9: Models for Pure and Mixed Forests

HANS PRETZSCH

9.1 INTRODUCTION

The previous chapter showed how forest growth is the sum of their species interactions with environment as mediated through physiological processes, and the dynamic nature of the responses of trees and stands. Long before forest scientists understood even some of the more basic processes governing the way trees grow, considerable empirical knowledge had accumulated through observation to quantify tree growth. While based on observation and not first causes, it is no less a contribution to understanding how trees grow and what affects them by looking at the way they respond in the 'field' or more properly the 'forest'!

This chapter reviews our understanding of tree and forest stand behaviour gained from empiricism (what has been observed), through quantifying systematically such observations (the yield table) to process-based modelling of both pure and mixed forest stands. For a deeper understanding of the introduced model types, the bibliography offers the most important references. A model's objective and existing knowledge about the observed system determine how complex the model approach has to be. Single-tree models, ecophysiological-based gap models and hybrid models are of particular interest for forest management as they are suitable across many stand types and forest conditions.

Forest growth models aggregate knowledge of individual processes of forest growth to predict stand or whole system functioning. Forest ecosystems may be modelled with varying degrees of temporal and spatial resolution. The time-scale may range from seconds to millenia, while the

spatial scale may encompass anything from cells and mineral surfaces to continents (Fig. 9.1). The slow processes on large spatial scales fix the boundary for quicker processes on smaller scales. Conversely, the rapid and spatially bounded processes determine the processes on higher levels. Model approaches that take into consideration these feedback loops between the different system levels can provide important contributions to system understanding as well as to management decision support. At our present state of system knowledge, single-tree and stand models, which model processes on temporal scales from a year to a century and on spatial scales from tree to stand level, best fullfil the demands of forest management. They model the stand dynamic on the basis of the classical growth and yield variables, like diameter, height, crown length, etc. Process models have a higher spatial and temporal resolution and approximate to the classical variables by scaling-up. However, the behaviour of the whole system can be more than the sum of the underlying processes. Forest sucession and biome shift models become an important tool for global change research in forest ecosystems.

9.2 PATTERNS AND DYNAMICS OF GROWTH: EMPIRICAL OBSERVATIONS

9.2.1 Periodicity and pattern in individual tree growth

Tree growth is periodic over short time-spans and follows a definite pattern in the long term. In temperate countries growth is overwhelmingly determined by the season, with growth confined to a period of a few weeks to perhaps several months

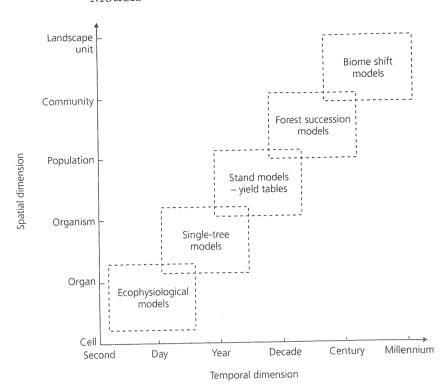


Fig. 9.1 Spatial and temporal dimensions of processes in forest ecosystems and models with increasing aggregation from ecophysiological models to biome shift models.

in any one year while warmth and moisture are adequate. Even in the moist tropics, with year-round favourable growing conditions, trees show periodicity under a measure of genetic control as recorded, for example, from measurements of multinodal tropical pines such as *Pinus caribaea* (Chudnoff & Geary 1973) and fast-growing hardwoods such as *Cordia alliodora* (Blake *et al.* 1976).

As well as periodicity in one year, trees exhibit a strong pattern of growth during their life. In relation to age the pattern is typically sigmoid, whether recording total height, diameter or volume over time.

9.2.2 Dynamics of stand growth

The dynamic nature of stand growth is a little less obvious than for a single tree, since superficially a stand seems to be a collection of individual trees the relations of which appear constant. That this is not so is seen by considering a small tree in a mature even-aged stand. At regeneration (or planting) this small tree will have been about the same size as its neighbours but subsequently will

have competed less successfully for light, nutrients or moisture to become inferior to its neighbours. As a stand develops any apparent uniformity disappears, with some trees developing vigorously and neighbours becoming suppressed, moribund and even dying. Thus the stand is continually changing – it is dynamic. It is not only a collection of individual trees, each with its own genetic potential for using the site, but also a collection of trees that interact and compete with one another.

Seedlings and regeneration

From the outset trees appear to grow at different rates. Even in new plantations of well-spaced trees of one species, and long before onset of between-tree competition, the growth of individual trees is not identical. Moreover, there is often no correlation between initial postgermination vigour and subsequent growth rate. Small seedlings, or plants from the forest nursery, do not necessarily lead to small slow-growing trees (see illustration of this for young *Pinus caribaea* in Evans 1992, p. 221).

Between-tree competition

As trees grow they eventually begin to compete with their neighbours. This has both an aboveground component, mainly competition for light, and a below-ground element in terms of root competition for nutrients and moisture. Such competition is most readily seen in suppression of side branches on the lower crown and a measurable impact on diameter increment. The timing of the onset of between-tree competition depends on distance between trees, but is usually first measurable in forest stands from about the time of canopy closure. The principal exception is in arid climates where competition between root systems for moisture greatly exceeds that for light, and trees and shrubs remain widely dispersed and rarely in contact above ground.

Differentiation into crown classes

As competition begins, growth of some trees slows more than others. These tend to be the smaller trees at the time of canopy closure and the competition reinforces their inferior status. Once dominated, few trees can recover unless a gap develops owing to death of a neighbour. Thus as a stand develops, a range of tree sizes emerges and, traditionally, these are classified into different crown classes according to the tree's relative position in the canopy.

9.2.3 Interventions and manipulations

These empirical relationships of how trees are observed to grow and how they develop and interact in a stand provide the basis for manipulating their behaviour. Adjusting spacing between trees, both when planted or through thinnings, or influencing the balance of a mix of species in a stand all impact on how a stand develops, on how the increment is distributed and hence on the composition of tree types, trees sizes and the total of woody growth that will result.

In summary, densely stocked forest leads to high volumes per unit area but small mean tree size compared with less well-stocked forest on a similar site and of the same age. In the latter case there will be fewer but larger diameter trees, although total volume of timber may be somewhat reduced. This allows forests to be managed in different ways to yield different assortments of products. How to model these relationships and outcomes in detail, beyond the purely empirical, forms the bulk of this chapter.

9.3 GROWTH MODELS

The history of forest growth models is not simply characterized by the development of continuously improved models replacing former inferior ones. Instead, different model types with diverse objectives and concepts were developed simultaneously. The objectives and structure of a model reflect the state of the respective research area at its time and document the contemporary approach to forest growth prediction. The history of growth modelling thus also documents the advancement of knowledge in the science of forest growth.

Beginning with yield tables for large regions as a basis for taxation and planning (such as those by Schwappach 1893 and Wiedemann 1932, 1939a,b, 1942), model development led to regional yield tables and site-specific yield tables and culminated in the construction of growth simulators for the evaluation of stand development under different management schemes. Vanclay (1994) provided an overview about growth and yield management models and their application to mixed tropical forests. The 1980s brought a new trend with the development of ecophysiological models, which give insight into the complex causal relationships in forest growth and predict growth processes under various ecological conditions. The emphasis in model research has shifted towards ecophysiological models and away from models aimed only at providing growth and yield information for forest management. These models attempt to simulate forest growth on the basis of fundamental ecophysiological processes. The scientific value of ecophysiological models cannot be overrated; however, they will not be applied in forest management for the next few years as they are in many ways not yet sufficiently validated. Also, input and output variables do not yet meet the demand of forest management practice.

A major change has taken place in model conception, i.e. the understanding of forest growth on which the model is based. The tables by Weise (1880), Schwappach and Wiedemann resulted from a purely descriptive analysis of sample area data in the form of total and mean values of observed processes of stand development. These descriptions were later combined with theoretical model concepts that also considered natural growth relationships and causal relations as far as they were known at the time. For example, yield tables for mixed stands of pine and beech created by Bonnemann (1939) characterize growth of beech in the middle and lower storey by mean values. The FOREST model of Ek and Monserud (1974) controls increment behaviour of lowerstorey trees by geometrical competition indices, and the ecophysiological growth models of Bossel (1994), Mäkelä and Hari (1986) and Mohren (1987) derive increment behaviour of lower-storey trees from light availability and performance in terms of photosynthesis.

The change in model objectives and concepts is closely related to a change in quality of the information generated. Pure management models aim at reliable prediction of forest yield values that are crucial for planning and control in forest management, e.g. height and diameter increment and associated economic value. Ecophysiological models aim at biomass development, nutrient input and loss, etc.; variables relevant to forest management are only of secondary importance in these models. For future planning in modern forestry, models meeting the information de-

mands of ecology as well as of economy will gain in importance.

