provide long-term predictions such as succession models. Full validation should include testing of individual tree growth and of intermediate outputs from the different sub-models (light interception, carbon fixation, soil carbon balance, etc.) or long-term observations. However, as model validation gets more difficult, it is more often omitted (Botkin et al., 1972; Kercher and Axelrod, 1984b; Busing, 1991; Fulton, 1991; Mohren et al., 1991; Pukkala et al., 1994; Bugmann, 1996; Williams, 1996; Jogiste, 1998; Riéra et al., 1998; Talkkari and Hypén, 1996; Kellomäki and Väisänen, 1997; Bugmann and Cramer, 1998; Chave, 1999; Bartelink, 2000a).

Model verification was largely used, mostly in DDTM and GM, to check the accordance between outputs and general knowledge or historical observations of forest succession (e.g. Busing, 1991), forest structure (e.g. Riéra et al., 1998), and species behaviour (e.g. Shugart et al., 1980). Consistency of model outputs was also assessed by comparison with the other models that were considered as a reference (GM: Fulton, 1991; yield tables: Talkkari and Hypén, 1996; Kellomäki and Väisänen, 1997; Jogiste, 1998; Bartelink, 2000a,b).

For tree models, validation of individual tree growth is difficult to realise: individual measurements from an independent dataset cannot be expected to match the individual tree level outputs, when the model was initiated with another dataset. Therefore, outputs integrated at the stand level (that is to say either average and total value for the stand or distributions per dimensional classes) are commonly compared to observations of similar stands (Shugart and West, 1977; Waldrop et al., 1986; Leemans and Prentice, 1987; Prentice and Leemans, 1990; Pacala et al., 1993; Courbaud et al., 1997; Kolstrom, 1998; Jorritsma et al., 1999; Miller and Urban, 1999a; Vettenranta, 1999).

On the other hand, model validation is largely used in average tree models (ATM), DM and GM. Outputs generally correspond to the dendrometric characteristics that are easily and classically measured in a stand, such as stand BA, tree number, DBH distribution, per species. As a consequence, comparisons between simulations and data are used commonly (Moser, 1972; Bruner and Moser, 1973; Shugart and West, 1977; Shugart et al., 1980; Ung et al., 1982; Hyink and Moser, 1983; Lynch and Moser, 1986; Solomon et al., 1986; Waldrop et al., 1986; Leemans and Prentice, 1987; Prentice and Leemans, 1990; Bossel and Krieger, 1991; Puettmann et al., 1992; Solomon and Bartlein, 1992; Kolstrom, 1993; Pacala et al., 1993; Alder, 1995; Keane et al., 1996a,b; Courbaud et al., 1997; Lin and Buongiorno, 1997; Monserud et al., 1997; Osho, 1997; Favrichon, 1998; Kolstrom, 1998; Sterba and Monserud, 1998; Jorritsma et al., 1999; Kolbe et al., 1999; Miller and Urban, 1999a; Vettenranta, 1999). However, experimental difficulties often result in a partial validation:

- Data on long-term forest dynamics are generally not available. Comparison of simulations to short chronosequences and steady-state measurements restrict validations to shorter periods than the whole simulated period (e.g. Pacala et al., 1993; first 10–50 years for a model simulation of 200 years, Favrichon, 1998).
- Models designed to include perturbations are validated under no perturbation. It is assumed that model performance will remain the same under perturbation (e.g. insect, Shugart and West, 1977; climatic changes, Solomon and Bartlein, 1992; fire, Keane et al., 1990, 1996a,b; grazing, Jorritsma et al., 1999).

As indicated by Bugmann (1996), comparison between simulations and site specific data are not sufficient to demonstrate the reliability of a model and sensitivity analysis to the parameters values are used increasingly to judge their quality (Keane et al., 1989, 1990; Bonan et al., 1990; Bossel and Krieger, 1991; Busing, 1991; Fulton, 1991; Osho, 1991; Wissel, 1992; Kolstrom, 1993; Bugmann et al., 1996a,b, 1997; Pacala et al., 1996; Williams, 1996; Moravie et al., 1997; Batista et al., 1998; Liu and Ashton, 1998; Chave, 1999). It is worth noting that mechanistic tree models were particularly used for sensitivity analysis.

### 4.3. Recruitment sub-models

Recruitment modelling is unsatisfactory in most models, whatever the type. Differences between observations and estimations are considerable: the Average tree model of Lynch and Moser (1986), e.g. underestimates by 35–47% the number of recruits. Errors in recruitment estimations using an ATM based on multiple regression techniques results in up to 20% of error on the final estimation of standing volume (Turner, 1966). The correlation between the number of recruits on the one hand, and the stand basal area, the tree number, and diameter on the other hand is used in most models, but such regressions result in poor statistical models (Lynch and Moser, 1986; Carpentier, 1996; Lin and Buongiorno, 1997; Favrichon, 1998). Gap models also showed difficulties in the representation of regeneration. FORCAT (Waldrop et al., 1986), e.g. was not able to represent the number of recruits per species of a mixed Oak–Hickory forest (Fig. 11).

Gap models present a specific parameter that alters recruitment estimation: gap size. A too large gap will favour shade-intolerant species whereas a too small gap will prevent their installation, resulting in incorrect species composition (Shugart and West, 1977; Shugart, 1984; Leemans and Prentice, 1987).

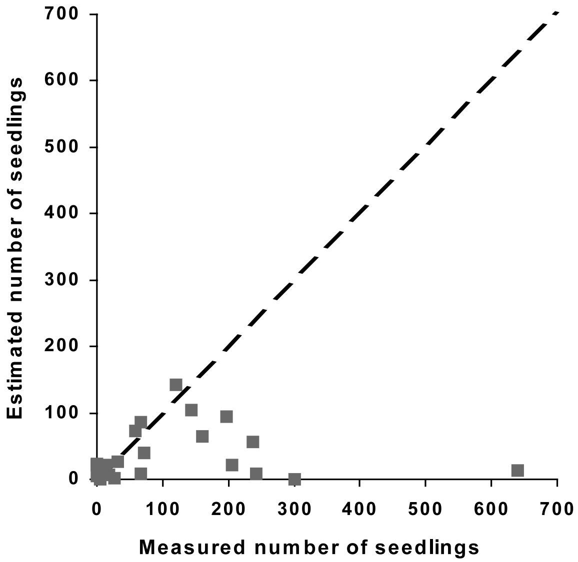

Fig. 11. Number of recruits per species estimated using the Gap model FORCAT of Waldrop et al. (1986) vs. the measured number of recruits. Each point corresponds to one species (1–24). The $Y = X$ line is represented (– –). Graph was constructed using values presented in their Table 6.

The consequence of the poor representation of recruitment on forest growth modelling was enquired by several authors. For example, Kolstrom (1993) presented a sensitivity analysis of the regeneration routine of a matrix model applied to uneven-aged Norway spruce stands: a ±25% change in the recruitment parameter results in a 17–18% change in the stand basal area over 100 years as well as an alteration of the diameter distribution. The gap model KOPIDE (Shao et al., 1994) was used to simulate the impact of the initial state and the regeneration processes on the evolution of a broadleaved-*Pinus koriensis* forest: Fig. 12 presents the evolution of the total stand volume when simulation started from bare ground, from a birch–aspen secondary forest ($\sim$ 30 years) or from an old-growth Ash dominated forest ($>200$ years). The effects on the stand characteristics were disappearing only when stand reached its state of maturity between 200 and 300 years.

Therefore, special attention must be paid to the modelling of early stages. Attempts to model recruitment with more mechanistic approaches were carried out in several DDTM's (Williams, 1996; Liu and Ashton, 1998; Chave, 1999). For example, TROLL (Chave, 1999) described seed production, dispersal, germination and installation to model recruitment. As a consequence, it required many parameters such as the age of maturation, the seed production per tree, and the average dispersal length. The forest dynamic model proved to be very sensitive to the values of these parameters. The accuracy of complex models to represent recruitment was not investigated much. Shugart (1984) indicated that the diversity of the processes involved in regeneration would impede the development of mechanistic models. However, as indicated by Liu and Ashton (1998), the representation of seed dispersal in forest dynamics models is all the more required to understand the recruitment of tree species without the presence of adults in the stand. Therefore, despite their com-

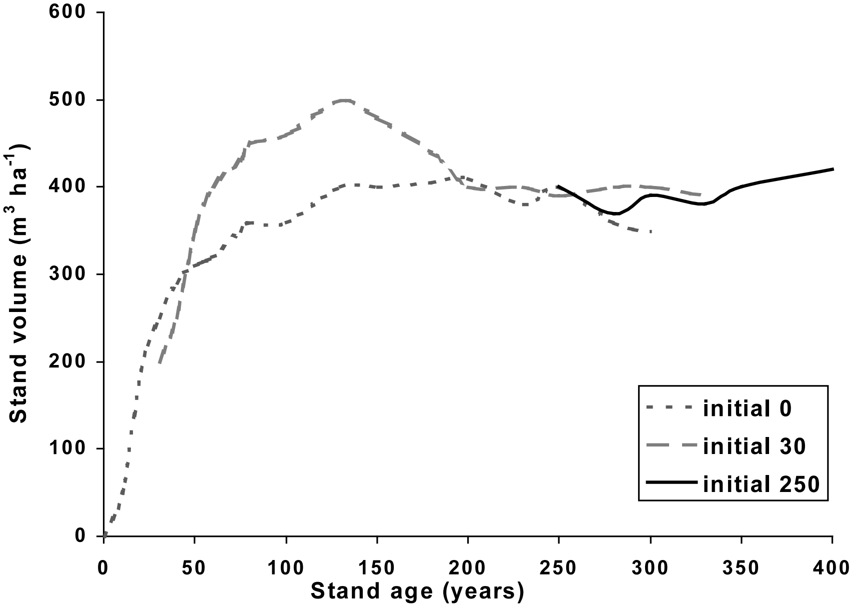

Fig. 12. Stand volume as estimated using the gap mode of Shao et al. (1994). Initial stand structure was either bare ground (- - -); a secondary growth forest (– –); or an old-growth forest (—). Graph was constructed using values presented in their Figs. 2–4a.

plexity, such models seem very promising to represent regeneration if they are coupled to intensive studies on the different processes from seed production to recruitment to improve their accuracy.

