A REVIEW OF FOREST GAP MODELS

HARALD BUGMANN

*Mountain Forest Ecology, Department of Forest Sciences, Swiss Federal Institute of Technology
Zürich, ETH-Zentrum, CH-8092 Zürich, Switzerland
E-mail: bugmann@fowi.ethz.ch*

Abstract. Forest gap models, initially conceived in 1969 as a special case of individual-tree based models, have become widely popular among forest ecologists for addressing a large number of applied research questions, including the impacts of global change on long-term dynamics of forest structure, biomass, and composition. However, they have been strongly criticized for a number of weaknesses inherent in the original model structure. In this paper, I review the fundamental assumptions underlying forest gap models, the structure of the parent model JABOWA, and examine these criticisms in the context of the many alternative formulations that have been developed over the past 30 years.

Four assumptions originally underlie gap models: (1) The forest is abstracted as a composite of many small patches of land, where each can have a different age and successional stage; (2) patches are horizontally homogeneous, i.e., tree position within a patch is not considered; (3) the leaves of each tree are located in an indefinitely thin layer (disk) at the top of the stem; and (4) successional processes are described on each patch separately, i.e., there are no interactions between patches. These simplifications made it possible to consider mixed-species, mixed-age forests, which had been difficult previously mainly because of computing limitations.

The structure of JABOWA is analysed in terms of the functional relationships used for formulating the processes of tree establishment, growth, and mortality. It is concluded that JABOWA contains a number of unrealistic assumptions that have not been questioned strongly to date. At the same time, some aspects of JABOWA that were criticized strongly in the past years are internally consistent given the objectives of this specific model.

A wide variety of formulations for growth processes, establishment, and mortality factors have been developed in gap models over the past 30 years, and modern gap models include more robust parameterizations of environmental influences on tree growth and population dynamics as compared to JABOWA. Approaches taken in more recent models that led to the relaxation of one or several of the four basic assumptions are discussed. It is found that the original assumptions often have been replaced by alternatives; however, no systematic analysis of the behavioral effects of these conceptual changes has been attempted to date.

The feasibility of including more physiological detail (instead of using relatively simple parameterizations) in forest gap models is discussed, and it is concluded that we often lack the data base to implement such approaches for more than a few commercially important tree species. Hence, it is important to find a compromise between using simplistic parameterizations and expanding gap models with physiology-based functions and parameters that are difficult to estimate. While the modeling of tree growth has received a lot of attention over the past years, much less effort has been spent on improving the formulations of tree establishment and mortality, although these processes are likely to be just as sensitive to global change as tree growth itself. Finally, model validation issues are discussed, and it is found that there is no single data source that can reliably be used for evaluating the behavior of forest gap models; instead, I propose a combination of sensitivity analyses, qualitative examinations of process formulations, and quantitative tests of gap models or selected submodels against various kinds of empirical data to evaluate the usefulness of these models for assessing their utility for predicting the impacts of global change on long-term forest dynamics.

1. Introduction

'The complexity of a forest ecosystem makes difficult any attempt to synthesize knowledge about forest dynamics or to perceive the implications of information and assumptions regarding forest growth.'

(D. B. Botkin et al., 1972, *J. Ecol.* **60**, 849).

The description, understanding and prediction of the long-term dynamics of forest ecosystems has fascinated ecologists for a long time (cf. Clements, 1916; Watt, 1925; Gleason, 1926; Tansley, 1936; Whittaker, 1953). In spite of this, quantitative theories of forest dynamics are difficult to construct because of an inadequate database on long-term processes, their environmental influences, associated feedback mechanisms, and the lack of tools to synthesize the available knowledge. Only in the late 1960s and early 1970s with the advent of digital computer technology, were researchers able to construct and numerically explore fairly complex mathematical models. Among these were fully three-dimensional, individual-based tree models (e.g., Newnham, 1964). At the 1969 annual meeting of the Ecological Society of America (ESA), Siccama et al. (1969) presented a simplified computer-based approach for studying successional processes in a small watershed in New England. The development of this model was pioneered by Daniel Botkin and was technically supported through a collaboration with the IBM Thomas J. Watson Research Center in Yorktown Heights, NY (Botkin et al., 1970, 1972a). The first ecological application of the model (Botkin et al., 1972b) was to become one of the citation classics in forest succession modeling.

In models of this type, the establishment, growth and mortality of individual trees on small patches of land are simulated as a function of biotic (competition) and abiotic factors (climate and soils). The mortality of a large, dominating tree produces a gap in the forest, which leads to the release of suppressed trees and increased tree recruitment rates, both of which drive succession; thus the name 'gap' models. The work of Botkin et al. (1972b) provided the basis for of a vast array of forest gap models that were developed for different forests worldwide (cf. Shugart and Smith, 1996), and the concept also proved successful for grasslands (e.g., Coffin and Lauenroth, 1990), alpine tundra (e.g., Humphries et al., 1996), and savannas (e.g., Gignoux et al., 1995).

In spite of these apparent successes, the basic problem of forest complexity encapsulated in the quote from Botkin (see above) remains a major challenge to ecologists involved in formalizing our knowledge on successional processes, or making projections of long-term forest dynamics. Ecologists seek to understand and predict natural phenomena and processes, and therefore it is obvious that a purely statistical approach to modeling forest succession is inappropriate. At the same time, it is impossible to scale up the behavior of ecosystems from knowledge of, for example, plant physiology alone. Hence, any useful model of long-term

forest dynamics must employ a combination of 'statistical' and 'mechanistic' approaches, and there is considerable room for the debate regarding what level of detail should be sought for the formulation of a specific process (cf. Bonan and Sirois, 1992; Pacala and Hurtt, 1993; Bonan, 1993; Bugmann and Martin, 1995; Fischlin et al., 1995; Loehle and LeBlanc, 1996; Schenk, 1996).

Gap models have been the subject of a number of reviews over the past 15 years (e.g., Shugart and West, 1980; Shugart, 1984, 1998; Dale et al., 1985; Urban and Shugart, 1992; Liu and Ashton, 1995; Shugart and Smith, 1996; Bugmann et al., 1996). These reviews have focused on the breadth of models that have been developed, model evaluation techniques, and their applications. The present review has two objectives: (1) to provide an overview of the fundamental ecological abstractions that form the nucleus of gap models, and (2) to evaluate the formulations that have been used in these models with respect to the question of how much physiological detail is necessary for simulating the long-term impacts of global change on vegetation.