Ecophysiological models and stand management models can give specific decision support (Fig. 9.2). Ecological and socioeconomic conditions define the framework and thus the 'foundations' for management decisions. Ecophysiological models can support the ecological elements of the framework, for example the effect of site conditions, species mixture and thinning variants on critical loads, water quality or acidification. Stand treatments of interest can be judged in this way as ecologically acceptable or unacceptable. Management models help to optimize the path from starting point to objective via the given framework, for example they support the decision between different thinning and pruning strategies.

With the shift from tree and stand management models with low resolution to more complex ecophysiological models, different source data are needed for model construction and for the determination of model parameters. Standard datasets derived from research sample plots (diameter, height, etc.) were used for the development of stand growth models for applied forestry. For the construction of single-tree models, additional data are required (crown dimension, tree position, etc.). The transition to ecophysiological models requires an additional database that can only be provided by broadening experimental concepts and cooperation with neighbouring disciplines.

Models are always an abstraction of reality and

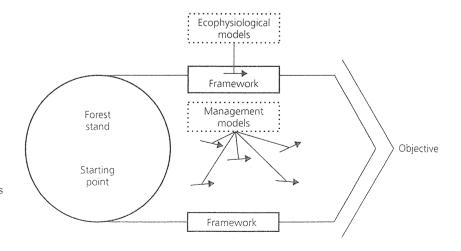


Fig. 9.2 Stand management models and ecophysiological models for decision support in forest ecosystem management.

are greatly influenced by the modeller's knowledge and perception of nature. This applies to the construction of yield tables as well as for ecophysiological models.

9.3.1 Stand growth models based on mean stand variables

With a history of over 250 years, yield tables for pure stands may be considered the oldest growth models in forestry science and forest management. They are representations of stand growth within defined rotation periods and are based on a series of measurements of diameter, height, biomass, etc. reaching far back into the past. From the late eighteenth to the middle of the nineteenth century, German scientists such as Paulsen (1795), von Cotta (1821), R. Hartig (1868), Th. Hartig (1847), G.L. Hartig (1795), Heyer (1852), Hundeshagen (1825) and Judeich (1871)

created the first generation of yield tables based on a restricted dataset. These original yield tables soon revealed great gaps in scientific knowledge. A series of long-term data-collection campaigns on experimental areas was therefore started. This was the birth of a unique network of long-term experimental plots in Europe that is still under survey. The old British yield table for Scots pine is shown as Fig. 9.3.

The second generation of yield tables, initiated towards the end of the nineteenth century and continued into the 1950s, follows uniform construction principles proposed by the Association of Forestry Research Stations (the predecessor organization of the International Union of Forest Research Organizations (IUFRO)), in 1874 and 1888 and has a solid empirical basis. The list of protagonists involved in this work includes Weise (1880), von Guttenberg (1915), Zimmerle (1952), Vanselow (1951), Krenn (1946), Grundner (1913)

Scots Pine Normal yield table: yield class 160

	Main crop after thinning							Yield from thinnings						Total production		Increment		
Age (years)	Number of	Top height	Mean BHQG	Basal area	Vol. (h. ft.) to diameter o.b.			Number of	Mean BHQG	Av. vol. per tree	Vol. (h. ft.) to top diameter o.b. of			Basal area	Vol. to 3 in.	CAI		MAI
	trees	(feet)	(in.)	sq. ft q. g.	3 in.	7 in.	9 in.	trees	(in.)	h. ft.	3 in.	7 in.	9 in.	sq. ft q. g.	h. ft.	Basal area	Vol. to 3 in.	Vol. to 3 in.
15 20	1650 765	27.5 36.0	2.75 3.5	86 65	750 1020	_	_	- 885	- 3.0	0.80	- 480	_	_	86 122	750 1500	7.3 [®] 7.2	130 168	50 75
25 30 35 40	478 333 250 199	44.0 51.0 57.5 63.5	4.75 6.0 7.25 8.5	71 80 90 100	1380 1830 2330 2840	120 610 1500 2350	- 95 580 1420	287 145 83 51	4.0 5.0 6.25 7.5	1.95 3.86 6.74 11.00	560 560 560 560	10 80 240 385	- 50 170	158 192 224 254	2420 3430 4490 5560	7.0 6.7 6.3 5.8	194 208 213 214	97 114 128 139
45 50 55 60	166 142 125 112	69.0 74.5 79.0 83.5	9.75 110.0 12.25 13.5	110 119 128 135	3350 3820 4255 4685	3590 4095	2270 3020 3650 4290	33 24 17 13	8.75 10.0 11.25 12.25	16.7 23.0 30.6 38.0	560 560 535 490	470 510 500 470	290 400 440 430	282 308 331 352	6630 7660 8630 9550	5.3 4.9 4.5 4.0	210 201 189 177	147 153 157 159
65 70 75 80	102 94 88 83	87.0 90.5 93.5 96.0	14.25 15.0 15.75 16.25	142 147 152 156	5455 5790	5310 5650	4650 5050 5390 5700	10 8 6 5	13.5 14.5 15.25 16.0	46.2 54.3 62.4 70.0	450 410 370 330	435 395 360 320	410 375 340 310	371 388 403 416	10400 11180 11885 12520	3.6 3.2 2.8 2.4	163 149 134 120	160 160 159 157
85 90 95 100	79 76 73 71	98.0 100.0 101.5 103.0	17.0 17.5 18.0 18.5	159 162 165 167	6805	6480 6680	5980 6220 6410 6580	4 3 3 2	16.5 17.0 17.25 18.0	77.2 83.6 88.6 94.5	295 260 225 195	275 240 210 180	275 240 210 180	427 437 446 453	13085 13580 14010 14370	2.1 1.8 1.5 1.3	106 92 79 68	154 151 147 144

Fig. 9.3 Facsimile of normal yield table of Scots pine used in the 1960s. Normal yield tables model the development of fully stocked stands on the basis of mean stand variables, e.g. number of trees per acre, mean diameter at breast height or basal area per acre. (From Bradley *et al.* 1966.) (Uses traditional (Imperial) measures.)

and, in particular, Schwappach (1893), Wiedemann (1932) and Schober (1967), who designed yield tables that were conceptually related and is still being used to this day. A brilliant example of their work is the yield tables for European beech. In the 1930s and 1940s the first models of mixed stands were contructed under the direction of Wiedemann. Data from some 200 experimental areas established by the Prussian Research Station led to the yield tables for even-aged mixed stands of pine and beech (Bonnemann 1939), spruce and beech (Wiedemann 1942), pine and spruce (Christmann 1949), and oak and beech (Wiedemann 1939a). The Second World War prevented Wiedemann from bringing the development of yield tables for uneven-aged pure and mixed stands to an end, but his studies initiated systematic research on mixed stands. Yield tables for mixed stands of this generation were never consistently used in forestry practice as they were restricted to specific site conditions, intermingling patterns and age structures.

Yield tables developed by Gehrhardt (1909, 1923) in the 1920s effected a transition from purely empirical models to models based on theoretical principles and biometric formulae and led to a third generation of yield tables. These models were designed by, among others, Assmann and Franz (1963), Hamilton and Christie (1973, 1974), Vuokila (1966), Schmidt (1971) and Lembcke et al. (1975), and at their core is a flexible system of functional equations. These functional equations are based as far as possible on natural growth relationships and are generally parameterized by means of statistical methods. The biometric models are usually transferred into computer programs and predict expected stand development for different spectra of yield and site classes. A wealth of data were available for the construction of these models and processed with modern statistical methods.

Since the 1960s a fourth generation of yield table models has been created, i.e. the stand growth simulations of Franz (1968), Hoyer (1975), Hradetzky (1972), Bruce et al. (1977) and Curtis et al. (1981, 1982), which simulate expected stand development under given growth conditions for different stem numbers at stand establishment and for different tending regimes. They describe

stand development at different sites and for varying treatments and varying numbers of trees at the time of establishment. Expected stand development under given growth conditions is simulated by means of computer programs and controlled by systems of suitable functions forming the core of the growth simulator. All information available on forest growth is synthesized into a complex biometric model that simulates stand development for a wide range of possible management alternatives and summarizes the results in tabular form similar to yield tables. These yield tables reflect the stand dynamic for a wide range of imaginable management scenarios. While table and model were identical for the yield tables of earlier generations. simulator-created yield tables now describe just one of many potentially computable stand development courses.

Despite a number of drawbacks, yield tables still form the backbone of sustainable forest management planning. When computing capacities and available data for model construction increased and with the rising demand for information in forestry, mean-value and sum-orientated growth models and yield tables were increasingly replaced by stand-orientated growth models, predicting stem number frequencies, and by single-tree growth models. Prodan (1965, p. 605) commented on the significance of yield tables in the context of silviculture and forest sciences: 'Undoubtedly, yield tables are still the most colossal positive advance achieved in forest science research. The realization that yield tables may no longer be used in the future except for more or less comparative purposes in no way detracts from this achievement'.