### *4.4. Growth and yield predictions*

#### *4.4.1. Stand models*

Many stand models developed for growth and yield predictions of boreal and temperate mixed or uneven-aged forests are ATM (Turner, 1966; Moser and Hall, 1969; Moser, 1972; Ung et al., 1982; Deusen and Biging, 1985; Lynch and Moser, 1986; Puettmann et al., 1992; Payandeh and Papadopol, 1994; Smith, 1996; Jogiste, 1998) and only a few examples of applications of this model type in tropical forests was found (Singh and Sharma, 1982, 1983; Atta-Boateng and Moser, 2000). On the one hand, it is probably due to the large amount of data required to construct the yield tables. On the other hand, ATM's characteristics appear to be believed to be less suitable to model the large diversity in terms of species composition and stand structure that can be found in tropical forest. Most of the ATM provides only yield estimates but some enable the user to manipulate the management regime and hence analyse the consequences of forestry measures. For example, the model by Jogiste (1998) was used to investigate the impact of the *Betula* sp. proportion on the total yield of a *Picea abies*/*Betula* sp. mixture, on a short- (50 years) and long-term (100 years). Stand density management diagrams were used to investigate the impacts of initial *Pseudotsuga meanziesii*/*Alnus rubra* proportion and stand density on the basal area increments per species (Puettmann et al., 1992).

Short-term predictions using ATM's seemed very accurate: estimations of number of trees and basal area per species over a 9–10 year period (Fig. 13) did not significantly differ from the values measured (Ung et al., 1982; Lynch and Moser, 1986).

However, the major drawback of these models is that, because of their simplified nature, they are valid for a limited range of conditions (stand structure, site, environment) only. For instance, the lack of simulating interactions between species restricted the prediction capacity to the first 7–8 years when the forest dynamics could be considered equal to the sum of the independent species dynamics (Ung et al., 1982). Without modelling tree death (Moser and Hall, 1969; Ung et al., 1982) and/or ingrowth (Puettmann et al., 1992; Jogiste, 1998), the lengths of the reasonable predictions are limited. Although Jogiste (1998) used his model over a 100 year period, interpretations of the long-term results provided by models not including these processes should be carefully looked upon. The empirical relationships used provide simple, straightforward models, with few variables and parameters. However, they strongly bind the model to the data used for fitting, impeding the direct extrapolation to different forests and environmental conditions. For instance, when Ung et al. (1982) wanted to apply the model of Moser (1972) for another forest but with the same objectives, they had to collect a whole new dataset and re-parameterise the whole model.

The second group of stand models used frequently for yield estimations are the distribution models (DM). The evolution of stand structure in terms of diameter class distributions of tree number or BA is estimated under natural conditions or different management practices. For example, a matrix model with transition probabilities function of stand BA (Lin and Buongiorno, 1997) was applied to simulate the evolution of DBH-distribution in a maple–birch forest after different periods without intervention, from 15 years to steady-state (360 years). Most of the time, silvicultural practices were simulated and the model was used to assess the impacts of management on stand structure (Hyink and Moser, 1983; Solomon et al., 1986; Kohyama, 1992a, 1993; Hinssen, 1994; Lin et al., 1996; Schulte and Buongiorno, 1998; Favrichon, 1998). A classical study consists of assessing the effects of thinning regimes: Fig. 14 illustrates the evolution of species composition in a mixed stand submitted to two different thinning regimes (Solomon et al., 1986). A more intensive thinning regime resulted in significant changes in species composition: fir increasing from 18 to 29% of the stand volume; red maple and yellow birch from 4–6% to 8–11%; while spruce, various hardwoods and softwoods proportions decreased.

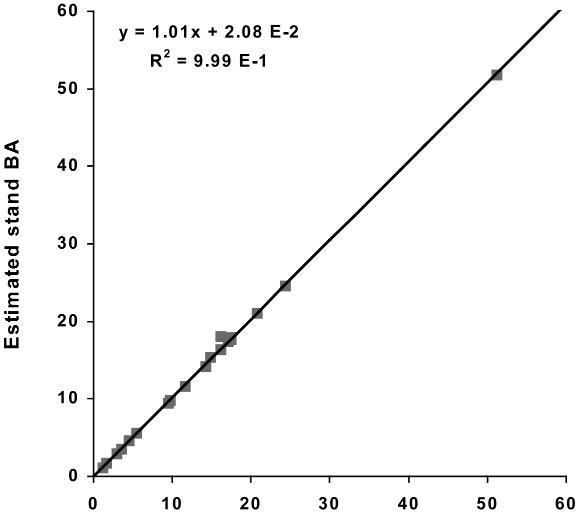

Fig. 13. Stand basal area estimated using the ATM of Ung et al. (1982) versus measured stand basal area. Each point corresponds to one species (1–19). The linear tendency (—) and equation are represented. Graph was constructed using values presented in their Table 2.

Some distribution models present a specific application which is to answer the practical questions of forest managers: what silviculture has to be applied in the actual forest to reach a specific economic (standing volume, proportion of saw-timber and pulpwood, income) or ecological (diversity, steady stand structure) goal (Haight et al., 1985; Haight and Getz, 1987; Yu and Zheng, 1989; Bruciamacchie et al., 1991; Buongiorno et al., 1995; Gove et al., 1995; Ingram, 1995; Ingram and Buongiorno, 1996; Lin et al., 1996; Volin and Buongiorno, 1996; Schulte and Buongiorno, 1998). The final objective is summarised using indices such as the Shannon index of diversity (based on the number and dimensions of the different species) or the NPV economical index (net present value based on the volumes and prices of saw-timber and pulpwood). The principle consists of estimating the initial stand structure and composition and the silvicultural practices (thinnings, harvesting) that will lead to the desired value of different indices.

The elaboration of these deterministic distribution models would require a lot of data including repeated measurements of diameter distributions,

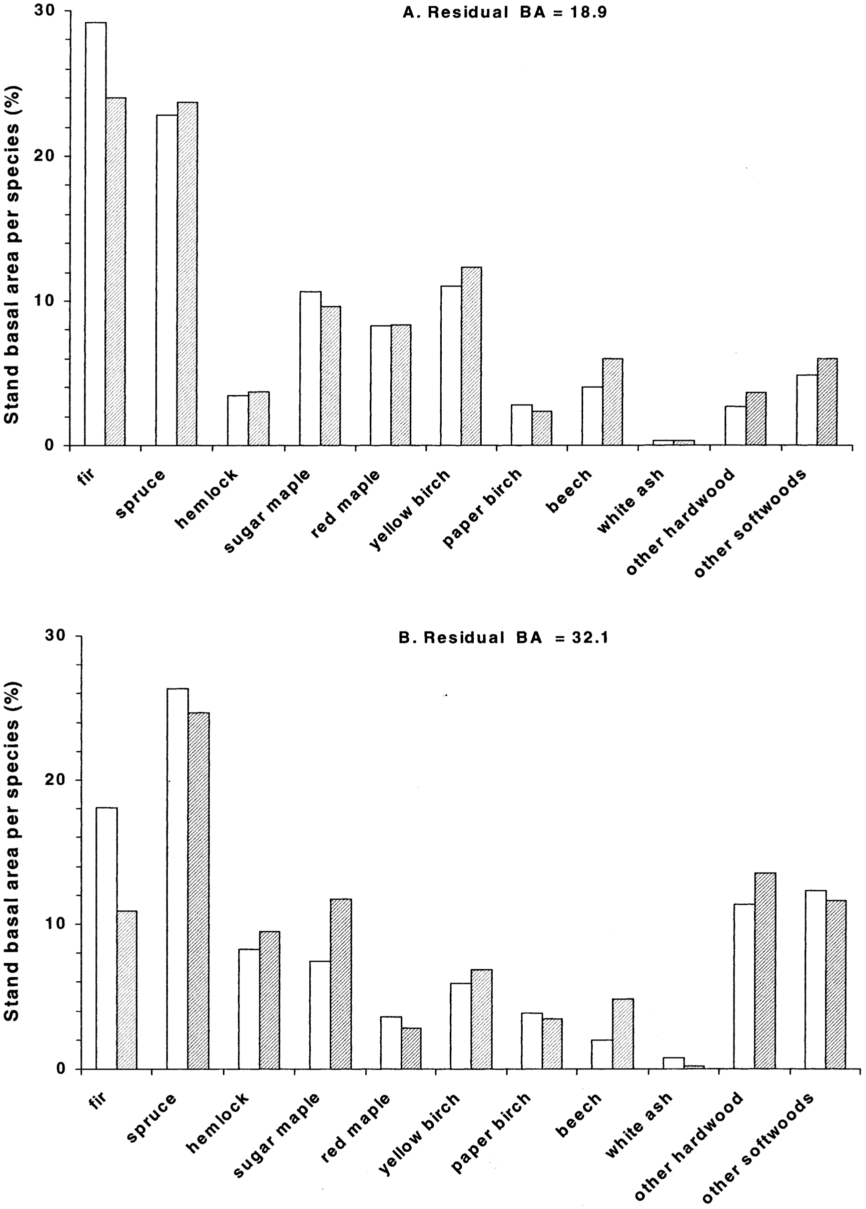

Fig. 14. Stand yield (% of total volume per hectare) per species for a mixed forest as measured □ and estimated ▨ using the DM of Solomon et al. (1986). The values are corresponding to stand volume after a 15 year-long rotation with 3 harvests. (A). the first intensive thinning regime resulted in a residual BA of 18.9. (B). The second less intensive regime resulted in a residual BA of 32.1. Graphs were constructed using values presented in their Table 5.

recruitment, death and harvesting on long-term periods. In general, time repetitions are difficult to achieve and unless previous studies provided large datasets (e.g. experimental plots designed in 1953 and re-measured every 5 years, Solomon et al., 1986) models were parameterised using growth measurements carried out only once over a 5 or 10 year-long interval (Ek, 1974; Hyink and

Moser, 1983; Kolstrom, 1993; Alder, 1995; Sanquetta et al., 1996; Geldenhuys et al., 1997; Lin and Buongiorno, 1997). In the end, the growth model depending on stand BA and/or class diameter represents between 8 and 58% of the variability observed in growth increments (Kolstrom, 1993; Alder, 1995; Buongiorno et al., 1995; Kolbe et al., 1999) which indicates that although the models based on variable parameters are significantly different from fixed parameter models (Lin and Buongiorno, 1997), the selected growth relationships are not sufficient. Anyway, the models seem quite satisfying: the short-term evolution of a mixed hardwood stand is predicted very accurately (Fig. 15(A); Bruner and Moser, 1973) and the long-term evolution of a maple–birch stand is coherent with observations of old stands (Fig. 15(B), Lin and Buongiorno, 1997).