First, I describe the classic JABOWA model because it is a relatively simple model whose structure is easy to understand, and because many of its formulations continue to be used in current gap models. Next, I describe changes in the basic assumptions that have been made in subsequent models, and variations in the formulation of the three fundamental processes of tree growth, tree establishment, and tree mortality. More detailed considerations regarding selected key processes in the models can be found in Norby et al. (2001), Wullschleger et al. (2001), Price et al. (2001) and Keane et al. (2001).

2. The Origin of the Models: JABOWA

The JABOWA model (Botkin et al., 1972b; acronym derived from the last names of the developers, Janak, Botkin, Wallis) was developed as a contribution to the Hubbard Brook Ecosystem study in New England, U.S.A. (cf. Bormann et al., 1970). As such, it served to study succession in a fairly small geographical area under the *current* environmental conditions.

2.1. BASIC ASSUMPTIONS

The developers of JABOWA made a number of keys that allowed them to formalize tree growth, tree establishment, and tree mortality in a relatively simple fashion (Figure 1):

1. *The forest stand is abstracted as a composite of many small patches of land, where each can have a different age and successional stage. The size of the patch is chosen so that a large individual organism can dominate the entire patch; in the case of trees, patch size thus is on the order of 100–1000 m^2.*

The spatial discretization of nature into small patches of land is supported by numerous empirical studies which suggest that 'patch dynamics' (cf. Pickett and White, 1985) underlie the successional dynamics of many communities dominated by sessile organisms. In the case of forests, the concept has proved valid in many different forest types, including tropical forests (Aubréville, 1938), European beech forests (Watt, 1925; Lemée, 1987), mixed forests and pine forests of Poland (Szwagrzyk, 1992; Andrzejczyk and Brzeziecki, 1995), forests of the Great Lakes region of the U.S. (Frelich and Lorimer, 1991), the southern Appalachian mountains (Busing, 1998) as well as coniferous forests of the Pacific Northwest of North America (Lertzman and Krebs, 1991; Lertzman et al., 1996).

2. *Patches are horizontally homogeneous, i.e., tree position within a patch is not considered. A consequence of this assumption is that all tree crowns extend horizontally across the entire patch.*

The assumption of horizontal homogeneity undoubtedly introduces a bias in the competitive relationships, particularly for small trees that do not usually interact fully with each other. However, the assumption is less restrictive than it appears: (1) in open patches, i.e., in the absence of large canopy dominants, there are usually many small trees so that the exact position of a small individual is not of prime concern and the 'smearing out' of an individual's crown across the whole patch has no strong effect; (2) on patches dominated by one or several large trees, the major influence on small trees is from the canopy dominants, and not from each other, so that it is again not crucial how their relative spatial arrangement is treated; and (3) with increasing tree size, the assumption becomes less and less critical because a tree's crown projection area converges towards patch size.

3. *The leaves of each tree are located in an indefinitely thin layer (disk) at the top of the stem.*

Schulze et al. (1977) found that in a *Picea excelsa* forest, more than 70% of the annual CO_2 uptake was attributable to the needles exposed to direct sunlight at the top of the crown, which supports this assumption. However, while it drastically reduces the effort required to calculate shading and thus competition, it introduces a significant bias because it sharply increases the asymmetry of competition. For example, two trees that are 25 m and 25.01 m tall will, in reality, compete strongly for light and other resources, whereas in the JABOWA context, taller trees are not shaded at all by smaller ones. As discussed below, this assumption seems especially critical at higher latitudes where sun angles are low.

4. *Successional processes can be described on each of those patches separately, i.e., there are no interactions between patches, and the forest is a mosaic of independent patches.*

In an era of limited computer resources, this assumption was essential because individual patches could be simulated sequentially. In reality, there are multi-
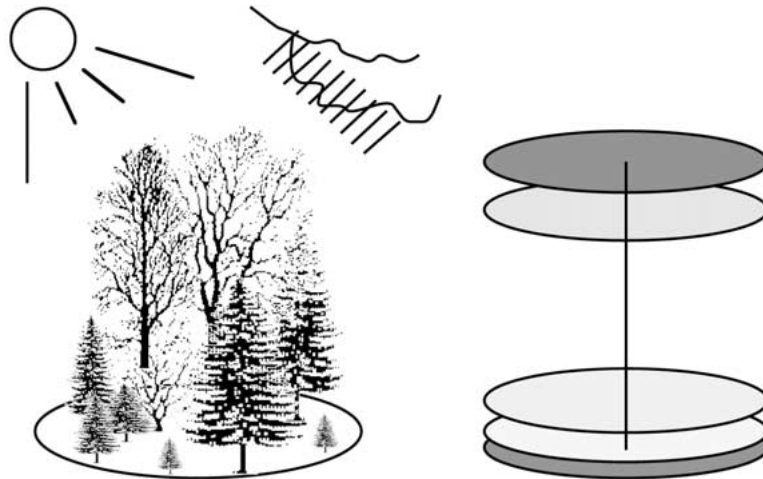
Figure 1. The concept of forest gap models is usually depicted as shown in (a), which masks the fact that the vertical canopy structure is much simplified in JABOWA and many successor models, and that horizontal tree position is neglected altogether (b).

ple relationships between adjacent patches, including shading, flow of water and nutrients, dispersal dynamics, etc. The ZELIG family of gap models (cf. Urban et al., 1991) was the first to introduce a parallel treatment of the patches with nearest-neighbor interactions (cf. Section 3).

The above four basic assumptions underlying JABOWA resulted in a geometry of the forest stand that was much simplified relative to distance-dependent approaches from forest growth modeling (e.g., Munro, 1974). However, this simplification was necessary to provide an efficient framework for including the complexity of mixed-age, mixed species stands, which are not usually considered in forest growth models. Unfortunately, it is currently unknown whether the bias that is introduced through these assumptions is small enough to go unnoticed in the model behavior, or whether other parts of the model implicitly compensate for this bias.