9.3.2 Stand-orientated management models predicting stem number frequency

With the transition towards new intensive treatment concepts, the demand for information in forestry has changed the emphasis from mean stand values towards single-tree dimensions of selected parts of a stand. This changed demand for information resulted in the 1960s in the creation of the first growth models, which enabled prediction of mean stand values as well as frequencies of

216 Chapter 9

single-tree dimensions. Until then, a stand served as the usual information unit on which all predictions were based; these predictions were now strengthened by statements about stem number frequencies in diameter classes (Fig. 9.4), which are needed for precise prediction of assortment yield and value of a stand. Depending on their concept and construction, stand-orientated growth models predicting stem number frequency are classified into differential equation models, distribution prediction models and stochastic evolution models.

Many natural processes in various disciplines of the natural sciences can be described by differential equations. Examples are the differential equations formulating change of yield descriptors for diameter classes of a stand, i.e. change of stem number, basal area and growing stock, depending on current yield state values. Stand development then results from the numerical solution of the differential equations. In the 1960s and 1970s, Buckman (1962), Clutter (1963), Leary (1970), Moser (1972, 1974) and Pienaar and Turnbull (1973) developed stand-orientated growth models based on differential equations.

In the mid 1960s, Clutter and Bennett (1965) proposed a completely new approach to stand growth modelling. They characterized the condi-

tion of a tree population by its diameter and height distribution and described stand development by extrapolation of these frequency distributions. The precision of such models is decisively determined by the flexibility of the distribution type on which it is based. The suitability of different distribution types, for example beta, gamma, lognormal, Weibull or Johnson, has to be assessed individually. Compared with those reviewed earlier, in these models stand development is not controlled by the age function of the individual yield descriptors but by the parameters of the underlying frequency distribution. Models of this type were initially constructed by Clutter and Bennett for North American spruce stands and further developed by McGee and Della-Bianca (1967), Burkhart and Strub (1974), Bailey (1973) and Feduccia et al. (1979).

The term 'evolution models' for stochastic growth models is derived from the fact that in these models stand development evolves from an initial frequency distribution, for example from a diameter distribution known from forest inventory. Thus these models, like distribution prediction models, predict frequencies of single-stem dimensions (see Fig. 9.4). However, the mechanism accounting for the extrapolation is based on a Markov process, giving the transition probabil-

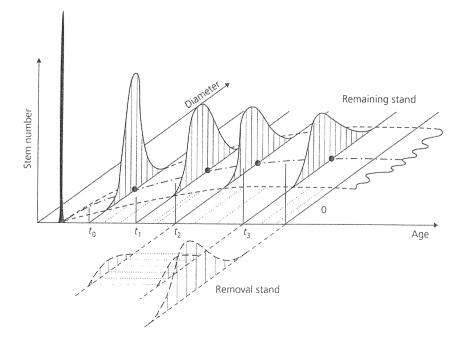


Fig. 9.4 Principle of management models predicting the shift of the diameter or height distribution along the time-axis. (After Sloboda 1976.)

ity for the shift between the diameter classes. Stochastic growth models were introduced to forestry science with the pioneering investigations by Suzuki (1971, 1983), and they continue to be linked to his name today. His growth models, for Japanese Chamaecyparis pure stands for example, have been consistently developed by Sloboda (1976) and his team since the mid 1970s: they are mainly interested in adapting the models, which are orientated to Japanese conditions, to the issues of German forestry and in model validation based on permanent test plot data. Stand-orientated growth models based on stochastic processes have been developed by Bruner and Moser (1973) and Stephens and Waggoner (1970) also for mixed stands.

9.3.3 Single-tree orientated management models

Single-tree models describe the stand as a mosaic of single trees and model individual growth and interactions with or without consideration of tree position. This has paved the way for the design of models of pure and mixed stands of all age structures and intermingling patterns. An equation system that controls growth behaviour of single trees depending on their constellation within the stand is the central module of all single-tree Position-independent or positionmodels. dependent competition indices are used to quantify the spatial growth constellation of each tree and to predict its increment of height, diameter, etc. in the following period. Compared with stand-orientated growth models based on mean stand descriptors and those predicting stem number frequencies, single-tree models work on higher resolution. The information unit in singletree models is the individual tree. However, results of lower-resolution models, for example mean tree development or diameter frequency distributions, can also be derived from single-tree model results by integration. Information about stand growth then results from summarizing and aggregating each individual single-tree development for a given growth period. Recent single-tree models are programmed to enable the user to influence a simulation run interactively. This allows stand development to be followed step by step during the simulation and permits the user to

specify other factors (e.g. thinning or influence of disturbance) at any time during the simulation process, thus influencing or diverting the current course of stand development.

After parameters for the control of the singletree model have been set, tree characteristics at the beginning of the prediction phase for the test area to be investigated are fed into the computer as initial values for the simulation (Fig. 9.5). This tree list can contain data on tree species, stem dimensions, crown morphology, stem position and other data about the stand individuals. These data usually originate from single-treebased inventories of indicator plots. Starting with these initial values, change (e.g. mortality or development of diameter, height or crowns) for all stand members depending on individual growth conditions is predicted using an appropriate control function; this is done for a first growth period, for example 5 years. Once the tree list has been processed, change of growth conditions (e.g. due to thinning or disturbance) can be specified prior to continuing to the next increment period. This will now influence single-tree growth in the following period. The modified state values of all trees resulting at the end of the first growth period also represent the initial values for the second growth period. These values are repeatedly extrapolated in every simulation cycle and interim results are given. The simulation continues until the envisaged prediction period has been completed step by step. In most models, time steps are 5 years, sometimes only 1 or 2 years. By removing single trees during a simulation run, the growth constellation and growth behaviour of the remaining individuals change in the next growth period. Growth reaction of the stand is thus explained by the reactions of all single trees to this intervention. By relating stand development back to growth behaviour of single trees and by modelling single-tree dynamics depending on growth constellation within the stand, single-tree models, after being initialized accordingly, enable evaluation of a wide range of treatment programs.

The first single-tree model was developed for pure Douglas fir stands by Newnham (1964). It was followed by the development of models for pure stands by Arney (1972), Bella (1970)

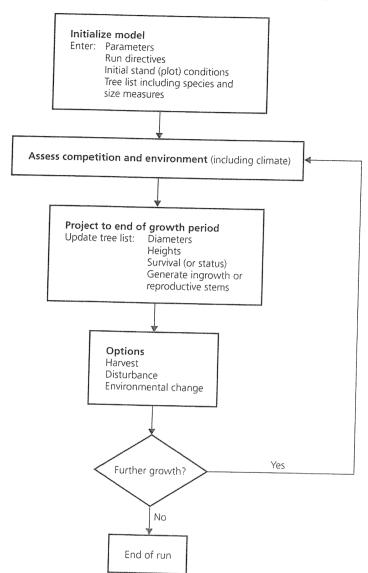


Fig. 9.5 Flow chart of single-tree models. (After Ek & Dudek 1980.)

and Mitchell (1969, 1975) and colleagues. In the mid 1970s, Ek and Monserud applied the construction principles for single-tree orientated growth models for pure stands to uneven-aged pure and mixed stands (Ek & Monserud 1974; Monserud 1975). Munro (1974) distinguished distance-dependent and distance-independent single-tree models, the former being able to refer to data about stem position and stem distance for the control of single-tree growth. The worldwide bibliography of single-tree growth models compiled by Ek and Dudek (1980) lists

more than 40 different single-tree models, which are grouped into 20 distance-dependent and 20 distance-independent models. Single-tree models developed since the 1980s (Wykoff et al. 1982; van Deusen & Biging 1985; Wensel & Koehler 1985; Pretzsch 1992, 1998, 1999; Sterba et al. 1995; Nagel 1996) in many ways go back to the methodological bases of their predecessors; however, owing to the rapidly improving technology of modern computers they are far more user-friendly than older single-tree models.

9.3.4 Ecophysiological growth models

All the models mentioned above rely on growth and yield data from long-term observation plots and hence have the advantage of being validated empirically. However, there is a drawback to historically deduced data in as much as growth conditions undergo changes, and reaction patterns from the past cannot simply be projected into the future. In the 1970s, model research was pointed in a new direction with the creation of high-resolution ecophysiological process models, which account for metabolism, organ formation, assimilation and respiration as well as biochemical and soil chemistry reactions. Pioneers of the ecophysiological process model for forest stands are Bossel (1994), Mäkelä & Hari (1986) and Mohren (1987). The term 'process model' is slightly misleading in the sense that all forest growth models describe processes. Only the temporal and spatial scales of modelled processes become more detailed and accurate in the transition from yield table models via single-tree management models and succession models to growth models based on ecophysiological data (see Fig. 9.1).