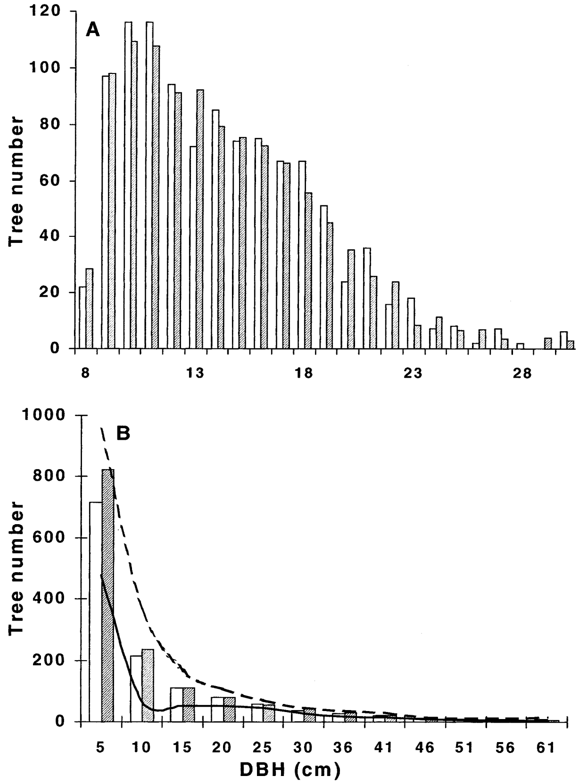

Fig. 15. Examples of comparisons between simulations and observations using Distribution models. (A) Tree number per diameter class as measured □ and estimated ▨ over 19 years using the constant parameter DM of Bruner and Moser (1973). Graph was constructed using values presented in their Table 4. (B) Tree number per diameter class as measured (mean value □, mininum — and maximum – – values) and estimated ▨ at steady-state over 360 years using the variable parameter DM of Lin and Buongiorno (1997). Graph was constructed using values presented in their Table 6.

Apart from comparisons between measurements and estimations, no further investigation on the quality of the models was generally carried out before applying them to various conditions. The application of a matrix model established in Wisconsin to the same kind of mixed hardwood forests (maple–beech–birch) in Michigan demonstrated the difficulty of extrapolating such models to different conditions: although a site index was added in the Wisconsin growth equations, the parameters were highly significantly different when using the Michigan, Wisconsin or mixed datasets to parameterise the model. Steady-state basal area for stands in the same initial conditions could be 25% higher when using the Michigan than the Wisconsin model (Kolbe et al., 1999).

### *4.4.2. Tree models*

With respect to tree models, both distance-dependent (DDTM) and distance-independent tree models (DITM) have been applied for growth and yield research, with only a few gap models strictly applied to management purposes (Shugart et al., 1980; Harrison and Ineson, 1988; Kienast and Krauchi, 1991; Mohren et al., 1991; Coates and Burton, 1997; Kolstrom, 1998). DDTM's as well as DITM's generally allow various thinning regimes to be simulated (Wykoff et al., 1982; Siekierski, 1991; Pretzsch and Kahn, 1996a; Wimberly and Bare, 1996; Chumachenko, 1998; Pretzsch, 1998; Pukkala et al., 1998; McLeish, 1999; Vettenranta, 1999; Bartelink, 2000b; Phillips et al., 2000a,b). For example, the DDTM models SILVA-2 (Pretzsch, 1992) and COMMIX (Bartelink, 2000a) have been used to calculate the impacts of thinning regimes and mixtures on productivity (Kahn and Pretzsch, 1997; Bartelink, 2000b) and to determine the financial consequences of stand composition and treatment (Knoke, 1998). The DITM PROGNOSIS was used to determine the species mixture that maximise stand yield (Bare and Opalach, 1987) or the impacts of thinning and management options

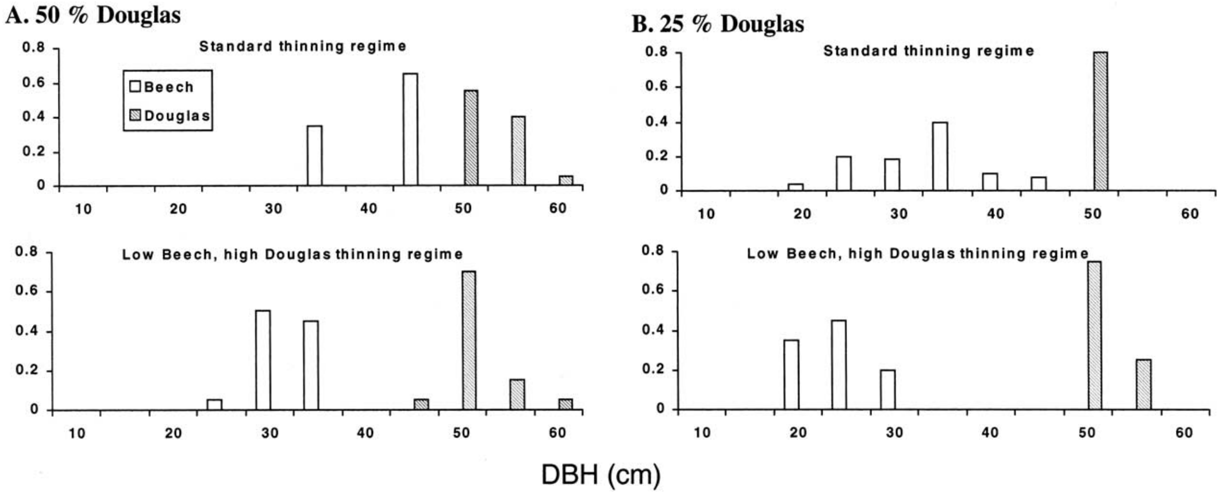

Fig. 16. Simulations of tree frequency per diameter class per species, for a Beech □ and Douglas ▨ mixture using the DDTM COMMIX of Bartelink (2000b). Top graphs represent simulations with a standard thinning scenario (low thinning intensity, selection from below) and bottom graphs with a selective thinning scenario that favours Beech compared to Douglas. (A) Left graphs represent simulations using a initial stand composition of 50 % Douglas–50 % Beech, and (B) right graphs using a initial mixture of 25 % Douglas–75 % Beech. Graphs were constructed using values presented on his Figures 7 and 8.

(Wykoff et al., 1982). In general, both DDTM's and DITM's are capable of predicting growth and yield of stand of various compositions in terms of species and age. Fig. 16 presents the simulations of the stand DBH distributions after 50 years of growth, with the impacts of thinning regime and initial species composition, using the DDTM COMMIX (Bartelink, 2000b).

Tree level outputs integrated at the stand level present a quality of prediction not as good as for stand level models but they are still consistent with short- and long-term observations (Shugart et al., 1980; Waldrop et al., 1986; van Daalen and Shugart, 1989; Keane et al., 1996b; Pacala et al., 1996; Moravie et al., 1997). Fig. 17 presents comparisons of measurements and simulations using the gap model OUTENIQUA (van Daalen and Shugart, 1989), the DDTM SORTIE (Pacala et al., 1996) and the DITM FIRE-BGC (Keane et al., 1996b): individual tree outputs were integrated to provide total basal area per species, average diameter increment and a diameter distribution (Fig. 17(A)–(C), respectively). Although fitting is not as accurate as observed with stand model, the general tendency of the predictions is in adequacy with the observations of stand DBH distribution, species composition or average tree increment.

### *4.5. Forest dynamics and succession*

Mostly gap models (GM) and distance-dependent tree models (DDTM) are used to describe forest dynamics and succession. Distance-dependent stand models (DDSM), some distribution models (DM) and distance-independent tree models (DITM) are less commonly used (Fig. 10). Apart from the DDTM SILVA 2 applied to simulate climate change impacts (Pretzsch and Kahn, 1996b), the DITM FIRE-BGC were used to study natural fire occurrence and prescribed burnings (Keane et al., 1996a,b) and the DM of Batista et al. (1998) which simulates hurricane disturbances in a beech forest in Florida, only GM include the effects of natural perturbations in the description of forest dynamics: wildlife impacts (Harrison and Ineson, 1988; Bonan, 1989; Jorritsma et al., 1999), fire occurrence (Kercher and Axelrod, 1984a; Miles et al., 1985; Bonan, 1989; Keane et al., 1989, 1990; Kienast and Kuhn, 1989a; Waldrop et al., 1986; Miller and Urban, 1999a,b), consequences of pollution (Kercher and Axelrod, 1984b; Harrison and Ineson, 1988) or climate change (Kienast and Kuhn, 1989b; Bonan et al., 1990; Solomon and Bartlein, 1992; Bowes and

Sedjo, 1993; Krauchi and Kienast, 1993; Burton et al., 1995; Fischlin et al., 1995; Post and Pastor, 1996; Shao, 1996; Shugart and Smith, 1996; Talkkari and Hypén, 1996; Yan and Zhao, 1996; Bugmann et al., 1997; Shugart et al., 1997; Talkkari et al., 1999). Other models focused on natural dynamics and succession without disturbances.