Additional basic features of JABOWA include the following: (5) the establishment, growth, and mortality of *each individual tree* is considered, i.e., the entity being modeled is the individual; (6) the model considers the tree composition and size structure of the forest, but it does not deal with forest functions such as biogeochemical cycling of carbon and nitrogen, or the flows of water through the ecosystem; and (7) the competition between trees and other life forms such as shrubs, herbs, or grasses is ignored. Deviations in subsequent models from these basic features will be discussed in Section 3.
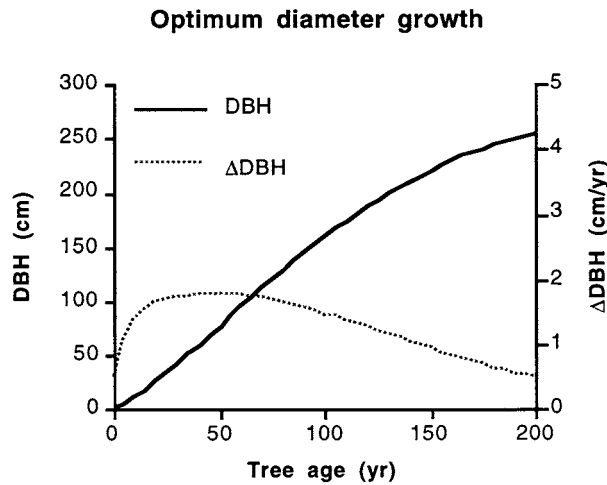
Optimum diameter growth

Figure 2. The JABOWA equation of maximum tree growth plotted for a tree with $H_{max} = 40$ m, $D_{max} = 285$ cm, and $G = 143$ cm/yr.

2.2. GROWTH SUBMODEL

In JABOWA, diameter at breast height of the trees (D) is the only state variable (cf. Section 3.2.1). Diameter growth is modeled as a deterministic process on an annual time step ($\Delta t = 1$ year), based on a consideration of the maximum possible growth, which is reduced by scalars that represent the extent of suboptimal conditions. The growth equation, which is illustrated in Figure 2, has the following form:

$$\frac{\Delta D}{\Delta t} = G \cdot D \cdot \left(1 - \frac{D \cdot H}{D_{max} \cdot H_{max}}\right) \cdot \frac{1}{b(D)} \cdot f(e), \tag{1}$$

where H is tree height (an allometric function of tree diameter, see below), $b(D)$ is a function encapsulating this allometric relationship, G is a growth rate parameter, and D_{max} and H_{max} are the maximum tree dimensions. An extensive review of the maximum growth equation (Equation (1)), including its limitations and various modifications, is given by Bugmann et al. (1996).

The influence of the abiotic and biotic environment on tree growth in Equation (1), $f(e)$, is a 0–1 scalar formulated as:

$$f(e) = g_1(AL) \cdot g_2(SBAR) \cdot g_3(DD), \tag{2}$$

where $g_1(AL)$ is a function of available light, $g_2(SBAR)$ is a function of stand basal area, and $g_3(DD)$ is a function of the annual degree-day sum. Hence, the only resource for which there is explicit competition in JABOWA is light. All other resources, specifically belowground resources such as water and nutrients, are summarized in the SBAR factor. Note also that the only climatic influence on tree growth is through the annual degree-day sum. Drought is not modeled explicitly because it was found to be unimportant in the Hubbard Brook area (Botkin et al.,

1972a, p. 109). The three factors that constitute $f(e)$ in Equation (2) are discussed below.

2.2.1. *Competition for Light (AL)*

To calculate light competition, tree height needs to be known for each individual. For this, an allometric relationship with a parabolic form is used (Ker and Smith, 1955; cf. Figure 3a):

$$H = b_1 + b_2 D + b_3 D^2 , \tag{3}$$

where b_i are parameters ($b_1 = 137$ cm, so-called 'breast height', and b_2 and b_3 are derived from H_{max} and D_{max}). A disadvantage of Equation (3) is that is contains the assumption that diameter growth comes to a halt when height growth stops, which is not true for many species. Parameter estimation procedures that are based on measured data will therefore tend to grossly underestimate D_{max}, whereas if the parameter values are derived from literature data on recorded maximum height and diameters of old, open-grown trees, an underestimation of early height growth results (cf. Bugmann et al., 1996).

Leaf area index must be known to simulate light competition, and it is calculated in JABOWA via a simple allometric relationship to diameter (Figure 3b):

$$LAI = cD^2/k , \tag{4}$$

where c is a species-specific parameter, and k is used to scale leaf weight per tree to projected leaf area (patch size is 100 m^2 in JABOWA). Botkin et al. (1972b) acknowledged that the exponent in Equation (4) is not a constant across species, but rather ranges from 1.5 to 3. Another concern is that leaf area does not increase indefinitely with diameter, but rather converges to a constant value with large diameters. With the JABOWA formulation, the amount of shade cast by large trees is overestimated, which unrealistically increases the competitive strength of such individuals.

From tree height and leaf area at the top of each tree, light extinction within the canopy is predicted using the Beer–Lambert law (Figure 3c), and relative light availability at the height of each tree is used to derive the AL scalar (Figure 3d, Equation (2)). The parameters for the two response curves (Figure 3d) were chosen 'to give reasonable fits to measured photosynthesis curves' (Botkin et al., 1972b, p. 856). This rationale contains a strong scaling assumption, because the relationship is used to modify *annual net tree growth*, whereas the response curves were from *instantaneous photosynthesis* measurements. Horn (1971) derived this scaling rule, but there may be scope for re-examining it in the light of more recent findings (e.g., Haxeltine and Prentice, 1996).

2.2.2. *Competition for Other Factors (SBAR)*

To account for the fact that there are other resources, e.g., water and nutrients, for which trees compete, a 'crowding-dependent' growth-reducing factor is used to
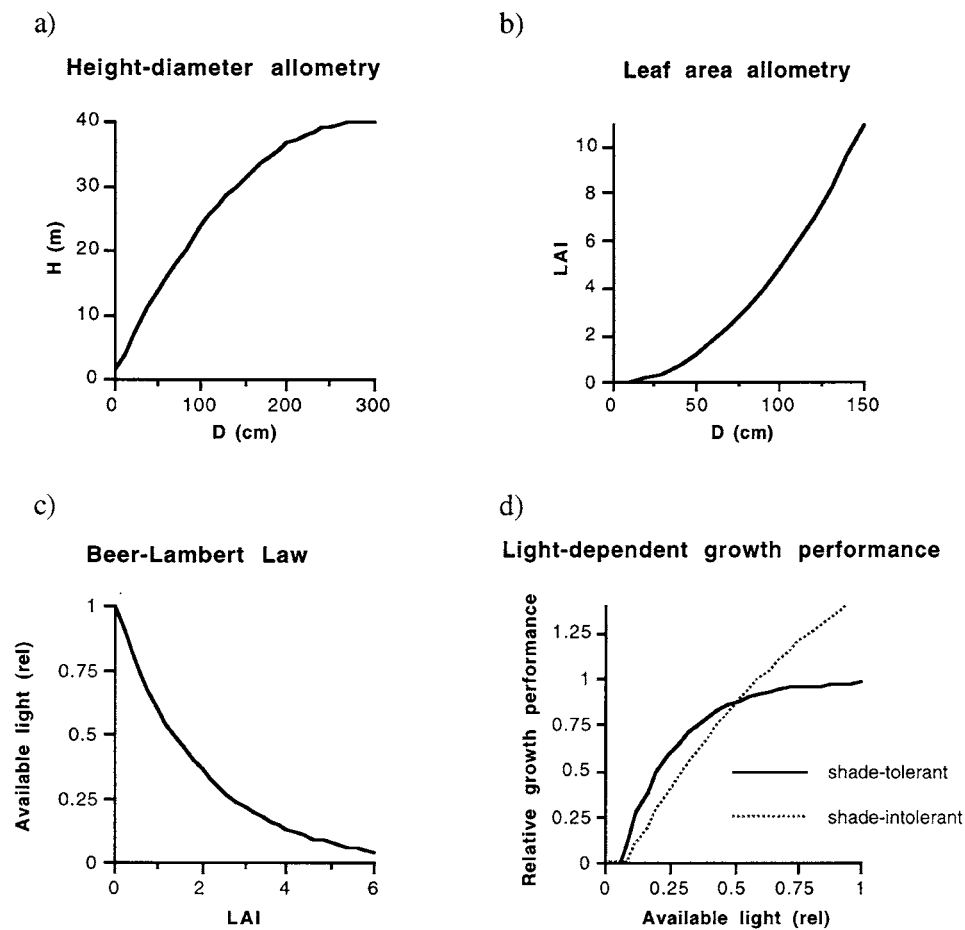
a)