The development of modern process models begins with a systems analysis and the selection of characteristic system components. A system to be analysed and modelled is first described using methods of systems analysis. Results of this description can be transferred into a system diagram (Fig. 9.6). The description breaks the system down into system components characteristic for all biological systems and identified by different symbols in the system diagram. By system parameters we mean those that remain constant during the lifetime of the system. Exogenous parameters are variables that control the system but which cannot be influenced by the system, e.g. stress caused by air pollutants. State variables are the actual output value of the model; their current values reflect the system's state. Important state variables in stand models are accumulated carbon quantities in needles, branches, stem and roots. The initial values of the state variables give the starting values of a system and thus crucially influence its further development. In a growth model for example, stem number and initial stand structure have to be specified as initial values. The rate of change of the state variables controls change, i.e. input and output of state variables. Examples are mortality rates or respiration rates, which control the change of the carbon quantities accumulated in the different components. Intermediary variables change simultaneously with the state variables and feed back into the system. The system components are indicated in the system diagram with different symbols and their interrelations are identified by arrows.

The model thus outlined is transferred into a mathematical model and subsequently into a computer program. For this, the system components and links are described by mathematical or logical relationships. Once the complete model is constructed, the causal relations implemented are parameterized. The system behaviour can be simulated with the developed computer programs. All suitable information known about the system is therefore consolidated in the system components and the system structure. The process of system analysis and model development concludes in the validation of the final model. For validation, i.e. testing if the causal relations assumed in the model realistically reflect growth of stands or single trees, empirical yield data can be used. If necessary, individual model assumptions are corrected or model parts revised.

A vastly improved understanding of ecophysiological processes in forest ecosystems paved the way for this model approach and it was the actual modelling of these processes that provided an idea of the functioning of the overall system. A further impetus to process model development was the need to understand and predict the reactions of forest ecosystems to an increasing number of adverse effects, such as industrial emissions, rise in atmospheric CO2 and climate change. In the context of environmental instability, highresolution and accurately detailed process models are certainly the ideal approach for understanding and predicting forest ecosystem behaviour. However, there are particular constraints in developing and applying process models due to considerable gaps in our knowledge of part processes in assimilation organs and in the soil.

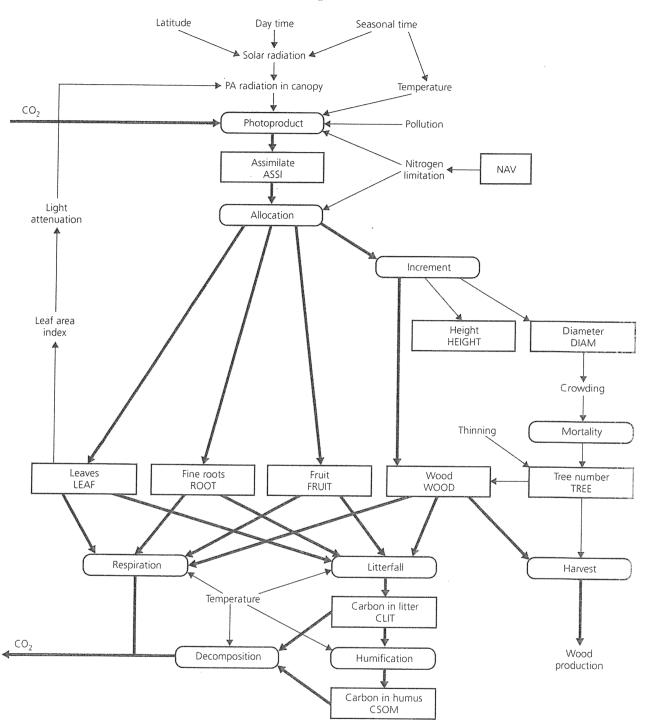


Fig. 9.6 Carbon flow (heavy arrows) in the TREEDYN3 forest simulation model, with the most important state variables, processes and flows indicated by boxes, ovals and arrows respectively. (After Bossel 1994.)

Also, the scaling-up of part processes to the behaviour of the overall system is still largely unresolved. Moreover, the introduction of process models still requires intensive research and extremely high-powered computers that are only rarely available in practice. To date, process models are therefore primarily research instruments rather than forest management planning tools.

9.3.5 Gap models and biome shift models

In the view of modern theoretical ecology, a spatially extensive system is composed of mosaiclike subunits and can be studied by analysing these subunits. Watt (1925, 1947), Bormann and Likens (1979) and others transferred this view of extensive ecosystems to the study and model representation of the growth dynamics of pure and mixed stands. This laid the foundations for the concept of gap models suitable to predict succession. According to this concept, a forest stand is an aggregation of gaps. The size of these gaps corresponds to the extent of a potential crown area of a dominant tree or tree group (areas of 0.04-0.08 ha). The actual information unit is the tree group in the gap; stand development results as the sum of the total spectrum of contributing gaps. Gap models imply that forest development in a gap occurs in a fixed cycle: A gap results from exploitation or death of a dominant tree, and thus the growth conditions of understorey trees improve and natural regeneration occurs. Growing trees successively close the gap and a new overstorey develops. The cycle is repeated with further losses of dominant trees (Fig. 9.7). Growth models using this approach were predominantly employed for investigations of competition and succession in semi-natural stands.

Gap models, such as those designed by Shugart (1984), Pastor and Post (1985), Aber and Melillo (1982) and Leemans and Prentice (1989), are primarily aimed at mixed stands. While in the models described above increment-determining factors have effects on stands or individuals respectively, gap models describe tree growth that depends on growth conditions in the individual gap. Gap models simulate growth dynamics for

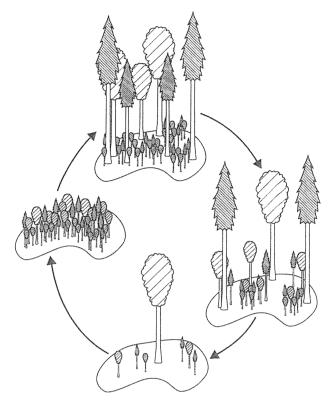


Fig. 9.7 Gap models imply that the stand dynamic occurs in a characteristic cycle: a gap results from exploitation or death of a dominant tree; growth conditions in the gap improve; young trees close the gap and form a new upper layer. (After Shugart 1984.)

single trees or tree classes in a gap; it is therefore possible to generate information about the development of diameter, height and volume of single trees as well as stands. However, regarding input and output variables they are less dependent on information available from, or required by, forestry practice; rather, they aim at predicting long-term succession in natural forest stands and the effects of altered growth conditions. The FORMIX2 model (Bossel & Krieger 1994) for virgin and logged Malaysian lowland dipterocarp forests is an example of an ecophysiological-based gap model with output variables that is useful as decision support in forest management.

Biome shift models, such as those of Box and Meentemeyer (1991) and Prentice *et al.* (1992), establish statistical relationships between regional climate and vegetation type. Based on relevant climatic conditions, the nature of poten-

tial biomes, i.e. communities, may be predicted on a regional and even global scale. Of all the models under discussion, these are the ones that provide the highest aggregation of data on vegetation development and forest growth. They have therefore gained increasing importance in research on global change.

9.3.6 Hybrid models for forest management

The transfer of specific components of ecophysiological models (based on solid process knowledge) into stand or single-tree management models (based on long-term experimental plots and increment series) leads to what Kimmins called 'hybrid growth models'. Models of this type were constructed by, among others, Botkin et al. (1972) and Kimmins (1993). Their objective is to make the best possible use of the newly acquired knowledge of ecophysiological processes combined with historical increment observations to assist in forest planning and management. On account of the implemented relationship between site conditions and species-specific growth, they can be used for pure and mixed stands. In the past 100 years mixed stands have gradually become the focus of forest research, particularly on account of studies by Gayer (1886), Wiedemann (1939b) and Assmann (1961), but to this day growth models for mixed stands are scarcely used as quantitative planning tools.

Only very recently have models created by Kolström (1993), Nagel (1996), Pretzsch (1992), Pukkala (1987) and Sterba et al. (1995) found use in forestry practice for planning work in pure and mixed stands. These are in effect site-sensitive single-tree models constructed from a broad base of ecophysiological and growth and yield data. Version 2.2 of the SILVA model, developed in Germany for pure and mixed stands, belongs to the category of hybrid models (Pretzsch 1992; Pretzsch & Kahn 1996; Kahn & Pretzsch 1997) and may be used as an example to explain the functional principles underlying this approach.

9.3.7 Management model SILVA 2.2 for pure and mixed stands

SILVA reflects the spatial and dynamic character of mixed-stand systems in as much as it models spatial stand structures at 5-year intervals. This permits the recording of the individual growth constellation of every tree and the control of tree increment in relation to growth constellation and the original dimensions of the tree (Fig. 9.8). The external variables determining tree increment and stand structure are treatment, risk and site factors. The model simulates the effects that tending, thinning, regeneration and natural hazards such as storms and wind have on the stand dynamic. The feedback loop, stand structure \rightarrow tree growth \rightarrow state of tree \rightarrow stand structure, forms the backbone of the model. The step-by-step modelling of the growth of all individual trees via differential equation systems provides information about the development of assortment yield, financial yield, stand structure, stability and diversity of the stand over and above the data, required in yield calculations, on height, diameter at breast height, number of stems, etc.