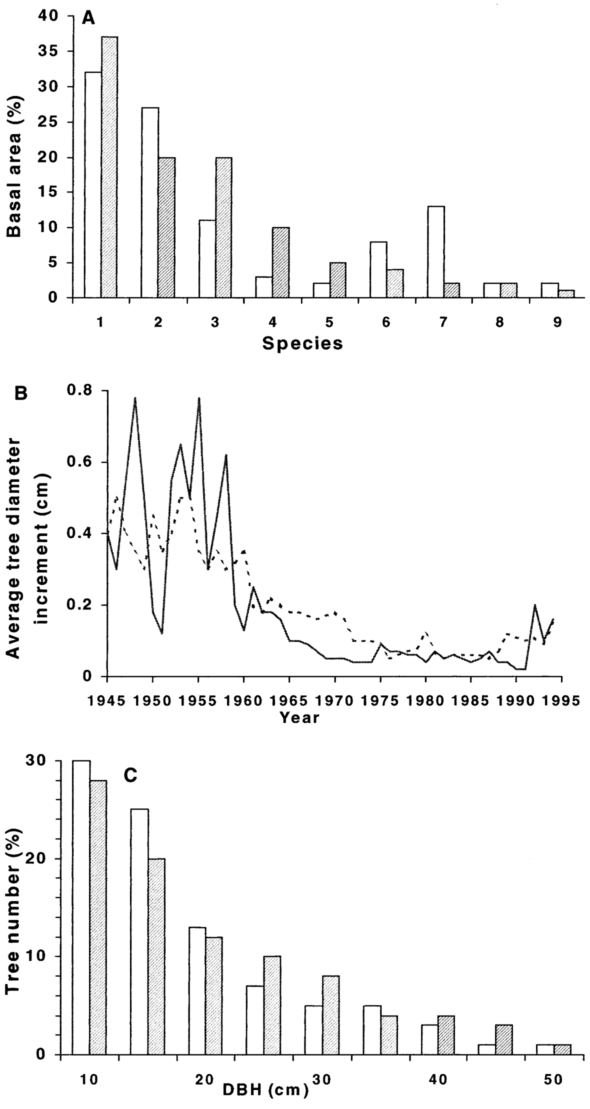

Fig. 17.

### 4.5.1. Stand models

At the stand level, DDSM and DM are applied to forest succession studies. Most of them focused on species dynamics only, without further information on the evolution of the stand structure (tree number, BA, DBH distribution etc.). Most of the DDSM enter in the first category whereas DM permits investigating both species composition and stand yield. However, by integrating space dependency, DDSM provide information on the spatial organisation of the forest when DM remains at the global scale. For example, the model by Riéra et al. (1998) based on transition probabilities of cells between four developmental stages investigates the evolution of the spatial patterns of a tropical forest (Fig. 18). Examples of DM (Fig. 19) applied to succession studies are models by Kohyama (1993) and Miles et al. (1985). The first model was used to represent the long-term evolution of BA per species for a temperate rain forest in Japan. On a mixed broadleaved-pine forest in China, a Markov model was applied to simulate the evolution of species composition over six successions.

The accuracy of these predictions over centuries is impossible to assess but the suitability of certain model types for such studies can be discussed. Hinssen (1994) stated that Markov chain approaches could be applicable to simulate forest dynamics only if the forest is 'large' enough: in that case, the large number of trees would permit

Fig. 17. Examples of comparisons between simulations and observations using Tree models. (A): Stand BA per species (1–9) as observed □ and simulated ▨ over 500 years for a Oak-northern hardwood forest in North America using the DDTM SORTIE of Pacala et al. (1996). 100 runs were simulated to obtain the average and confidence interval values. Data from the literature on old-grown stands were complied to obtain the average and confidence interval values. Graph was constructed using values presented in their Table 6. (B): Annual average tree diameter increment as measured (—) and simulated (– – ) for *Pinus radiata* in a *P. radiata–Abies lasiocarpa* mixture using the DITM FIRE-BGC of Keane et al. (1996b). Graph was constructed using the values presented on their Figure 12. (C): Relative DBH distribution of trees as observed □ and estimated ▨ for a mixed evergreen forest in South Africa using the GM OUTENIQUA of van Daalen and Shugart (1989). Graph was constructed using values presented on their Figure 3b.

to suppose that the changes in transition probabilities are constant in time. On the contrary, looking at the lack of fit between observations of the composition of a hardwood forest and simulations using a stationary Markov model, Binkley (1980) considered the approach not at all suitable to study forest succession. Usher (1979) concluded that since most ecological successions are not stationary, Markov models could be used to represent successions provided transition probabilities are changing in time or that constant probabilities are being used over non-constant transition periods. In general, distribution models are established on restricted datasets and consider that the relationships hold through time. At least, precautions should be taken during the interpretation of such long-term dynamics (e.g. 10 000 years for Kohyama's model).

### *4.5.2. Tree models*

At the tree level, particularly gap models are applied to simulate forest developments (Botkin et al., 1972; Shugart and West, 1977; Harrison and Ineson, 1988; van Daalen and Shugart, 1989; Kienast and Kuhn, 1989a; Prentice and Leemans, 1990; Kellomäki et al., 1992; Leemans, 1992; Coffin and Urban, 1993; Shao et al., 1994; Acevedo et al., 1995, 1996; Kolstrom, 1998). Such models constitute tools to support decision making in ecosystem management. They simulate the evolution of stand structure and composition under the pressure of many natural disturbances, providing indications useful to the forest manager. For example, impacts of fire disturbance are presented in Fig. 20. With SILVA (Kercher and Axelrod, 1984a) fires limit fir expansion and favour the dominance of pine, whereas the evolution of the same mixture without disturbance would almost lead to a co-dominant stand.

FORGRA (Jorritsma et al., 1999) simulates the species dynamics over 100 years according to the number of ungulates per hectare and to their species and grazing habits. Stand composition is highly changed under grazing pressure (Fig. 21), going as far as the full disappearance of birch when one cow is present on the stand or leading to the disappearance of pine and a favoured development of birch when one roe deer is present per hectare.

Model outputs can hardly be compared with observations since authors do not dispose of long-term succession data. The reliability of the results is assessed by comparison between the steady-state estimations and observations on old stands or between the simulated successional states and general forest behaviour as it was derived from the observations in the field (e.g. Shugart et al., 1980; Busing, 1991; Williams, 1996; Chave, 1999).

Sensitivity analysis were also used to assess the model quality. For instance, Chave (1999) indicated that the forest structure simulated by TROLL was highly dependent on the formulation and parameterisation of regeneration and tree fall. Similarly, there is a general agreement that model

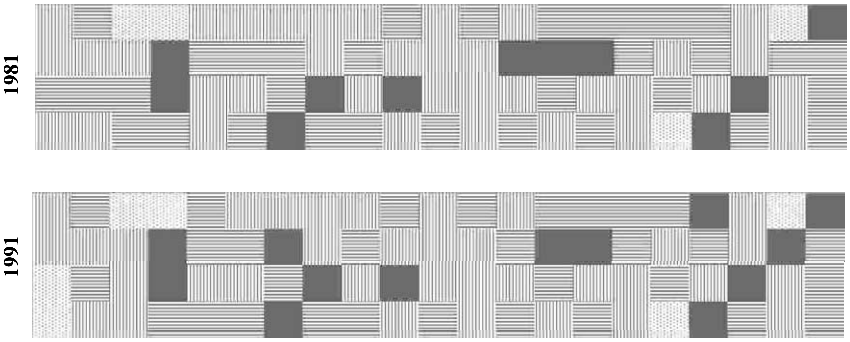

Fig. 18. Evolution of the spatial pattern of a tropical forest in French Guinea over 10 years using the DDSM of Riéra et al. (1998). Each unit cell was characterised by its state in the succession (defined by tree species and tree dimensions): ░ = nude land after tree fall, ▥ = colonisation steps, ▤ = cover of intermediate and/or small trees, ■ = presence of dominant trees. Graphs were constructed based on their Figure 3.

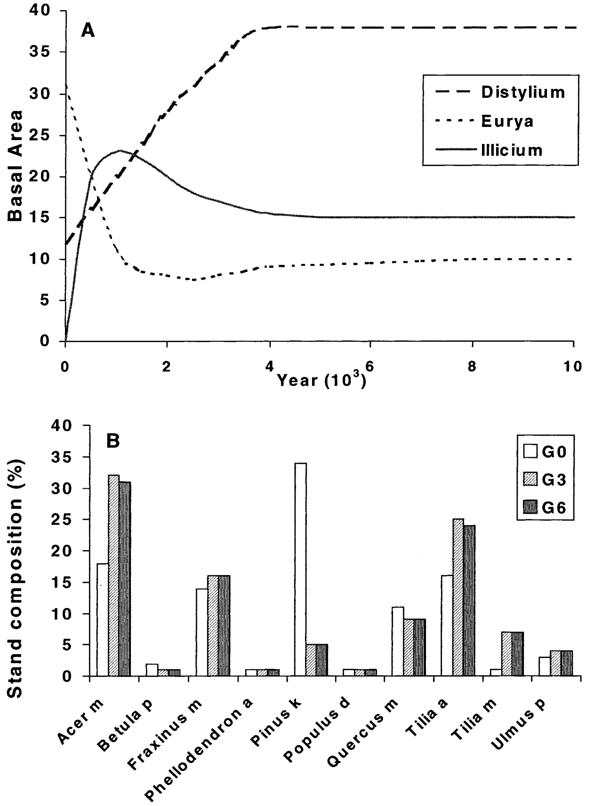

Fig. 19. Examples of succession simulations using DM. (A): Stand BA per species as simulated over 10000 years using the model of Kohyama (1993). Graph was constructed using values presented on their Figure 4b. (B): Evolution of stand composition from the initial forest (G0, □) to the next generation forests (G3, ▨ and G6, ▥) using the model of Miles et al. (1985). Graph was constructed using the values presented in their Table 3.

characteristics, from general structure to more specific parameterisations, should be compared and tested carefully to determine the limitations and suitability of the models to reach certain objectives. Excessive or poor sensitivity of the model to some specific parameters can limit its application under different conditions, or at least require a new parameterisation. For example Bugmann (1996) and Fischlin et al. (1995) underline the inadequacy of certain models to be extended along temperature and draught gradients. Attention was also directed on the impact of the spatial structuration of the model. Shugart et al. (1997) underlined the importance of the joint study of structure and function saying that the structural pattern is created by the processes (growth, regeneration, etc.) and that patterns influence the quantity and the trend of evolution of these processes. As any individual model, GM simulates the tree as an independent entity, and in addition, the gap structure allows to: (i) integrate the action of the environmental conditions on the tree response; and (ii) represent the feedback of the tree response on the local environmental conditions, through the local structure. But the gap structure and especially the gap size have large impacts on recruitment and stand composition (Shugart, 1984; Leemans and Prentice, 1987; Shugart and West, 1977; Liu and Ashton, 1998). Smith and Urban (1988) used the model ZELIG with a gap size of 0.01 ha and a varying interacting zone from 0.01 to 1 ha. They demonstrated that the resulting forest structure (tree diameter class distribution) was highly altered by the selected scale. Lett et al. (1999) compared the impacts of the regular structure of a gap model to the irregular structure of a distance-dependent tree model to conclude that the simulation results are quite similar but that the space-oriented model is more suitable to study natural disturbances (fire, wind tree fall, etc.) whereas the tree-oriented model is more appropriate to study the close interactions between the trees and biological agents (seed dispersing birds and mammals, human beings, etc.).