Height-diameter allometry

b)

Leaf area allometry

c)

Beer-Lambert Law

d)

Light-dependent growth performance

Figure 3. Functional form of the equations used in JABOWA to derive light availability and the associated growth reduction for a given tree.

prescribe a linear decrease of tree growth with increasing stand basal area (Figure 4a). The parameterization is not species-specific (i.e., the parameter *maxBA* in Figure 4a is the same across all species). Accordingly, the strongest effect of the factor is to determine the biomass that can be achieved on the patch, whereas its effect on species composition is much weaker (cf. Bugmann, 1996).

2.2.3. *Temperature Effects on Tree Growth (DD)*

Climate-growth relationships are parameterized in JABOWA through the annual sum of degree-days (DD), which thus serves as an index of the available energy for plant growth:

$$DD = \sum_{m=\text{Jan}}^{\text{Dec}} (T_m - 4.4) \cdot d_m \,, \tag{5}$$

a)

Crowding-dependent growth performance

b)

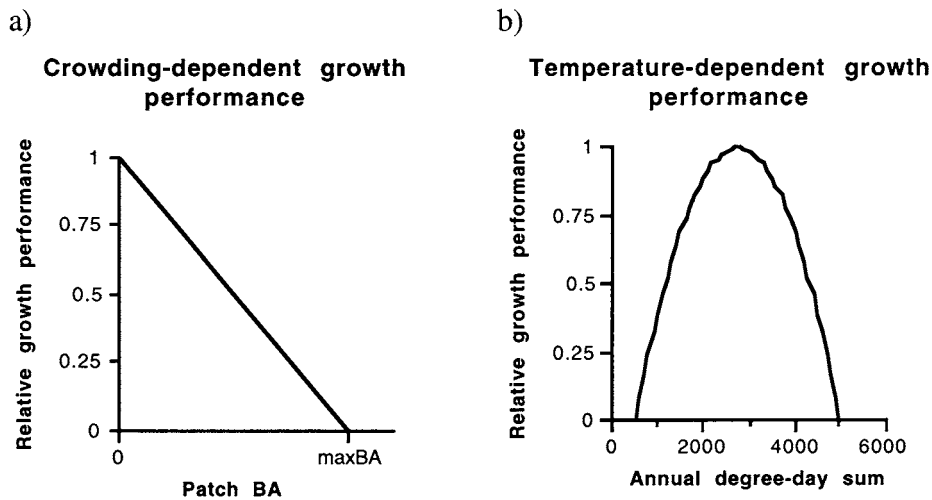**Temperature-dependent growth performance**

Figure 4. (a) The crowding-dependent growth factor in JABOWA. BA = basal area. Note that the parameter *maxBA* is not species-specific. (b) The temperature-dependent growth factor in JABOWA. For details, see text.

where T_m is monthly mean temperature (°C), d_m is the number of days in month m, and 4.4 °C is the base temperature (i.e., 40 °F). A parabolic relationship (Figure 4b) is used to scale tree growth according to the annual degree-day sum. This equation, which has been used in about half of the current gap models, has been critically reviewed several times (e.g., Bonan and Sirois, 1992; Pacala and Hurtt, 1993; Schenk, 1996; Loehle and LeBlanc, 1996) with respect to its functional form and its parameter estimation procedure. In the context of a model that lacks any drought effects on tree growth, it is reasonable to interpret the right half of the parabola (Figure 4b) as a growth reduction induced by drought and not by temperature *per se*, based on the often-observed correlation between high temperatures and the occurrence of drought. In many later gap models, where drought was introduced as an independent response variable, the degree-day parabola was retained, which was inconsequential (cf. Bugmann et al., 2000).

2.3. ESTABLISHMENT SUBMODEL

As a consequence of the lack of interactions, such as seed dispersal between neighboring patches, it is reasonable to assume that at the scale of a JABOWA patch (100 m²), seeds of all tree species are always present. New trees are added as a function of the current biotic (light) and abiotic (temperature and moisture) conditions, as follows:

- Light availability at the forest floor must be higher than a species-specific threshold, which is parameterized as a maximum leaf area index (LAI).
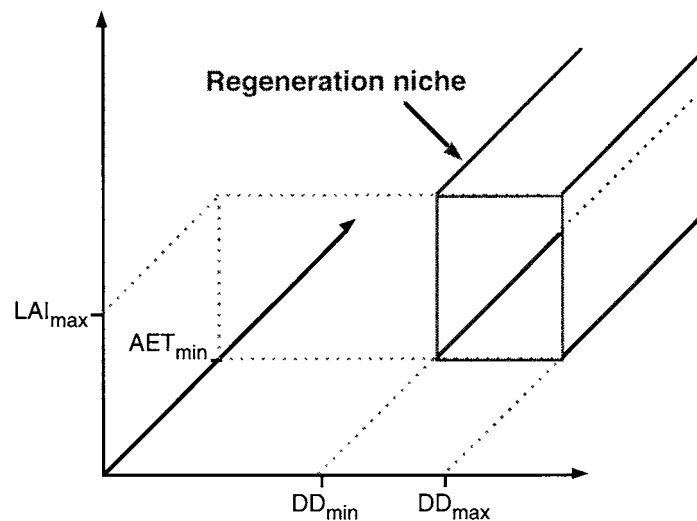
Figure 5. The three-dimensional regeneration niche of the tree species as encapsulated in the JABOWA model.