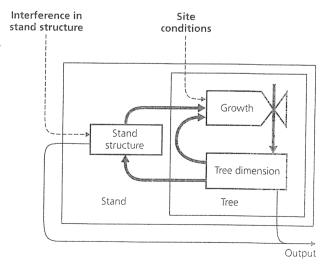


Fig. 9.8 Simplified system diagram of the growth model SILVA 2.2 showing the levels 'stand' and 'tree', the external variables 'interference in stand structure' and 'site conditions' and the feedback loop 'stand structure \rightarrow growth \rightarrow tree dimension \rightarrow stand structure'.

Input and output data used in the model correspond to the data available from, or required in, forestry practice, for example only site variables available on a large scale are considered. With models of this type a weighting between yield-related, socioeconomic and ecological aspects of stand development in pure and mixed stands becomes possible. Parametrization relies on yield and site characteristics of pure and mixed stands that have been under observation for over 100 years.

The position-dependent individual tree model SILVA 2.2 breaks down forest stands into a mosaic of individual trees and reproduces their interactions as a space-time system (Fig. 9.9). It can therefore be used for pure and mixed stands of all age combinations. Primarily it is designed to assist in the decision-making processes in forest management. Based on scenario calculations SILVA 2.2 is able to predict the effects of site con-

ditions, silvicultural treatment and stand structure on stand development, and therefore also serves as a research instrument.

A first model element reflects the relationship between site conditions and growth potential and aims at adapting the increment functions in the model to actual observed site conditions (Fig. 9.10). With the aid of nine site factors reflecting nutritional, water and temperature conditions, the parameters of the growth functions are determined in a two-stage process (Kahn 1994). The stand structure generator STRUGEN facilitates the large-scale use for position-dependent individual tree growth models. The generator converts verbal characterizations as commonly used in forestry practice (e.g. mixture in small clusters, single tree mixture, row mixture) into a concrete initial stand structure with which the growth model can subsequently commence its forecasting run (Pretzsch 1997). The three-dimen-

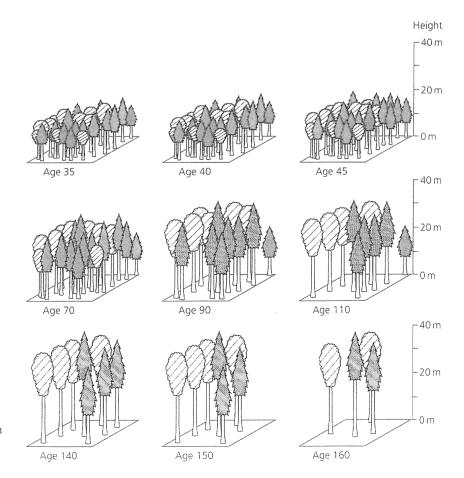


Fig. 9.9 SILVA 2.2 breaks down forest stands into a mosaic of individual trees and reproduces their interactions as a space–time system. Extract of a simulation run for a mixed stand with two species (slight thinning from below).

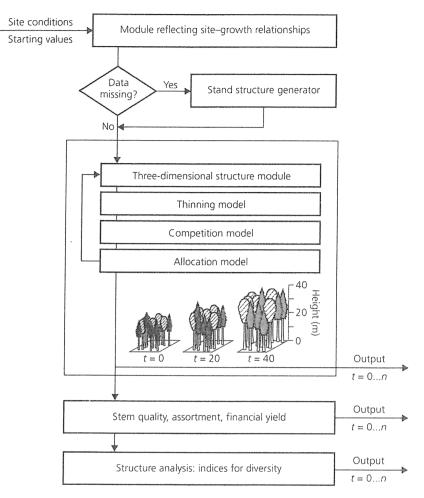


Fig. 9.10 Essential elements of the SILVA 2.2 simulator for pure and mixed stands.

sional structure module uses tree attributes such as stem position, tree height, diameter, crown length, crown diameter and species-related crown form to construct a spatial model of the stand in question. The thinning model is also based on individual trees and can model a wide spectrum of treatment programs (Kahn 1995). The core of the thinning model is a fuzzy logic controller. In the simulation studies described below the thinning model simulates various thinning methods (thinning from below and selective thinning) and thinning intensities (slight, moderate and heavy). The competition model employs the light-cone method (Pretzsch 1992) and calculates a competition index for every tree on the basis of the three-dimensional stand model. The allocation model controls the development of individual stand elements. Tree diameter at height 1.3 m, tree height, crown diameter, height

of crown base, crown shape and survival status are controlled, at 5-year intervals, in relation to site conditions and interspecific and intraspecific competition. Finally classical yield information on stand and single-tree level for the prognosis period are compiled in listings and graphs. Additional information on stem quality, assortment and financial yield complete the growth and yield characteristic. At every stage of the simulation run, a program routine for structural analysis calculates a vector of structural indices that serve as indicators for habitat and species diversity and form a link to the ecological assessment of forest stands.

The algorithmic sequence for predicting forest development comprises the following steps (Fig. 9.10). Step 1 is the input of data on the initial structure and site conditions of the monitored stand. In step 2, the parameters of the growth

functions are adapted to actual site conditions. Once the starting values for the prognostic run are complete, monitoring can begin. If there are no initial values, for example stem positions are unknown, the missing data can be realistically complemented with the help of the stand structure generator (step 3). Once the spatial model has been constructed (step 4) the silvicultural treatment program is specified in step 5. The competition index calculated for each tree through the three-dimensional model in step 6 is used, in step 7, to control individual tree development. Steps 4–7 are repeated until the entire prognostication period has been run through in 5-year steps.

To date, model research has had little success in substituting the yield tables for pure stands by an improved information system for pure and mixed stands. This can in no way be attributed to a deficit in methodological principles, data or technical equipment. Rather, the causes lie in the fact that new models are not properly adapted to practical requirements. The recent introduction of the growth model SILVA 2.2 for forest management use led to a range of operational requirements and outputs demanded from the management models that will be used in decision-making processes at stand and forest enterprise levels.

- 1 The natural management of forests is currently making great headway. In the long run only those growth models capable of simulating the growth of pure and mixed stands of all age compositions and structural patterns will find approval.
- 2 Models need to be operable at stand and forest enterprise levels and able to simulate growth behaviour under different thinning regimes and different processes of artificial and natural regeneration.
- 3 Flexibility of the model is essential so as to permit simulation of growth reactions to site alterations and interference factors on a large regional scale.
- 4 Apart from tree and stand characteristics such as volume production, assortment yield, wood quality and financial yield should also include structural parameters determining the recreational and protective functions of forests as well

as indicators showing the impact of hazards or ecological instability.

5 Forestry practice is interested, first and foremost, in calculating scenarios at stand and forest enterprise levels. This can only be achieved if input and output data of the model consider what information is available and which data are needed in forestry practice. Furthermore, achieving this goal also depends on whether the model forms part of a comprehensive forestry information system and, lastly, whether hardware specifications are acceptable in practice.

For decades forestry practice has been hoping for improved growth models to assist with research, planning, operations and control in forest management. The general acceptance of new models by practitioners calls for close cooperation between forest science and forest practice, from the design and development of the model to its actual introduction in forest management.

REFERENCES

Aber, J.D. & Melillo (1982) FORTNITE: A Computer Model of Organic Matter and Nitrogen Dynamics in Forest Ecosystems. Research Bulletin R3130, College of Agriculture and Life Sciences, University of Wisconsin, Madison, Wisconsin.

Arney, J.D. (1972) Computer simulation of Douglas-fir tree and stand growth. PhD thesis, Oregon State University

Assmann, E. (1961) Waldertragskunde. BLV Verlagsgesellschaft, München.

Assmann, E. & Franz, F. (1963) *Vorläufige Fichten- Ertragstafel für Bayern*. Institut für Ertragskunde der Forstlichen Forschungsanstalt, München.

Bailey, R.L. (1973) Development of unthinned stands of Pinus radiata in New Zealand. PhD thesis, University of Georgia, Athens, Georgia.

Bella, I.E. (1970) Simulation of growth, yield and management of aspen. PhD thesis, Faculty of Forestry, University of British Columbia, Vancouver.

Blake, J., Rosero, P. & Lojan, L. (1976) Interaction between phenology and rainfall in the growth of *Cordia alliodora. Commonwealth Forestry Review* 55, 37–40.

Bonnemann, A. (1939) Der gleichaltrige Mischbestand von Kiefer und Buche. *Mitt. a. Forstwirtschaft und Forstwissenschaft* 10(4), 45 pp.

Bormann, F.H. & Likens, G.E. (1979) Pattern and Process in Forested Ecosystems. Springer-Verlag, New York.