Among the natural perturbations, impacts of global warming on mixed forest dynamics was investigated recently using tree models (Bonan et al., 1990; Solomon and Bartlein, 1992; Bowes and Sedjo, 1993; Krauchi and Kienast, 1993; Burton et al., 1995; Fischlin et al., 1995; Bugmann and Fischlin, 1996; Bugmann et al., 1996b; Post and Pastor, 1996; Pretzsch and Kahn, 1996b; Shao, 1996; Shugart and Smith, 1996; Talkkari and Hypén, 1996; Yan and Zhao, 1996; Kellomäki and Väisänen, 1997; Shugart et al., 1997; Shugart, 1998; Talkkari et al., 1999). Except for the DDTM SILVA 2 (Pretzsch and Kahn, 1996b), all models were gap models. Most of the models present important limitations which should prevent them from being used in climate change studies:

- Models are only sensitive to one or two climatic variables, generally temperature and precipitations. Other variables such as air $CO_2$ concentration, soil nutrient contents were rarely considered (Post and Pastor, 1996; Pretzsch and Kahn, 1996b; Yan and Zhao, 1996). This resulted directly from the model construction: most of the time, only light, water availability and temperature are considered to limit the potential individual tree growth. For example, in FORENA (Solomon and Bartlein, 1992), growth is limited by cold temperatures and the sum of degree-days (to represent the length of the growing season): the model was applied to simulate the evolution of stand biomass per species over 1000 years, under changing environment, drawing conclusions on the future evolution of the mixed coniferous-hardwood forests in Michigan. SILVA (Pretzsch and Kahn, 1996b) used the same concept of reducing factors than many gap models but multiple dependency on factors such as air $CO_2$ concentration, soil nutrient supply, precipitation, draught, mean and minimum temperature was represented. This permitted to dispose of a more complete model, reasonable to investigate global change impacts on forest growth.
- In most models, tree growth is the only process sensitive to climate factors. Most of the time recruitment is indirectly altered by climate change, through modifications of the stand structure and light availability. However, recruitment can be altered directly by minimum winter temperatures, sum of degree-days and/or soil water content (Fischlin et al., 1995; Post and Pastor, 1996; Talkkari and Hypén, 1996; Kellomäki and Väisänen, 1997).
- In most models, sensitivity to climate change was represented using empirical functions which resulted in independent and constant responses to climatic changes through time. LINKAGES (Post and Pastor, 1996) presents a mechanistic modelling of forest trees and soil dynamics, including the nutrient, water and carbon cycles, which is particularly interesting to understand the evolution of a forest under concomitant changes in temperature, $CO_2$ concentration, water and nitrogen availability, in-

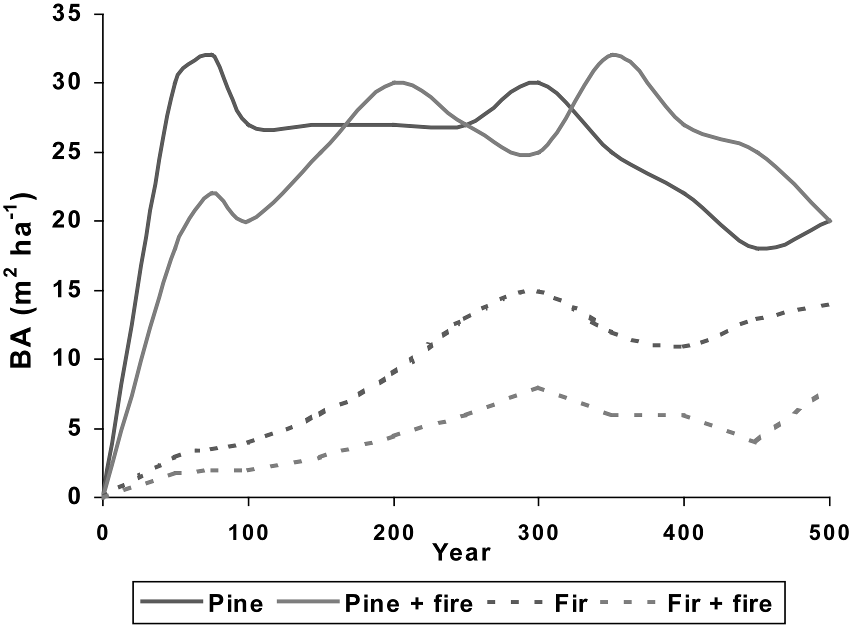

Fig. 20. Simulation of stand BA dynamics per species over 500 years, as undisturbed (—) and disturbed (– –) by fire occurrence using the gap model SILVA of Kercher and Axelrod (1984b). Graph was constructed using the values presented in their Fig. 7.

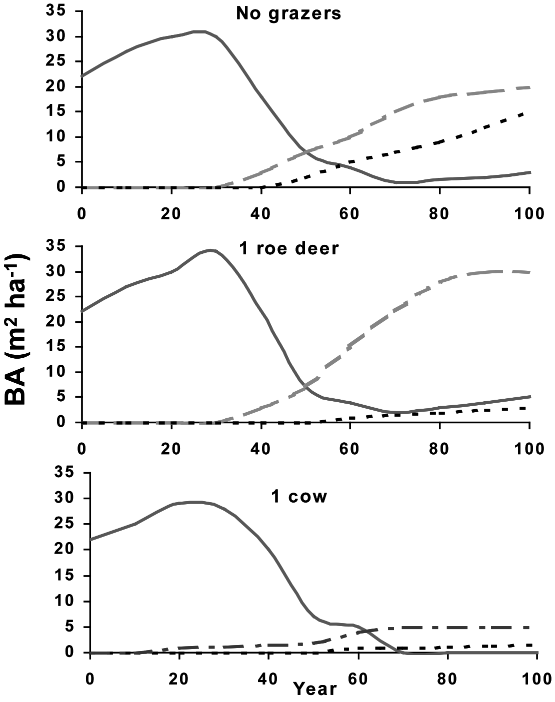

Fig. 21. Simulation of stand BA dynamics per species over 100 years, as undisturbed or disturbed by the presence of grazers using the gap model FORGRA of Jorritsma et al. (1999). (—) *Pinus*; (– – –) *Betula*; (- - -) *Quercus*; (— –) *Sorbus*. Graph was constructed using the values presented in their Fig. 4.

cluding feedback effects such as the interaction of species composition on the ecosystem mineral cycle. As a consequence, LINKAGES can be used under a wide range of conditions: Fig. 22 presents the simulations of the cumulated stand biomass per species under different climate change scenarios and for two different soil types. The effects of increased rainfall (scenario A to scenario B) and the interaction between soil type and climate conditions (scenario A to scenario C) are evident; the latter was attributed to the difference in the alteration of the decomposition rates of organic matter.

In their current state, most models seemed unreliable to predict the impact of global warming. A quasi-exhaustive analysis of the sensitivity to specific climatic parameterisation was carried out on FORECE and FORCLIM (Fischlin et al., 1995; Bugmann, 1996; Bugmann et al., 1996b; Bugmann and Cramer, 1998) that underlined the

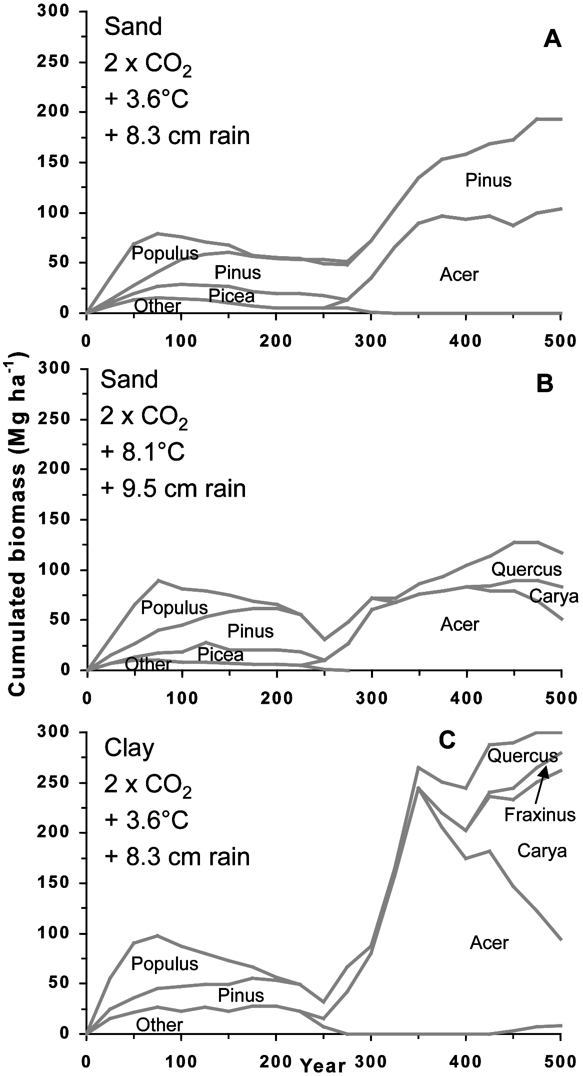

Fig. 22. Simulation of cumulated stand biomass species over 200 years under current climate conditions, 100 years under changing climate conditions and 200 years under the new climate using the gap model LINKAGES of Post and Pastor (1996). (A) Sandy soil, average increase in temperature + 3.6 °C, average increase in precipitations + 8.3 cm. (B) Sandy soil, average increase in temperature + 8.1 °C, average increase in precipitations + 9.5 cm. (C) Clay soil, average increase in temperature + 3.6 °C, average increase in precipitations + 8.3 cm. Graph was constructed using the values presented in their Fig. 2.

importance of the formulation of climate dependency. Compared to FORECE, FORCLIM includes a soil dynamics sub-model and improved climate-dependent functions (Bugmann, 1996). When applied to the sites for which the models were developed, both models perform equally well. However, when used to simulate the evolution of forest along temperature and drought gradients, FORECE was not able to represent the species composition correctly (Bugmann, 1996). Fischlin et al. (1995) and Bugmann and Cramer (1998) demonstrated that changing the formulation of the water balance alone drastically modified the simulations of species composition. Therefore, future improvements should come from focusing on mechanistic approaches including not only demographic and environmental interactions but also the vegetation physiological responses to provide reliable simulations of climate change impacts simulations (Fischlin et al., 1995; Bugmann and Fischlin, 1996; Bugmann et al., 1996b; Post and Pastor, 1996; Shugart and Smith, 1996). Accuracy of parameter estimates could also be improved using experimental results of species tolerance (Bugmann and Cramer, 1998).