- The annual sum of actual evapotranspiration (AET) must lie above a species-specific threshold value. This prevents establishment of species whose seedlings would wilt and die before they have access to deeper soil horizons. AET is calculated with the Thornthwaite and Mather (1958) soil water submodel running at a monthly time step.
- The annual sum of degree-days (DD) must lie within a range that is tolerated by the species.

These variables define a three-dimensional regeneration niche for each species (cf. Figure 5). The current-year values of the three variables are evaluated against species-specific thresholds; if they permit establishment, a number of trees with a diameter at breast height of 0.5 cm plus 'a small random addition' (Botkin et al., 1972b, p. 857) are 'planted'. Obviously, these trees are more than one year old, but the environmental conditions across the early phase of tree life are assumed to be reasonably correlated with those of the current year.

The establishment submodel is stochastic, where the number of trees to be established per species depends on their shade tolerance, and a uniformly distributed random number is used to determine the actual number of trees to be established. For shade tolerant species, intermediate species, and shade-intolerant species, 0–200, 0–1300, and 6000–7500 trees ha^{-1} yr^{-1} are established, respectively.

2.4. MORTALITY SUBMODEL

Tree mortality is modeled as a stochastic process, and is assumed to consist of two components (Figure 6): (1) a 'background' mortality that allows only 2% of
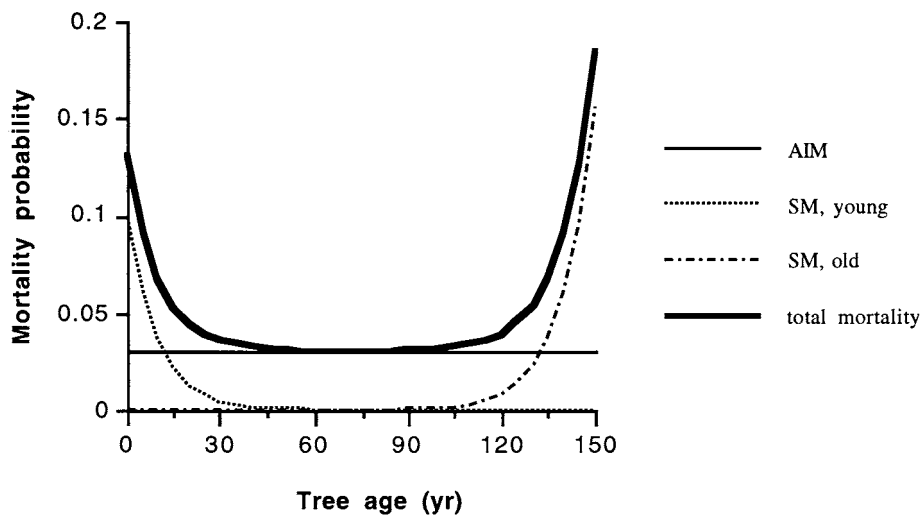
Figure 6. Changes of mortality patterns with tree age (cf. Goff and West, 1975; Harcombe, 1987) and their approximation in the JABOWA model. AIM – age-independent 'background' mortality; SM – stress-related mortality. For details, see text.

the trees to survive to maximum tree age (a model parameter) where the annual mortality probability is constant across tree life; and (2) a stress-related mortality that acts when diameter increment is less than 0.01 cm for any given year and species. A tree has a 1% chance of surviving 10 stress years; as soon as there is no stress, the stress-related mortality ceases to be effective. Hence, it is assumed that there are no lags between the occurrence of stress and the associated mortality, and that stress tolerance is not species-specific.

In spite of these simplifications, JABOWA portrays the crucial features of natural tree mortality: Young trees have a large potential increment, but often they are shaded strongly; thus, their realized growth rate is often below the 0.01 cm threshold, so that stress-related mortality is high for small trees. Large trees have small maximum increments, and thus their realized growth rate often is below the 0.01 cm threshold as well. In essence, this results in a U-shaped mortality curve across tree life (Figure 6). However, the criterion for defining 'stress' in JABOWA clearly is not satisfactory, and the model fails to recognize species-specific differences in the stress-related mortality.

3. Variations in the Formulations

Over the past 30 years, almost all of the assumptions and equations described above have been challenged, scrutinized, or replaced by alternative formulations in specific gap models. This has led to a large variety of gap models, most of which continue to share many features. Below, important deviations in the conceptual-

ization and formulation details of several recent gap models are reviewed, starting with their basic assumptions, followed by an evaluation of growth processes, establishment, and mortality. Given the present variety of gap models, it is impractical to list all the models that use a specific assumption or formulation. Where individual models are mentioned below, these examples focus on (1) those models that introduced a new assumption or formulation; (2) those that are widely used or have had a particularly high impact in the field; and (3) those that were involved in the model comparison exercises described by Badeck et al. (2001), Shao et al. (2001), and Bugmann et al. (2001).

3.1. BASIC ASSUMPTIONS

3.1.1. *The Forest as a Mosaic of Small Patches*

In all gap models except SORTIE (Pacala et al., 1993, 1996), the fundamental spatial unit – the patch – consists of an area of 100–1000 m^2. In the SORTIE model, which emphasizes light competition as the major driver of forest succession, much larger tracts of land are considered, and within this area the position of each tree is kept track of to allow for the accurate calculation of light conditions. Whereas the SORTIE approach certainly is more realistic and accurate than the original abstractions used in the other gap models, it comes at great cost in terms of parameterization efforts as well as computation time.

3.1.2. *Horizontal Structure within a Patch*

Almost all current gap models retain the assumption that patches are horizontally homogeneous. Patch sizes vary from 100 m^2 (as used in JABOWA) to around 1000 m^2, the latter especially in high-latitude forests where a single narrow-crowned tree never dominates a larger area (i.e., an entire patch; cf. Leemans and Prentice, 1989; Prentice et al., 1993). The exact choice of patch size is less critical than it may appear (cf. Shugart and West, 1979), and variations by $\pm 50\%$ typically have a small effect on the simulated dynamics as long as the range of 100–1000 m^2 is not exceeded (Bugmann, unpublished).