- Bossel, H. (1994) Treedyn 3 Forest simulation model. Berichte des Forschungszentrums Waldökosysteme, Reihe B 35, 118 pp.
- Bossel, H. & Krieger, H. (1994) Simulation of multispecies tropical forest dynamics using a vertically and horizontally structured model. *Forest Ecology and Management* **69**, 123–44.
- Botkin, D.B., Janak, J.F. & Wallis, J.R. (1972) Some ecological consequences of a computer model of forest growth. *Journal of Ecology* **60**, 849–72.
- Box, E.O. & Meentemeyer, V. (1991) Geografic modeling and modern ecology. In: Esser, G. & Overdieck, D., eds. *Modern Ecology: Basic and Applied Aspects*, pp. 773–804. Elsevier, Amsterdam.
- Bradley, R.T., Christie, J.M. & Johnston, D.R. (1966) Forest Management Tables. Forestry Commission Booklet no. 16, HMSO, London.
- Bruce, D., De Mars, D.J. & Reukema, D.C. (1977) Douglas-fir Managed Yield Simulator: DFIT User's Guide. USDA Forest Service General Technical Report PNW-57, PNW Forest and Range Experimental Station, Portland, Oregon.
- Bruner, H.D. & Moser, J.W. (1973) A Markov chain approach to the prediction of diameter distributions in uneven-aged forest stands. *Canadian Journal of Forest Research* 3, 409–17.
- Buckman, R.E. (1962) Growth and Yield of Red Pine in Minesota. USDA Technical Bulletin no. 1272, US Forest Service, Lake States Forest Experiment Station, St. Paul, Minnesota.
- Burkhart, H.E. & Strub, M.R. (1974) A model for simulation of planted loblolly pine stands. In: Fries, J., ed. *Growth Models for Tree and Stand Simulation*, pp. 128–35. Royal College of Forestry, Research Notes No. 30, Stockholm, Sweden.
- Christmann (1949) Ertragstafel für den Kiefern-Fichten-Mischbestand. In: Wiedemann, E., ed. Ertragstafeln der Wichtigen Holzarten bei Verschiedener Durchforstung Sowie Einiger Mischbestandsformen. Schaper, Hannover, 1949.
- Chudnoff, M. & Geary, T.F. (1973) Terminal shoot elongations and cambial growth rhythms in *Pinus caribaea*. Commonwealth Forestry Review 52, 317–24.
- Clutter, J.L. (1963) Compatible growth and yield models for loblolly pine. *Forest Science* **9**, 354–71.
- Clutter, J.L. & Bennett, F.A. (1965) *Diameter Distributions in Old-field Slash Pine Plantations*. Georgia Forestry Research Council Report, no. 13. US Forest Service SE Experiment Station, Ashville, Carolina.
- Curtis, R.O., Clendenen, G.W., De Mars, D. & J. (1981) A New Stand Simulator for Coast Douglas-fir: User's Guide. USDA Forest Service General Technical Report PNW-128, PNW Forest and Range Experimental Station, Portland, Oregon.
- Curtis, R.O., Clendenen, G.W., Reukema, D.C., De Mars, D. & J. (1982) *Yield Tables for Managed Stands*

- of Coast Douglas-fir. USDA Forest Service General Technical Report PNW-135, PNW Forest and Range Experimental Station, Portland, Oregon.
- Ek, A.R. & Dudek, A. (1980) Development of Individual Tree Based Stand Growth Simulators: Progress and Applications. Department of Resources Staff Paper no. 20, College of Forestry, University of Minnesota, St. Paul.
- Ek, A.R. & Monserud, R.A. (1974) Trials with program FOREST: growth and reproduction simulation for mixed species even- or uneven-aged forest stands. In: Fries, J., ed. *Growth Models for Tree and Stand Simulation*, pp. 56–73. Royal College of Forestry, Research Notes No. 30, Stockholm, Sweden.
- Evans, J. (1992) *Plantation Forestry in the Tropics*, 2nd edn. Oxford University Press, Oxford.
- Feduccia, D.P., Dell, T.R., Mann, W.F. & Polmer, B.H. (1979) Yields of Unthinned Loblolly Pine Plantations on Cutover Sites in the West Gulf Region. USDA Research Paper SO-148, Southern Forest Experiment Station, New Orleans, Louisiana.
- Franz, F. (1968) Das EDV-Programm STAOET: zur Herleitung mehrgliedriger Standort-Leistungstafeln. Manuskriptdruck, München.
- Gayer, K. (1886) *Der gemischte Wald*. Paul Parey, Berlin. Gehrhardt, E. (1909) Über Bestandes-Wachstumsgesetze und ihre Anwendung zur Aufstellung von Ertragstafeln. *Allgemeine Forst-und Jagdzeitung* 85, 117–28.
- Gehrhardt, E. (1923) Ertragstafeln für Eiche. Buche, Tanne Fichte und Kiefer. Verlag Julius Springer, Berlin.
- Grundner, F. (1913) Normalertragstafeln für Fichtenbestände. Springer-Verlag, Berlin.
- Hamilton, G.J. & Christie, J.M. (1973) Construction and Application of Stand Yield Tables, British Forestry Commission Research and Development Paper no. 96, Forestry Commission, London.
- Hamilton, G.J. & Christie, J.M. (1974) Construction and application of stand yield models. In: Fries, J., ed. *Growth Models for Tree and Stand Simulation*, pp. 222–39. Royal College of Forestry, Research Notes No. 30, Stockholm, Sweden.
- Hartig, G.L. (1795) Anweisung Zu Taxation der Forsten Oder Zur Bestimmung Des Holzertrages der Wälder. Heyer-Verlag, Gießen.
- Hartig, R. (1868) Die Rentabilität der Fichtennutzholz-Und Buchenbrennholzwirtschaft Im Harze und Im Wesergebirge. Cotta-Verlag, Stuttgart.
- Hartig, Th. (1847) Vergleichende Untersuchungen Über Den Ertrag der Rotbuche. Förstner-Verlag, Berlin.
- Heyer, G. (1852) Über die Ermittlung der Masse, des Alters und des Zuwachses der Holzbestände. Verlag Katz, Dessau.
- Hoyer, G.E. (1975) Measuring and Interpreting Douglasfir Management Practices. Washington State Deart-

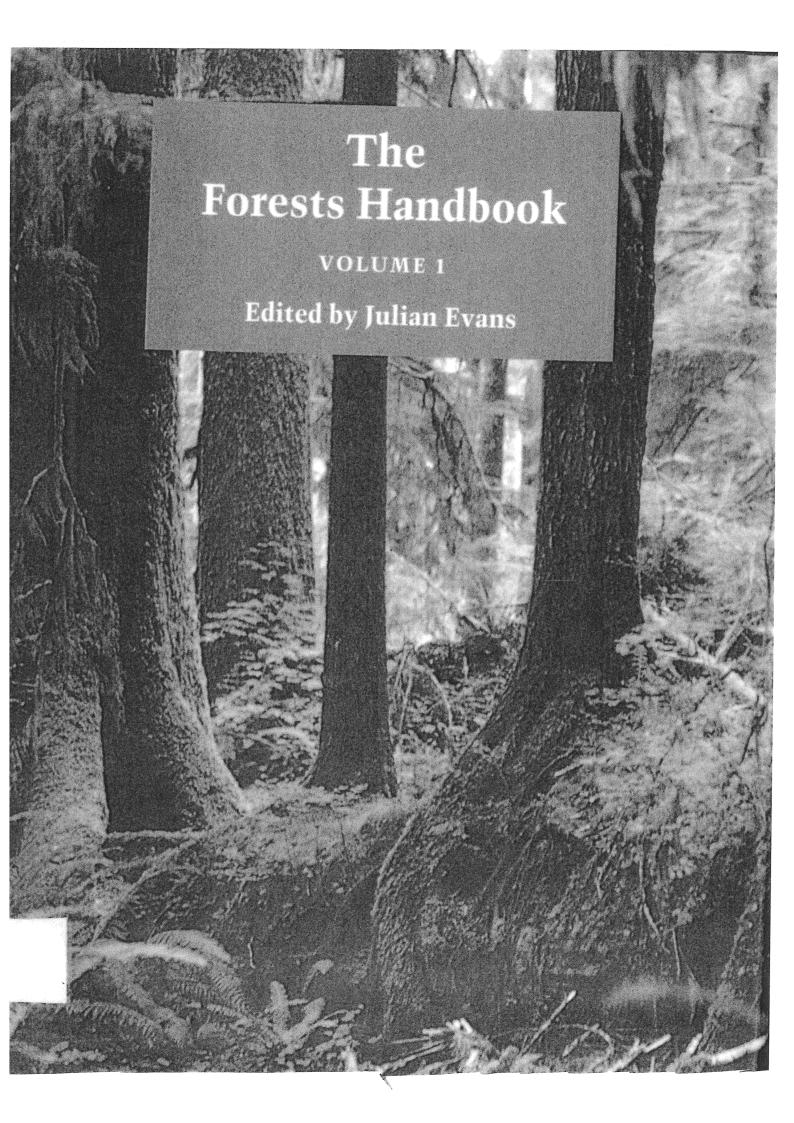
- ment of Natural Resources Report no. 26, Olympia, Washington.
- Hradetzky, J. (1972) Modell eines integrierten Ertragstafel-Systems in modularer Form. PhD thesis, University of Freiburg.
- Hundeshagen, J.C. (1825) Beiträge zur gesamten Forstwirtschaft. Verlag Laupp, Tübingen.
- Judeich, F. (1871) *Die Forsteinrichtung*. Schönfeld-Verlag, Dresden.
- Kahn, M. (1994) Modellierung der Höhenentwicklung ausgewählter Baumarten in Abhängigkeit vom Standort. Forstliche Forschungsberichte. München 141.
- Kahn, M. (1995) Die Fuzzy Logik basierte Modellierung von Durchforstungseingriffen. *Allgemeine Forst-und Jagdzeitung* **166**, 169–76.
- Kahn, M. & Pretzsch, H. (1997) Das Wuchsmodell SILVA: Parametrisierung für Rein- und Mischbestände aus Fichte und Buche. Allgemeine Forstund Jagdzeitung 168, 115–23.
- Kimmins, J.P. (1993) Scientific Foundations for the Simulation of Ecosystem Function and Management in FORCYTE-11. Information Report NOR-X-328, Forestry Canada, Northwest Region Northern Forestry Centre, Vancouver, Canada.
- Kolström, T. (1993) Modelling the development of unevenaged stand of *Picea abies. Scandinavian Journal of Forest Research* 8, 373–83.
- Krenn, K. (1946) Ertragstafeln für Fichte. Schriftenreihe der Badischen Forstlichen Versuchsanstalt, Freiburg. 3.
- Leary, R.A. (1970) System Identification Principles in Studies of Forest Dynamics. USDA North Central Forest Experimental Station Research Paper NC-45, St. Paul, Minnesota.
- Leemans, R. & Prentice, I.C. (1989) FORSKA: a General Forest Succession Model Vol. 2, pp. 1–45. Institute of Ecology and Botany, University of Uppsala, Meddelanden fran Växtbiologiska Institutionen.
- Lembcke, G., Knapp, E. & Dittmar, O. (1975) Die neue DDR-Kiefernertragstafel 1975. Beiträge für die Forstwirtschaft 15, 55–64.
- McGee, C.E. & Della-Bianca, L. (1967) Diameter Distributions in Natural Yellow-poplar Stands. USDA South East Forest Experimental Station Research Paper SE-25, US Forest Service, Ashville, Carolina.
- Mäkelä, A. & Hari, P. (1986) Stand growth model based on carbon uptake and allocation in individual trees. *Ecological Modelling* 33, 205–29.
- Mitchell, K.J. (1969) Simulation of the Growth of Evenaged Stands of White Spruce. Yale University School of Forestry Bulletin no. 75, New Haven, Connecticut.
- Mitchell, K.J. (1975) Dynamics and simulated yield of douglas-fir. Forest Science Monograph 17.
- Mohren, G.M.J. (1987) Simulation of forest growth, applied to douglas fir stands in the Netherlands. PhD thesis, Agricultural University Wageningen.