## 5. Concluding remarks

Many models for mixed-species forests have been developed during the past decades. From this review it appears that a wide variety of modelling approaches occurs, running from highly empirical stand-level descriptions (e.g. Wiedemann's empirical yield table from 1949) to sophisticated, spatially explicit computer models. Although more recently models have been developed that do contain causal relationships between tree growth and environmental conditions, it seems that the two paths (empirical versus mechanistic) are still only marginally 'merged': there are still contrasts between biologically based process models and management-oriented growth and yield models (Mohren and Burkhart, 1994). It is also clear that there is a strong relationship between the model type and the research questions to be answered: differences between models arise because authors use their specific research aims as driving principles for designing their models.

There are two main applications of the models presented here. The first one concerns growth and yield estimations including the effects of forest management practices, and the second one aims at studying forest dynamics and succession, including the effects of natural disturbances and stand structure. Which model type is applied depends partly on the research objectives. Average tree models and distance-independent (non-gap) tree models appear to have been used almost exclusively for growth and yield predictions, whereas distance-dependent stand models are used only in forest succession studies. Distribution models are mostly used for growth and yield applications whereas gap models are mainly applied to forest dynamics studies. Distance-dependent models, finally, are applied for both purposes.

Not all models were developed to serve the same purpose, and likewise, not all models are suitable for all applications. The more empirical, the more accurate the models are in their (generally short-term) predictions. However, empirical models are highly dependent on the dataset used for parameter fitting and are therefore limited with respect to application in other growing or environmental conditions. The inexhaustible number of species combinations, management regimes, and site-dependent interactions in mixed forests indicates that a purely empirical approach will be unsuitable for most problems to be solved. Bringing in mechanistic relationships would improve the model validity, because then the reliability of the model depends more on the state of knowledge of physiological processes and responses to the growing conditions of the species involved than just on a statistical fit to a particular set of empirical data (Burkhart and Tham, 1992; Kelty and Cameron, 1994; Bartelink, 1998). According to Vanclay (1989), models with yield purposes should be a mix between empirical content so that the model is efficient and include sufficient physiological and ecological basis to remain realistic under different site and stand conditions. A drawback of mechanistic models is that on some occasions they over-do the job: for certain questions related to forest management problems, a high level of ecophysiological detail might not be necessary. Nevertheless, there is a clear trend in literature towards the inclusion of more mechanistic approaches, especially when complex systems have to be simulated (Judson, 1994).

In complex systems like mixed forests, tree-level models will be necessary to account for competition effects: the differing characteristics of the species and the spatial distribution of the trees have a different and in most cases a much stronger impact on stand development than is the case in monospecific forest stands. The descriptions of tree-to-tree interactions are thus necessary to provide reliable estimates of stand development. Yield tables, e.g. have been used successfully to manage pure stands, but this approach is less suitable for application to mixed forests, mainly because these are more complex and diverse in terms of their structure and composition (Pretzsch, 1992).

Due to the required spatial detail, tree models, in many cases, seem to offer the best opportunities to support silvicultural research and forest management decision taking. The simulation of inter-tree competition allows in principle a detailed prediction of stand structure, growth and yield, and biodiversity and is hence a promising tool. A minor disadvantage of tree models is that they may require a lot of computation time, especially when detailed physiological processes are simulated: this, however, can first be considered a temporarily hardware problem and can also be overcome by simplifying too complex models to the only necessary relationships and parameters.

## Acknowledgements

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## Appendix A. List of models of mixed forest stands

Classification of the models in alphabetical order by first author. The model name is indicated as well as the model type according to our classification. The model description consists in a short list of the main characteristics of the model (input and output variables, modelling principal, main applications).

| First author | Model name | Model type | Model description |
|---|---|---|---|
| Acevedo, M.F., 1995, 1996 | – | Distribution model | Markov chain model that simulates the transition probabilities of cells between different states of development. Used for long-term succession simulations |
| Alder, D., 1995 | CAFOGROM | Distribution model | Cohort model: annual increment, mortality and recruitment are modelled per species group and canopy class, using regression on stand or tree BA<br>Growth and yield productions, management of tropical forest |
| Alder, D., 1997 | SIRENA CAFOGROM | Average tree model + distribution model | Cohort model: annual increment, mortality and recruitment are modelled per species group and canopy class, using regression on stand or tree BA<br>Growth and yield productions, management of tropical forest |
| Alimi, R.J., 1977 | – | Average tree model | Yield table |
| Andonov, A.D., 1967 | – | Average tree model | Yield table |
| Antonovsky, M.Y., 1989 | – | Average tree model | Yield table |

**Appendix (continued).**

| First author | Model name | Model type | Model description |
|---|---|---|---|
| Armasescu, S., 1972 | – | Average tree model | Yield table |
| Atta-Boateng, J., 2000 | – | Average tree model + distribution model | Stand BA, diameter, nb trees/species using differential equations depending on initial BA or sum of diameters and density<br>Parameters of a Weibull distribution are fitted on data and expressed as a function of BA sum DBH/species<br>Prediction of yield per species and distribution for a tropical forest |
| Azevedo, C.P., 1994 | – | Distribution model | Matrix model for prediction of short and long-term evolution of diameter distributions in uneven-aged stands |
| Baginskii, V.F., 1982 | – | Average tree model | Yield table |
| Bare, B.B., 1987 | PROGNOSIS | Distance-independent (non-gap) tree model | Application of the prognosis model (Wykoff et al., 1982; Monserud et al., 1997) to answer a management question: find the species mix that optimises volume and income |
| Bartelink, H.H., 1998 | COMMIX | Distance-dependent tree model | Mechanistic model of growth depending on radiation availability and competition. No regeneration<br>Effects of silviculture (thinning regime, species composition) on forest productivity for temperate mixture |
| Batista, W.B., 1998 | – | Distribution model | Matrix model simulating demographic responses to hurricanes |
| Beky, A., 1978 | – | Average tree model | Yield table |
| Bernetti, G., 1980 | – | Average tree model | Yield table |
| Bonan, G.B., 1989, 1990 | | Gap model | Simulate the impact of climatic and environmental conditions on forest structure and vegetation patterns. As a management tool, determines the best management to achieve in order to compensate the growth modifications as a result of climate changes. |
| Bossel, H., 1991, 1994 | FORMIX2 | Distance-dependent stand model | Natural and managed development of a tropical forest according to the light conditions. Evaluating management practices |
| Botkin, D.B., 1972 | JABOWA | Gap model | First gap model: designed to model forest succession and competition in a mixed forest |
| Bowes, M.D., 1993 | | Gap model | Climate change and management evaluation using a gap model |
| Bowling, E.H., 1989 | – | Distribution model | Prediction of stand DBH distribution per species using the Weibull function. Stand-level BA was derived |
| Bruciamacchie, M., 1991 | – | Distribution model | Application to evaluate the effect of changes in forest structure on the income produced by uneven aged coniferous mountain forests |
| Bruner, H.D., 1973 | – | Distribution model | Stationary Markov model with probabilities of dying, growing, being harvested which are constant<br>No ingrowth, no species distinction<br>Forest dynamics and diameter distributions predictions |
| Bugmann, H., 1996 | FORECE | Gap model | See Kienast and Krauchi, 1991; Kienast and Kuhn, 1989a,b |
| Bugmann, H., 1996, 1997, 1998 | FORCLIM | Gap model | Long-term forest dynamics and sensitivity to climate change |
| Buongiorno, J., 1980 | – | Distribution model | Deterministic matrix model where probability to die, grow or not are constant. No species distinction<br>Ingrowth is a linear function of BA and tree number per class<br>Management (effects of thinnings intensities) and economic returns on short and long time scales |
| Buongiorno, J., 1995, 1996 | – | Distribution model | Deterministic matrix model where probability to die, grow or not are functions of BA and diameter/class/species. Ingrowth is a linear function of BA and tree number per class/species<br>Management (effects of thinnings). Long-term evolution of forest species composition and diameter distribution |
| Burton, P.J., 1995 | Zelig | Gap model | Impact of frost and climate change on growth of different forests |
| Busing, R.T., 1991 | SPACE | Gap model + distance-dependent tree model | Gap model where trees are located inside the gap to emphasise the spatial aspect in the model. Long-term study of the spatial pattern of a forest |