The assumption of horizontal homogeneity was found to cause problems in some of the more recent gap models that simulate photosynthesis and respiration from ecophysiological principles (e.g., 4C model, Bugmann et al., 1997). When the assumption of horizontal homogeneity was made, small understory trees failed to grow in 4C, because too little light reached the forest floor as a consequence of the presence of leaves from larger trees across the whole patch. The situation was improved by taking into account an estimate of the crown projection area of each tree, thus effectively leaving part of the patch unshaded (Badeck, personal communication).
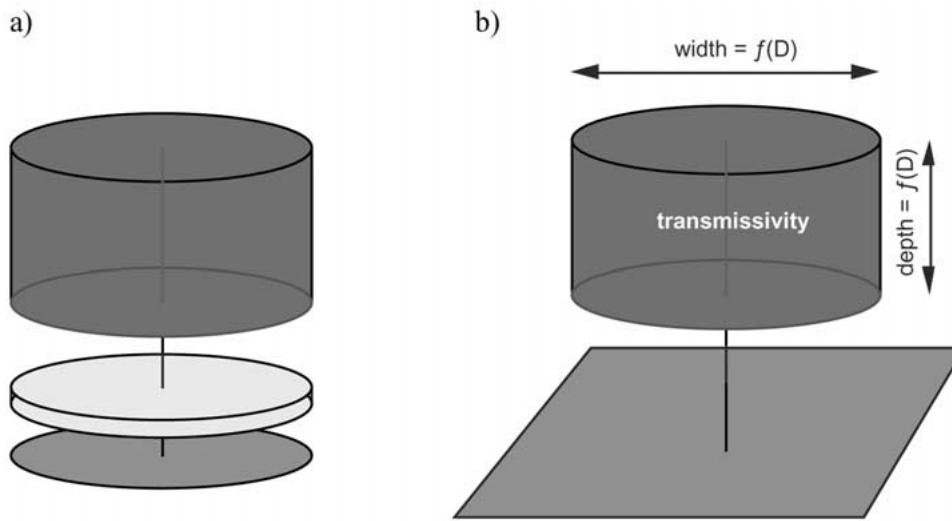
Figure 7. Variations in the conceptualization of crown architecture in gap models (cf. Figure 1): (a) the formulation introduced in FORSKA (Leemans and Prentice, 1989); (b) the 3-D formulation used in SORTIE (Pacala et al., 1993).

3.1.3. *Vertical Canopy Structure*

The majority of current gap models retain the original assumption that all the leaves are located in a disk at the top of the stem (cf. Figure 1); alternative approaches that are used in some lineages of gap models are discussed below.

Leemans and Prentice (1989) argued that for deep-crowned conifers in the boreal zone, where sun angles are low, a more realistic representation would be a cylindric crown model (Figure 7a). In their FORSKA model, two new state variables were introduced: (1) the height of the bole (or, alternatively, the length of the crown); and (2) the amount of leaf area, which is not determined from an allometric relationship to diameter, but derived from the pipe model theory (Shinozaki et al., 1964). The resulting vertical overlap of tree crowns reduces the strong asymmetry of light competition inherent in the JABOWA formulation. This feature may be a key reason why a whole family of FORSKA-based models have been developed (e.g., Price and Apps, 1995, 1996; Desanker, 1996; Lindner et al., 1996, 1997).

Leemans (1992) conducted an elegant comparison of two variants of FORSKA (cylindric crown geometry; Figure 7a) and ZELIG (disk crown geometry; Figure 1). The models were set up to be similar in their process representations, while differing primarily in the treatment of crown geometry and, thus, light competition. Leemans (1992) showed that FORSKA is capable of accurately simulating stem size distributions of a near-natural *Picea-Pinus* forest in Sweden, whereas ZELIG fails to simulate realistic distributions, especially for shade-intolerant species, suggesting that the cylindric crown model is superior to the disk model, at least in high
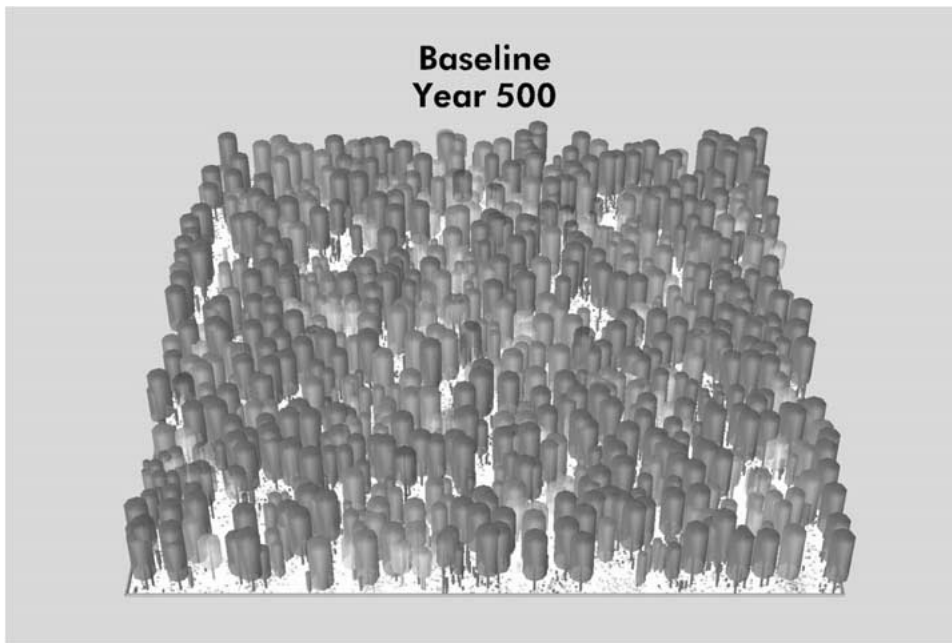
Figure 8. The spatial representation of trees in the SORTIE model (Pacala et al., 1993, 1996). Image courtesy of Catherine Devine and Linda Buttel at the Cornell Theory Center, kindly provided by Douglas Deutschman (cf. http://www.sciencemag.org/feature/data/deutschman/home.htm).

latitudes. More recent versions of ZELIG (e.g., Weishampel and Urban, 1996) have abandoned the disk model and adopted the cylinder model instead.

The cylindric model for crown geometry also has proved advantageous in those gap models that resolve photosynthesis and respiration explicitly (e.g., Keane et al., 1996; Friend et al., 1997; Bugmann et al., 1997). Moreover, recent models that deal with fire, fire propagation, and fire-induced mortality are often based on the cylindric model because of the relative ease of determining fire damage to the crown (e.g., Keane et al., 1996).