Monserud, R.A. (1975) Methodology for simulating Wisconsin northern hardwood stand dynamics. PhD thesis, University of Wisconsin-Madison, Dissertation Abstracts 36(11).

- Moser, J.W. (1972) Dynamics of an uneven-aged forest stand. *Forest Science* **18**, 184–91.
- Moser, J.W. (1974) A system of equations for the components of forest growth. In: Fries, J., ed. *Growth Models for Tree and Stand Simulation*, pp. 260–87. Royal College of Forestry, Research Notes No. 30, Stockholm, Sweden.
- Nagel, J. (1996) Anwendungsprogramm zur Bestandesbewertung und zur Prognose der Bestandesentwicklung. Forst und Holz 51, 76–8.
- Newnham, R.M. (1964) The development of a stand model for Douglas-fir. PhD thesis, Faculty of Forestry, University of British Columbia, Vancouver.
- Pastor, J. & Post, W.M. (1985) Development of a Linked Forest Productivity-Soil Process Model. Oak Ridge National Laboratory, Environmental Science Division, Oak Ridge, Tennessee.
- Paulsen, J.C. (1795) Kurze praktische Anleitung zum Forstwesen. Verfaßt von einem Forstmanne. Hrsg. von Kammerrat G. F. Führer, Detmold.
- Pienaar, L.V. & Turnbull, K.J. (1973) The Chapman–Richards generalization of von Bertalanff's growth model for basal area growth and yield in evenaged stands. *Forest Science* 19, 2–22.
- Prentice, I.C., Cramer, W., Harrison, S.P., Leemans, R., Monserud, R.A. & Solomon, A.M. (1992) A global biome model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography* 19, 117–34.
- Pretzsch, H. (1992) Konzeption und Konstruktion von Wuchsmodellen für Rein- und Mischbestände. Forstliche Forschungsberichte München 115.
- Pretzsch, H. (1997) Analysis and modeling of spatial stand structures. Methological considerations based on mixed beech-larch stands in Lower Saxony. *Forest Ecology and Management* 97, 237–53.
- Pretzsch, H. (1998) Structural diversity as a result of silvicultural operations, *Lesnictvi—Forestry* **44**(10), 429–39.
- Pretzsch, H. (1999) Modelling growth in pure and mixed stands: a historical overview. In: Olsthoorn, A.F.M., Bartelink, H.H., Gardiner, J.J., Pretzsch, H., Hekhuis, H.J. & Franc, A., eds. *Management of Mixed-species Forest: Silviculture and Economics*, pp. 102–7. Wageningen.
- Pretzsch, H. & Kahn, M. (1996) Wuchsmodelle für die Unterstützung der Wirtschaftsplanung im Forstbetrieb, Anwendungsbeispiel: Variantenstudie Fichtenreinbestand versus Fichten/Buchen-Mischbestan. *Allgemeine Forstzeitschrift* 51, 1414–19.
- Prodan, M. (1965) *Holzmesslehre*. J. D. Sauerländer's Verlag, Frankfurt am Main.

- Pukkala, T. (1987) Simulation model for narural regeneration of *Pinus sylvestris*, *Picea abies*, *Betula pendula* and *Betula pubescens.Silva Fennica* 21, 37–53.
- Schmidt, A. (1971) Wachstum und Ertrag der Kiefer auf wirtschaftlich wichtigen Standorteinheiten der Oberpfalz. Forstliche Forschungsberichte. München 1.
- Schober, R. (1967) Buchen-Ertragstafel für mäßige und starke Durchforstung. In: Schober, R., ed. Die Rotbuche 1971. J.D. Sauerländer's Verlag, Frankfurt am Main.
- Schwappach, A. (1893) Wachstum und Ertrag Normaler Rotbuchenbestände. Verlag Julius Springer, Berlin.
- Shugart, H.H. (1984) A Theory of Forest Dynamics. The Ecological Implications of Forest Succession Models. Springer-Verlag, New York.
- Sloboda, B. (1976) Mathematische und stochastische Modelle zur Beschreibung der Statik und Dynamik von Bäumen und Beständen: insbesondere das bestandesspezifische Wachstum als stochastischer Prozess. Habil.-Schrift, University of Freiburg.
- Stephens, G.R. & Waggoner, P.E. (1970) The Forests Anticipated from 40 years of Natural Transitions in Mixed Hardwoods. Connecticut Agricultural Experimental Station Bulletin no. 707, New Haven.
- Sterba, H., Moser, M. & Monserud, R. (1995) Prognaus-Ein Waldwachstumssimulator für Rein- und Mischbestände. Österreichische Forstzeitung 5, 1–2.
- Suzuki, T. (1971) Forest transition as a stochastic process. *Mitteilungen der Forstlichen Bundesversuchsanstalt Wien* **91**, 137–50.
- Suzuki, T. (1983) Übergang des Waldbestandes als ein stochastischer Prozess. *Beiträge zur biometrischen Modellbildung in der Forstwirtschaft* **76**, 23–58.
- Vanclay, J.K. (1994) Modelling Forest Growth and Yield: Applications to Mixed Tropical Forests. CAB International, Wallingford, UK.
- van Deusen, P.C. & and Biging (1985) STAG: A Stand Generator for Mixed Species Stands, Version 2.0. Research Note 11, Northern California Forest Yield Cooperative, Department of Forestry and