**Appendix (continued).**

| First author | Model name | Model type | Model description |
|---|---|---|---|
| Carpentier, J.P., 1996 | BOJRES | Distance-independent (non gap) tree model | Empirical model for growth and yield prediction, including recruitment, mortality and growth at the tree level |
| Chave, J., 1999 | TROLL | Distance-dependent tree model | Mechanistic model of forest succession using dependence to light availability to model photosynthesis, radial growth, establishment. Tree fall (mechanistic approach) insures gap formation. Uses functional groups<br>Used to study the stand structure, the long-term dynamics, the spatial dynamics of a tropical rain forest. |
| Chumachenko, S.I., 1998 | – | Distance-dependent tree model | Model driven by light availability determined by tree position and structure.<br>Simulates silvicultural actions (thinnings), natural disturbances on the short and long-term forest dynamic |
| Coffin, D.P., 1993 | ZELIG | Gap model | Comparison of the dynamics of forested and grass areas, with extension of the dynamics in time and space |
| Courbaud, B., 1997 | – | Distance-dependent tree model | Empirical model for uneven-aged spruce forest dynamics: tree height and diameter are modelled using a potential Chapman Richards function altered by a multiplicative function of a light availability index. Non-regeneration, no mortality |
| Croc, E., 1994 | – | Distance-dependent stand model | Mosaic model to study the dynamics of the evolution of the patch composition |
| Cuprov, N.P., 1970 | – | Average tree model | Yield table |
| Daalen, J.C., van, 1989 | OUTENIQUA | Gap model | Gap model applied to tropical forest primarily to serve as a research tool integrating the present knowledge. Simulate species dynamics and impacts of management |
| Desanker, P.V., 1994 | MIOMBO | Gap model | Development of the African dry forest including drought sensitivity |
| Deusen, P.C., 1985 | – | Average tree model | – |
| Ek, A.R., 1974 | FOREST | Distance-dependent tree model | Management tool to assess silvicultural effects on forest growth and reproduction (via germination, seed production) |
| Ek, A.R., 1974 | – | Distribution model | Deterministic matrix model where probability to die or grow is a function of stand BA and density, diameter class. Ingrowth is a function of stand BA and density. No species distinction<br>Growth and dynamics over 20 years |
| Favrichon, V., 1997, 1998 | – | Distribution model | Deterministic matrix model where probability to die, grow or not are functions of BA and/or diameter/class/group species. Ingrowth is a function of BA or tree number/group species<br>Tropical management: effects of thinnings on species composition, long-term stand density or BA<br>Application of Solomon et al. (1986) |
| Fischlin, A., 1995 | FORCLIM | Gap model | Used to assess the importance of climate change on the steady state composition of the Alpin forests. Used to test the sensitivity of the model to climate parameterisation |
| Frelich, L.E., 1993 | MOSAIC | Distance-dependent stand model | Succession model used for long-term dynamics of species replacements. Interaction between patches are considered and resulted in a spatial organisation of the sub-forest mosaic |
| Fulton, M.R., 1991 | FLAM | Distribution model | Simplification from a gap model to a distribution model structured on height classes. Annual volume increment is modelled per species and height class, using a continuous function (relation to net photosynthesis). Mortality is a function of relative growth rate. Establishment is depending on a minimum light availability<br>Dynamics of temperate forest |

**Appendix (continued).**

| First author | Model name | Model type | Model description |
|---|---|---|---|
| Geldenhuys, C.J., 1997 | – | Average tree model+distribution model | Stand BA related to abiotic site factors.<br>Matrix model to project the diameter distribution of mixed forests in South Africa. Purposes are to determine the regulation of yield through timber harvest that will permit to reach a sustainable steady state |
| Gove, J.H., 1995 | – | Distribution model | Discussion on the possible use of a distribution model to optimise diameter diversity in the stands |
| Haight, R.G., 1985, 1987 | – | Distribution model | Distribution model using non-linear density-dependent regressions to model regeneration and growth<br>Used to find the optimum harvest system to maintain equilibrium in diameter distribution |
| Hanewinkel, M., 2000 | SILVA 2 | Distance-dependent tree model | Empirical model of production for all aged pure and mixed forest.<br>Growth is potential with parameters depending on ecological (nutrient, temp, water) site factors, and limitations by competition (mainly for light)<br>No regeneration |
| Hann, D.W., 1980 | – | Distribution model | Matrix model to study the forest dynamics and processes (ingrowth, growth, mortality) for uneven-age pine stands |
| Harrison, A.F., 1988 | FORTNITE | Gap model | Gap model coupled to a soil decomposition module to assess the impact of management and pollution on growth and yield |
| Hinssen, P.J.W., 1994 | HOPSY | Distribution model | Stationary Markov model: constant transition probability/species are average values coming from data<br>Designed to help decision making in management policies (thinning regime on species composition, wood production) |
| Hyink, D.M., 1983 | – | Average tree model+distribution model | Stand volume increment, ingrowth, mortality modelled with differential equations depending on tree number, sum of diameters<br>Parameters of Weibull distribution are depending on ingrowth, stem nb, sum DBH<br>Uneven-aged forest yield and distribution estimations |
| Ingram, C.D., 1995, 1996 | – | Distribution model | Application of the model of Buongiorno and Michie (1980) to a tropical forest<br>Designed for helping decision making in management: simulates the long-term effects of management on stand composition, annual income, steady state maintenance, annual yield |
| Jogiste, K., 1998 | – | Average tree model | Multivariate linear regression using a of stand BA, initial DBH age, proportion of species to estimate mean diameter growth and number of trees per tree group<br>Yield estimation with investigating the importance of percent species into total yield |
| Johnstone, W.D., 1977 | – | Average tree model | Yield table |
| Jonsson, B., 1962 | – | Average tree model | Yield table |
| Jorritsma, I.T.M., 1999 | FORGRA | Gap model | Gap model used to simulate the impact of grazing on the forest dynamics and composition |
| Kahn, M., 1997 | SILVA 2 | Distance-dependent tree model | Empirical model of production for all aged pure and mixed forest (see Pretzsch, 1992, 1998, 1999; Pretzsch and Kahn, 1996a,b).<br>Growth is potential with parameters depending on ecological (nutrient, temp, water) site factors, and limitations by competition (mainly for light)<br>No regeneration |

**Appendix (continued).**

| First author | Model name | Model type | Model description |
|---|---|---|---|
| Keane, R.E., 1989, 1990 | FIRESUM | Gap model | Gap model used to simulate the long-term succession of forest with different fire regime disturbances |
| Keane, R.E., 1996 | FIRE-BGC | Distance-independent (non gap) tree model | Combination of the mechanistic model FOREST-BGC and the gap model FIRESUM. Carbon, water, mineral cycles described, seed dispersal, establishment, growth, mortality. Different levels from tree to landscape. A lot of parameters<br>Used to study the impacts of fire on long-term forest dynamics |
| Kellomäki, S., 1992 | SIMA | Gap model | Highly mechanistic gap model, including soil water and nutrient model, growth, mortality and recruitment sensitive to environmental conditions, with light capture, photosynthesis, respiration rates, and allocation. Applied to an uneven-aged Scots pine boreal forest |
| Kellomäki, S., 1997 | FINNFOR | Distance-dependent tree model | Highly mechanistic model, including soil water and nutrient model, growth, mortality and recruitment sensitive to environmental conditions, with light capture, photosynthesis, respiration rates, and allocation. Applied to an uneven-aged Scots pine boreal forest for climate change studies |
| Kercher, J.R., 1984 | SILVA | Gap model | Long-term dynamics of a forest as disturbed by fire and $SO_2$ pollution |
| Kienast, F., 1989, 1991 | FORECE | Gap model | Long-term analysis of a forest dynamics in natural conditions, managed conditions, disturbed by storm and fire |
| Knoke, T., 1998 | SILVA 2 | Distance-dependent tree model | Empirical model of production for all aged pure and mixed forest (see Pretzsch, 1992, 1998, 1999; Pretzsch and Kahn, 1996a,b)<br>Application to estimate the harvest system to optimise DBH distribution, target tree DBH, stocking value |
| Kohler, P., 1998 | FORMIND | Distribution model | Mechanistic model for tropical forest. Simulates carbon fixation, respiration rate, tree and crown dimension per cohort (functional group × DBH class). Used to asses the impacts of logging |
| Kohyama, T., 1992, 1993 | – | Distribution model | The forest is modelled as a group of even-agreed sub-forests. Mortality, recruitment, growth of each sub-forest is modelled using a continuous distribution model using forest and sub-forest BA, tree DBH or BA, sub-forest age<br>Used to simulate long-term dynamics/species |
| Kolbe, A.E., 1999 | – | Distribution model | Deterministic matrix model: modification of Lin et al. (1996, 1998) with a site index to extend the model to larger areas<br>Applied to forest growth and species dynamics on short and long terms (500 years) |
| Kolstom, T., 1993 | – | Distribution model | Deterministic matrix model applied to management purposes (effect of thinnings, BA on sustainable harvest production) in uneven-aged Spruce stands |
| Kolstom, M., 1998 | – | Gap model | Used to analyse the diversity of boreal forests, with impacts of forest management |
| Kozlovskij, V.B., 1967 | – | Average tree model | Yield table |
| Krstanov, K.N., 1979 | – | Average tree model | Yield table |
| Krauchi, N., 1993 | FORSUM | Gap model | Gap model including a sensitivity to soil water availability. Used to assess the impact of climate change on species composition and stand biomass |
| Leemans, R., 1987, 1992 | FORSKA | Gap model | Include light interception and assimilation rates. Used to study the dynamics of stand composition and long-term succession |
| Lett, C., 1999 | – | Gap model + distance-dependent tree model | Comparison of the limitations and potential uses of a theoretical gap model and a theoretical distance-dependent tree model |