In the SORTIE model (Pacala et al., 1993, 1996), where the assumption of horizontal homogeneity of the patch was abandoned (cf. Section 3.1.1), it became necessary to keep track of the depth and width of tree crowns (Figure 7b), both of which are determined from tree diameter. In SORTIE, crown transmissivity is treated explicitly as well. Hence, SORTIE represents a further sophistication relative to the FORSKA crown geometry (cf. Figure 8).

3.1.4. *Neighborhood Relationships between Patches*
No horizontal interactions between individual patches were considered in gap models until Urban (1990) introduced ZELIG, which can be set up in three modes: (1) a 'classic' mode (horizontally zero-dimensional), where patches are simulated independent from each other; (2) a 'transect' mode (1-D), where patches are arranged

linearly, taking into account the direction from where the sun is shining; and (3) a full '2-D' mode, where patches are arranged in a rectangular grid. In the latter two modes, the influence of the spatial arrangement of forest patches on the light regime, light availability for individual trees, and the resulting competitive relationships are explicitly considered.

A second horizontal interaction, seed dispersal, was included in SORTIE (Pacala et al., 1993, 1996), PICUS (Lexer and Hönninger, 1998a,b) and FORGRA (Jorritsma et al., 1999), thus relaxing the assumption of unlimited seed availability. In PICUS, seed availability depends on the presence of adult trees within the effective seeding distance of the species; dispersal agents considered are wind and animals, and the frequency of mast years is also taken into account to capture the different quantities of seeds that are available in time and space. SORTIE and FORGRA use similar approaches.

A third type of spatial interaction between patches was included in the FORMIX model of Malaysian rainforest dynamics (Huth et al., 1998). In FORMIX, falling boles induce physical damage and mortality of the trees in the patch into which the bole is falling. Hence, the potential arises that the mortality of a large tree leads to a gap that is larger than its own crown projection area (i.e., larger than the patch where it grew), which can be important for the recruitment of shade-intolerant tree species.

The inclusion of interactions between adjacent patches has implications that call for an explicit simulation of disturbances of varying sizes. This is because in a gap model that does not consider horizontal shading interactions between patches, the death of a large tree induces a radical change of the light regime towards open-field conditions. However, when horizontal shading effects are taken into account and patch size is relatively small, even the death of a large, dominating tree does not induce a strong change of the light environment on the patch, because a significant amount of shading is simulated to occur from the surrounding patches. Urban et al. (1991) found that under these circumstances, it is necessary to impose disturbances that are larger than the patch size to avoid unrealistically low abundance of shade-intolerant species.

3.1.5. *Entities Being Modelled*

Because traditional gap models must follow the fate of individual trees, they are time-consuming to run even on modern workstations. The stochasticity that is inherent in the formulation of establishment and mortality further adds to this computational complexity. As a result, a systematic evaluation of their behavior e.g. in climate space is prohibitive (cf. Bugmann, 1996). Moreover, the models are not amenable to analytical methods such as stability analysis, or closed-form solutions. Hence, model properties remain relatively poorly known although many research teams around the world are working with these models. Based on such considerations, there have been several different lines of development towards

making gap models computationally more efficient and to derive the 'statistical mechanics' of forest community dynamics.

The simplest approach is based on the observation that while simulating each individual tree is intuitively attractive, it is somewhat cumbersome to establish and follow large numbers of trees of the same species that differ only marginally in their diameter at breast height. Bugmann (1994) showed that trees that are similar at the beginning of a simulation will remain similar throughout their entire life span. If the initial random variation of the diameters of small trees is removed (cf. Section 2.3), trees of a given species that are established in a given year will remain identical throughout their life span, because tree growth is deterministic in all gap models. Consequently, Bugmann (1996) introduced a cohort approach in the ForClim model, i.e., all trees of a given species established in a given year are assumed to be identical. Yet, mortality still removes individual trees from the cohorts. This conceptual change reduced simulation time considerably (by a factor four) without having any significant impact on the simulation results. A cohort approach is also used in the 4C model (Bugmann et al., 1997).

At least two approaches have been designed to reduce further the complexity of individual-based or cohort-based gap models, resulting in models that are based on tree population dynamics in height classes across the canopy. FLAM (Fulton 1991, 1993) was designed to mimic FORSKA in its processes, but it considers only a few height classes, thus greatly reducing the computational demand of the model. FORMIX (Huth et al., 1998) adopts a similar approach for simulating the dynamics of tropical rainforests based on a few plant functional types, but with a relatively detailed treatment of physiological processes.

Finally, two types of approaches have been used to derive the 'statistical mechanics' of forest community dynamics. First, Acevedo et al. (1995) fitted a semi-Markov model to the average output of the gap model ZELIG (note that a related approach was taken in the ROPE model by Shao et al. (1995)). The Markov model considered the transition probabilities between different states of the vegetation simulated by ZELIG as well as the holding times for these states. The resulting model, MOSAIC, was used to evaluate the behavior of the gap model at a spatial scale that would have been virtually impossible to explore with ZELIG, covering ≈200,000 patches of 900 m^2 each. The disadvantage of this approach is that the meta-model (i.e., MOSAIC) is derived from the *behavior* and not from the *structure* of the gap model, so that (1) a certain amount of simulation with the gap model needs to be done, and (2) the properties of the meta-model depend on the exact (and appropriate) choice of the gap model simulations, with an inherent uncertainty regarding the accuracy and precision of the meta-model. This type of approach has been discussed in more detail by Urban et al. (1999).

Second, several independent attempts have been made to predict the forest behavior through partial differential equations (PDEs) derived from the structure and parameters of gap models (Lischke et al., 1998: *DisCForM* model; Hurtt et al., 1998, cf. Figure 9). The appeal of these approaches is that they do not require
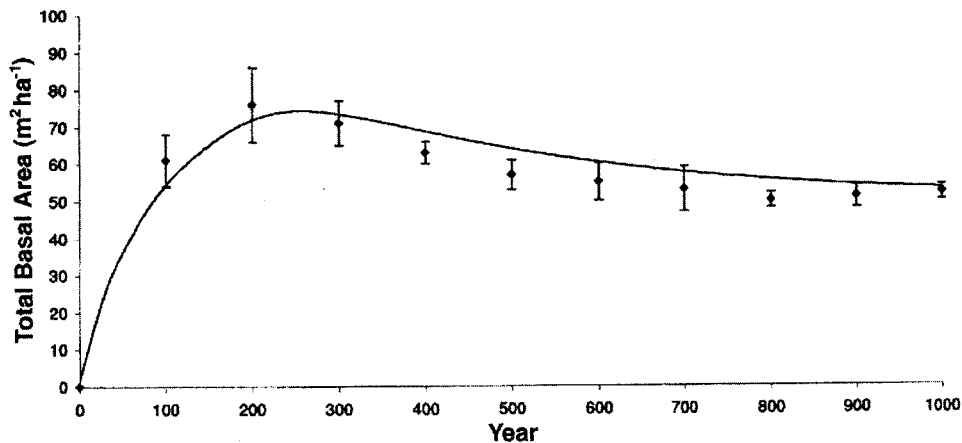
Figure 9. Comparison of total aboveground biomass simulated by the full SORTIE model (dots; the error bars denote one standard deviation) and by a PDE approximation of the SORTIE model (from Hurtt et al., 1998).