- Research Management, University of California, Berkeley, USA.
- Vanselow, K. (1951) Fichtenertragstafel für Südbayern. *Forstwissenschaftliches Centralblatt* **70**, 409–45.
- von Cotta, H. (1821) Hülfstafeln für Forstwirte unf Forsttaxatoren. Arnoldische Buchhandlung, Dresden.
- von Guttenberg, A. (1915) Wachstum und Ertrag der Fichte im Hochgebirge. Wien, Leipzig.
- Vuokila, Y. (1966) Functions for variable density yield tables of pine based on temporary sample plots. *Communicationes Instituti Forestalis Fenniae* **60**.
- Watt, A. & S. (1947) Pattern and process in the plant community. *Journal of Ecology* 35, 1–22.
- Weise, W. (1880) Ertragstafeln für die Kiefer. Verlag Springer, Berlin.
- Wensel, L.C. & Koehler, J.R. (1985) A Tree Growth Projection System for Northern California Coniferous Forests. Research Note no. 12, Northern California Forest Yield Cooperative, Department of Forestry and Research Management, University of California, Berkeley.
- Wiedemann, E. (1932) Die Rotbuche 1931. Mitteilungen aus Forstwirtschaft und Forstwissenschaft 3.
- Wiedemann, E. (1939a) Untersuchungen der Preußischen Versuchsanstalt über Ertragstafelfragen. Mitteilungen aus. Forstwirtschaft und Forstwissenschaft 10.
- Wiedemann, E. (1939b) Ertragskundliche Fragen des gleichaltrigen Mischbestandes aus der Preußischen Versuchsanstalt. *Der deutsche Forstwirt* 51.
- Wiedemann, E. (1942) Der gleichaltrige Fichten-Buchen-Mischbestand. *Mitteilungen aus Forstwirts*chaft und Forstwissenschaft 13.
- Wykoff, W.R., Crookston, N.L.U. & Stage, A.R. (1982) User's Guide to the Stand Prognosis Model. US Forestry Service General Technical Report INT-133, Ogden, Utah.
- Zimmerle, H. (1952) Ertragszahlen für Grüne Douglasie. Japaner Lärche und Roteiche in Baden-Württemberg. Ulmer-Verlag, Stuttgart.



EDITORIAL ADVISERS

0

P: G

D

Fo

Pi

G

Fc

St

N Bi Pl Bi

Pá

36

M ic ir ic

D.C. MALCOLM

Institute of Ecology and Resource Management University of Edinburgh, Edinburgh, United Kingdom

L.A. MORRIS

Daniel B. Warnell School of Forest Resources, University of Georgia, Athens, United States of America

EDITORIAL ASSISTANTS

Claire Holmes (Forest Research, UK)

Delia Sandford (Blackwell Science Ltd)

The Forests Handbook

VOLUME 1
AN OVERVIEW OF
FOREST SCIENCE

EDITED BY JULIAN EVANS

OBE BSc, PhD, DSc, FICFor

T.H. Huxley School of Environment, Earth Sciences and Engineering, Imperial College of Science, Technology and Medicine, The University of London

Bibliothek

Lehrstubl für Valdwachstumskunde München

FV. W 25/06

Stand: E

Nr. 539

Blackwell Science © 2001 by
Blackwell Science Ltd
Editorial Offices:
Osney Mead, Oxford OX2 0EL
25 John Street, London WC1N 2BS
23 Ainslie Place, Edinburgh EH3 6AJ
350 Main Street, Malden
MA 02148 5018, USA
54 University Street, Carlton
Victoria 3053, Australia
10, rue Casimir Delavigne
75006 Paris, France

Other Editorial Offices: Blackwell Wissenschafts-Verlag GmbH Kurfürstendamm 57 10707 Berlin, Germany

Blackwell Science KK MG Kodenmacho Building 7–10 Kodenmacho Nihombashi Chuo-ku, Tokyo 104, Japan

First published 2001

Set by Excel Typesetters Co., Hong Kong Printed and bound in Great Britain at MPG Books Ltd, Bodmin, Cornwall

The Blackwell Science logo is a trade mark of Blackwell Science Ltd, registered at the United Kingdom Trade Marks Registry The right of the Author to be identified as the Author of this Work has been asserted in accordance with the Copyright, Designs and Patents Act 1988.

All rights reserved. No part of this publication may be reproduced, stored in a retrieval system, or transmitted, in any form or by any means, electronic, mechanical, photocopying, recording or otherwise, except as permitted by the UK Copyright, Designs and Patents Act 1988, without the prior permission of the copyright owner.

A catalogue record for this title is available from the British Library

ISBN 0-632-04821-2 (vol. 1) 0-632-04823-9 (vol. 2) 0-632-04818-2 (set)

Library of Congress Cataloging-in-Publication Data

The forests handbook/edited by Julian Evans.
p. cm.

Includes bibliographical references.
Contents: v. 1. An overview of forest science.
ISBN 0-632-04821-2
1. Forests and forestry.
I. Julian Evans.
SD373.F65 2000
333.75—dc21 00-021516

DISTRIBUTORS
Marston Book Services Ltd
PO Box 269
Abingdon, Oxon OX14 4YN
(Orders: Tel: 01235 465500
Fax: 01235 465555)

USA
Blackwell Science, Inc.
Commerce Place
350 Main Street
Malden, MA 02148 5018

(Orders: Tel: 800 759 6102 781 388 8250 Fax: 781 388 8255)

Canada
Login Brothers Book Company
324 Saulteaux Crescent
Winnipeg, Manitoba R3J 3T2
(Orders: Tel: 204 837-2987)

Australia
Blackwell Science Pty Ltd
54 University Street
Carlton, Victoria 3053
(Orders: Tel: 3 9347 0300
Fax: 3 9347 5001)

For further information on Blackwell Science, visit our website: www.blackwell-science.com

- 7.2.1 Soil chemistry and nutrient cycling,
- 7.2.2 Roots and the rhizosphere, 162
- 7.3 Litter and soil organic matter, 164
 - 7.3.1 Litter and litter decomposition, 164
 - 7.3.2 Carbon in forest soils, 166
- 7.4 Forest soils and acidic inputs, 170
 - 7.4.1 Forest decline, 170
 - 7.4.2 Nitrogen saturation, 172
- 7.5 Timber harvesting and sustainability, 173
 - 7.5.1 Timber harvesting, nutrient removal and sustained productivity, 173
 - 7.5.2 Timber harvesting, soil compaction and sustainability, 179
- 8 Ecophysiology of Forests, 188 Richard H. Waring and Anthony R. Ludlow
 - 8.1 Introduction, 188
 - 8.2 Responses of forests to variation in climate, 188
 - 8.2.1 Determination of temperature optimum and limits, 189
 - 8.2.2 Physiological definition of soil drought, 189
 - 8.2.3 Sapwood as a water reservoir in trees,
 - 8.2.4 Transpiration by forests, 191
 - 8.3 Responses of forests to variation in nutrient availability, 192
 - 8.3.1 Optimum nutrition, 192
 - 8.3.2 Internal recycling of nutrients, 193
 - 8.4 Carbon balance analyses, 193
 - 8.4.1 Canopy photosynthesis, 194
 - 8.4.2 Autotrophic respiration, 195
 - 8.4.3 Net primary production, 196
 - 8.4.4 Allocation of carbon resources, 197
 - 8.5 Susceptibility of forests to herbivores and pathogens, 199
 - 8.5.1 Biochemical and structural defences, 199
 - 8.5.2 Biochemical and allocation ratios, 200
 - 8.6 Ecophysiological models of forest growth, 202
 - 8.7 Summary, 204
- 9 Models for Pure and Mixed Forests, 210 Hans Pretzsch
 - 9.1 Introduction, 210

- 9.2 Patterns and dynamics of growth: empirical observations, 210
 - 9.2.1 Periodicity and pattern in individual tree growth, 210
 - 9.2.2 Dynamics of stand growth, 211
 - 9.2.3 Interventions and manipulations, 212
- 9.3 Growth models, 212
 - 9.3.1 Stand growth models based on mean stand variables, 214
 - 9.3.2 Stand-orientated management models predicting stem number frequency, 215
 - 9.3.3 Single-tree orientated management models, 217
 - 9.3.4 Ecophysiological growth models, 219
 - 9.3.5 Gap models and biome shift models, 221
 - 9.3.6 Hybrid models for forest management, 222
 - 9.3.7 Management model SILVA 2.2 for pure and mixed stands, 222
- 10 Forests and the Atmosphere, 229 Paul G. Jarvis and David G. Fowler
 - 10.1 Introduction, 229
 - 10.1.1 Spatial and temporal scales, 229
 - 10.1.2 Historical development, 231
 - 10.1.3 The stand system, 232
 - 10.2 Stand energy balance, 232
 - 10.3 Radiation exchange, 234
 - 10.3.1 Solar radiation albedo, 234
 - 10.3.2 Long-wave radiation exchange, 235
 - 10.3.3 Net all-wave radiation balance, 235
 - 10.4 Momentum exchange, 236
 - 10.5 Exchange of scalars, 236
 - 10.5.1 Aerodynamic conductance/ resistance, 238
 - 10.5.2 Surface conductance/resistance,
 - 10.6 Evaporation and transpiration, 239
 - 10.6.1 Driving variables and constraints,
 - 10.6.2 Evaporation of intercepted water, 240
 - 10.6.3 Evaporation of transpired water, 241
 - 10.6.4 Some conclusions, 244
 - 0.7 Carbon dioxide exchange, 244
 - 10.7.1 The policy imperative, 244
 - 10.7.2 Forests as a carbon pump, 245