**Appendix (continued).**

| First author | Model name | Model type | Model description |
|---|---|---|---|
| Lin, C.R., 1997 | – | Distribution model | Comparison of fixed (Buongiorno and Michie, 1980) and variable parameter models (Solomon et al., 1986, 1987, 1995; Kolbe et al., 1999 Buongiorno et al., 1995, 1996 |
| Lin, C.R., 1996, 1998 | – | Distribution model | Matrix model involving harvest and net present values, distance dependent<br>Radial growth, mortality, ingrowth/diameter class<br>No species distinction |
| Lindner, M., 2000 | FORSKA-M | Gap model | A modified version of FORSKA (Prentice and Leemans, 1990) to include a description of the soil compartment different height increment model. Applied to assess the impact of climate change on forest management in mixed forest in East Germany. |
| Liu, J.G., 1998 | FORMOSAIC | Distance-dependent tree model | Empirical model with different structure levels: trees in cells, in a forest, in a landscape, mostly for recruitment. Growth and mortality based on stand BA, tree DBH, distance to watered areas etc.<br>Applied to forest dynamics and species diversity in tropical forest |
| Lynch, 1986 | – | Average tree model + distribution model | Stand BA, diameter, nb trees/species using differential equations depending on initial BA or sum of diameters and density<br>Parameters of a Weibull distribution are fitted on data and expressed as a function of BA sum DBH/species<br>Prediction of yield per species and distribution |
| MacLeod, W.K., 1955 | – | Average tree model | Yield table |
| Magin, R., 1957 | – | Average tree model | Yield table |
| Matsui, Z., 1959 | – | Average tree model | Yield table |
| McLeish, M., 1999 | SYMFOR | Distance-dependent tree model | Empirical model for tropical forest growth with effects of forest management. Includes recruitment and mortality (probabilities) and a deterministic DBH increment model with spatial competition indices |
| McTague, J.P., 1995 | – | Distance-independent (non gap) tree model | Individual radial growth model, adjusted to match a stand level model of BA, and species proportion model. Not always distinction between species<br>Management purposes |
| Miles, C., 1985 | – | Distribution model | Markov model of stand succession (uses probability that a tree from one species be replaced by another one) |
| Miller, C., 1999 | ZELIG + fire model | Gap model | Gap model coupled to a fuel and fire occurrence model to simulate the interactions between fire, climate and forest structure |
| Mohren, G.M.J., 1991 | ZELIG<br>+ FORECE | Gap model | Simulate the natural development of different forest mixtures on sandy soils. Used for management decision making |
| Monserud, 1997 | PROGNAUS | Distance-independent (non gap) tree model | Adaptation of PROGNOSIS (Wykoff et al., 1982) to Austria. Empirical model of growth, with recruitment, mortality, individual growth with stand level competition |
| Moravie, M.A., 1997 | – | Distance-dependent tree model | Theoretical model: forest dynamics depends on competitive development of canopy, mostly in circular structures. Partly empirical fittings, partly theoretical<br>Applied to canopy dynamics in tropical forest |
| Moser, 1969, 1972 | – | Average tree model | BA, cumulated volume using differential equations depending on initial BA and time elapsed from initial step till now<br>No species distinction<br>Prediction of yield for the whole stand |
| Mulloy, G.A., 1947 | – | Average tree model | Yield table |
| Nakashizuka, T., 1991, 1995 | – | Distribution model | Matrix model with constant probabilities to study the long-term dynamics of different types of species in the stand |
| Nilsson, N.E., 1961 | – | Average tree model | Yield table |
| Ojo, L.O., 1991 | – | Distribution model | Matrix model use to predict the future species composition of tropical forests |

**Appendix (continued).**

| First author | Model name | Model type | Model description |
|---|---|---|---|
| Osho, J.S.A., 1991, 1997 | – | Average tree model + distribution models | Compares a Weibull distribution model and a matrix model. Comparison with a regression average tree model on estimating total BA<br>Management purposes for tropical forests |
| Pacala, S.W., 1993, 1995, 1996 | SORTIE | Distance-dependent tree model | Empirical model where growth, recruitment, mortality are depending on distance to neighbours, light availability depending on neighbour crowns and on tree DBH<br>Used to simulate long-term dynamics (species composition BA) of temperate mixtures |
| Payandeh, B., 1986, 1996 | – | Average tree model | Prediction of yield per species in mixtures |
| Phillips, P., 2000 | SYMFOR | Distance-dependent tree model | Empirical model for tropical forest growth with effects of forest management. Includes recruitment and mortality (probabilities) and a deterministic DBH increment model with spatial competition indices |
| Poker, J., 1993 | – | Distance-independent (non gap) tree model | Individual based model to study stand development, mosaics, and floristic composition. Designed for mid-term forest dynamics study (response to felling, relation structure–growth rates) in tropical forest |
| Post, W.M., 1996 | LINKAGES | Gap model | Interactions between climate change, global carbon cycle, stand composition and structure |
| Prentice, I.C., 1990 | FORSKA | Gap model | Include light interception and assimilation rates. Used to study the dynamics of stand composition and long-term succession |
| Pretzsch, H., 1992, 1995, 1996, 1998 | SILVA 2 | Distance-dependent tree model | Empirical model of production for all aged pure and mixed forest. Growth is potential with parameters depending on ecological (nutrient, temp, water) site factors, and limitations by competition (mainly for light)<br>No regeneration |
| Prudov, B., 1984 | – | Average tree model | Yield table |
| Puettmann, 1992 | – | Average tree model | Stand density model diagram: graphical representation of the link between BA, density, species proportions<br>Management purposes, predicting yield with effects of density species composition |
| Pukkala, T., 1994, 1998 | – | Distance-dependent tree model | Empirical spatial individual tree growth model. Model radial increment/species every 5 years, height, mortality (or not, 1994) with regressions depending on tree dimensions, competition indexes, stand BA or height. No regeneration<br>Production and management purposes: the impact of mixtures, thinnings, stand spatial disposition (distance between trees) on yield or income (1998) |
| Riéra, B., 1998 | – | Distance-dependent stand model | The forest is described in cohorts defined by tree DBH and the forest development stage. A transition model permits to simulate the evolution of the forest mosaic |
| Sanquetta, C.R., 1996 | – | Distribution model | Transitional matrix model predicting growth and yield for decision making in management (effects of thinning regimes) |
| Schulte, B.J., 1998 | SOUTH-PRO | Distribution model | Deterministic matrix model: application of Lin et al. (1998)<br>Purposes of helping in management decision making: simulate impacts of management on productivity, diversity, income |
| Shao, G.F., 1994, 1996 | KOPIDE | Gap model | Investigate forest dynamics and succession after disturbances like harvesting, linked to a G.I.S. to predict forest dynamics at the landscape level. Used to assess the impacts of climate change |
| Shugart, H.H., 1977 | FORET | Gap model | Long-term (1000 years) development of a forest. |
| Shugart, H.H., 1980 | KIAMBRAM | Gap model | Short-term (30 years) impacts of logging on a tropical forest |
| Siekierski, K., 1991 | – | Distance-independent (non gap) tree model | Empirical model including growth, recruitment, mortality, for management purposes (effects of thinnings) in Poland |
| Singh, 1982, 1983 | – | Average tree model | Yield table |

**Appendix (continued).**

| First author | Model name | Model type | Model description |
|---|---|---|---|
| Smith, D.J., 1996 | – | Average tree model | Stand density diagram model. Management purpose: to describe effects of silviculture on stand development |
| Smith, T.M., 1988 | ZELIG | Gap model | Long-term (750 years) succession model |
| Solomon, D.S., 1986, 1987, 1995 | FIBER 3.0 | Distribution model | Deterministic matrix model where processes are linear function of BA and mean class diameter<br>Predicting yield, management effect (density, thinnings, species composition, harvest intervals) |
| Solomon, A.M., 1992 | FORENA | Gap model | Long-term gap model develop on data from 10 000 year-old climate data and used to simulate the forest dynamics under post-glacial, actual and future global climate conditions |
| Sterba, H., 1998 | PROGNAUS | Distance-independent (non gap) tree model | Application of the model PROGNAUS: simulation of forest growth and comparison to an independent dataset |
| Talkkari, A., 1996, 1999 | SIMA | Gap model | Modification of Kellomäki et al.'s model SIMA. Highly mechanistic gap model coupled to a soil model used to assess the impacts of climate change on boreal forest growth |
| Turner, B.J., 1966 | – | Average tree model | Empirical model using regressions fitted on data to estimate BA and volume increment of recruits and non-recruits.<br>Yield and production prediction for uneven-aged mixture with 80% Eucalypts |
| Ung, C.H., 1982 | – | Average tree model | Prediction of yield for the whole stand<br>Application of Moser (1972) to Canadian mixed forests |
| Urban, D.L., 1991 | ZELIG | Gap model | Extension of the gap models to the landscape level |
| Vanclay, 1989 | – | Distribution model | Cohort model where radial growth, Ingrowth, mortality/species group are modelled using continuous regression<br>Prediction of yield for tropical forest |
| Vettenranta, J., 1999 | – | Distance-dependent tree model | Close to Pukkala model. Empirical regressions on tree and stand dimensions, competition index based on tree height. No regeneration<br>Production and management purposes: the impact of mixtures, thinnings, stand spatial disposition (distance between trees) |
| Virgilietti, P., 1997, 1998 | – | Distribution model | Matrix model: short-term growth and long-term dynamics. Done for management purposes in uneven-aged and mixed mountain forest. |
| Volin, V.C., 1996 | – | Distribution model | Matrix model: long-term effects of management regimes (amount and dimension of the harvested trees, maintenance of a species) on BA, species composition, harvest income. Dynamics |
| Waldrop, T.A., 1986 | FORCAT | Gap model | Used to simulate impacts of clear cutting on forest development. Problems in estimating the young stages |
| Walker, J., 1986 | – | Distribution model | Markov model which includes competition for nutrients, light, and water into a growth parameter. Purposes: effects of competition on growth rates and regeneration in a semi-arid woodland (Australia) |
| Wiedemann, E., 1949 | - | Average tree model | Yield table |
| Williams, M., 1996 | ARCADIA | Distance-dependent tree model | Process based model (light intercept, photosynthesis, partitioning, etc.) with environmental effects, competition for resource (light)<br>Used for long-term (1200 years) dynamics (BA, LAI, /species). Impacts of tree structure, light environment |
| Wimberly, M.C., 1996 | – | Distance-independent (non gap) tree model<br>+ distance-dependent tree model | Comparison of a distance-dependent and distance-independent tree models. Competition is spatial or not, and concludes to no improvement of distance dependency |
| Wissel, C., 1992 | – | Distance-dependent stand model | Evolution of a spatial mosaic of beech at different developmental stages, as influenced by the neighbours through light availability |
| Wykoff, W.R., 1982 | PROGNOSIS | Distance-independent (non gap) tree model | Empirical model of growth, with recruitment, mortality, individual growth with stand level competition |
| Yan, X.D., 1996 | NEWCOP | Gap model | Response of the forest growth and the landscape structure to climate change |
| Yu, Z.Z., 1989, 1998 | – | Distribution model | Matrix model for yield purposes. Applied to determine the optimal values of growing stock, diameter distribution and economical income according to the cutting cycle length, species composition (mixed broadleaves, China) |

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