knowledge of the behavior of the gap model and thus can be quite powerful for exploring system behavior under a wide range of conditions. The disadvantage is that their derivation is based on a number of simplifying assumptions (cf. Löffler and Lischke, 2001), so that the PDE approximation may deviate significantly in its behavior from that of the gap model. Still, the value of a PDE approximation lies in its potential to perform systematic behavior analyses of the gap model with respect to both its parameter space as well as driving variables such as climate. The gap model itself can (and probably should) still be used to double-check the behavior of the PDE approximation in those cases where very sensitive or 'peculiar' trajectories result from the approximation.

In a related approach, Kohyama (1993, 1994) and Kohyama and Shigesada (1995) developed models that are based directly on the consideration of the dynamics of size structure, aimed at interpreting mechanisms at the population and community level. They derived these models from theoretical considerations, and not from detailed mathematical models of tree population dynamics such as gap models. Overall, while there is a remarkable congruence between the approaches of Lischke et al., Hurtt et al., and Kohyama et al., we still have a long way to go to fully explore the potential of these new approaches.

3.1.6. *Ecosystem Structure and Function*
Traditionally, gap models have focused on the dynamics of forest structure and composition, and have paid little attention to physiology and ecosystem function (such as the fluxes of carbon, nitrogen, and water between the land surface and the atmosphere). For example, early studies that addressed the effects of CO_2 fertilization on long-term forest dynamics (Botkin et al., 1973; Shugart and Emanuel, 1985; Solomon, 1986; Kienast, 1991) assumed that CO_2 would act to increase

the *G* parameter of the maximum growth equation (Equation (1)), i.e., that it has a direct effect on annual net growth proportional to the stimulation of photosynthesis, which is unlikely to be true (cf. Reynolds et al., 1993; Körner, 1996). Over the past years, it has been increasingly recognized that we cannot predict the long-term dynamics of ecosystem structure without considering changes in ecosystem function (including physiology), and vice versa (cf. Cramer et al., 1999).

In several recent efforts, gap modelers have attempted to provide a framework for projecting long-term forest dynamics based on the linked consideration of ecosystem structure and function. Both HYBRID (Friend et al., 1993, 1997) and FIRE-BGC (Keane et al., 1996) address this by replacing formulations in existing gap models by physiology-based submodels of photosynthesis, respiration, and plant growth, which also implies abandoning the annual time step of the model (cf. Equation (1)). Depending on the model, a daily or even sub-daily time step is used instead. These developments resulted in fairly complex models that are characterized by many parameters that are difficult to estimate for a large number of species. The 4C model (Bugmann et al., 1997) attempts to avoid the complexities of linking a physiological model with a gap model. Instead, it aims at deriving simplified formulations from physiological models that are scaled in their temporal and process resolution to the specific needs of the gap model (cf. Reynolds et al., 1993). However, no stable model version has been achieved so far (Badeck, personal communication).

Gap models that incorporate linked descriptions of forest structure and function are also referred to as 'physiology-based gap models' below.

3.1.7. *Multiple Life Forms*
In virtually all gap models, trees are established with a diameter at breast height of 0.5–1.5 cm. Usually, this corresponds to a tree height of 2–3 m. Shorter trees are not considered for two reasons: (1) the high stochasticity in and the lack of knowledge on growth and mortality rates of seedlings and saplings; and (2) the computational demand of handling thousands or even hundred thousands of small individuals, the vast majority of which do not survive to breast height. Consequently, it is difficult to simulate the interactions between different life forms (e.g., grasses and trees) in the framework of present gap models, although these interactions are known to be crucial for certain systems, e.g., savannas (Belsky and Canham, 1994; Gignoux et al., 1995).

Especially in the context of simulating forest function and biogeochemical fluxes with a gap model, it is evident that there is more to the forest than the trees: herbs, shrubs, and grasses can significantly alter the ecosystem balance of C, N, and H_2O in forests. Models that include different life forms to predict biogeochemistry are FIRE-BGC (Keane et al., 1996) and HYBRID (Friend et al., 1997), whereas a number of approaches do so mainly to provide a proxy for the intensity of competition between trees and grasses, such as SIMA (Kellomäki et al., 1992) and FLAM (Fulton, 1993).

3.2. GROWTH SUBMODEL

Below, variations in the formulation of gap models will be reviewed in five respects: (1) choice of state variables; (2) plant production; (3) allocation; (4) competition, including the question for which resources competition is modeled; and (5) environmental influences. The processes of above- and belowground growth are reviewed in detail by Norby et al. (2001) and Wullschleger et al. (2001), respectively.

3.2.1. *State Variables*

As mentioned in Section 2, JABOWA is based on one single state variable per tree, i.e., diameter at breast height. A number of models, including FORET (Shugart and West, 1977), BRIND (Shugart and Noble, 1981), FORTNITE (Aber and Melillo, 1982), FORICO (Doyle, 1981), CLIMACS (Dale and Hemstrom, 1984), SILVA (Kercher and Axelrod, 1984), FIRESUM (Keane et al., 1990) and also JABOWA II (Botkin, 1993) share this feature with the original version of the model (Botkin et al., 1972a,b).

Solomon (1986) was the first to introduce a second state variable in a gap model (FORENA). Trees typically are able to withstand several years of low growth before their mortality increases (cf. Waring, 1987; Allen and Breshears, 1998), but in JABOWA mortality was assumed to increase in response to a single stress year. Hence, a second state variable, i.e., a counter for the number of stress years was added, and it was assumed that three years of consecutive low growth have to occur before the risk of mortality increases. There is a large number of gap models that are based on the FORENA approach with two state variables, among others LINK-AGES (Pastor and Post, 1985), FORECE (Kienast, 1987), EXE (Martin, 1992), SIMA (Kellomäki et al., 1992), and ForClim (Bugmann, 1996).

Due to its more complex crown geometry, the FORSKA (Leemans and Prentice, 1989) family of models is characterized by a slightly larger set of state variables. In these models, bole height and leaf area are modelled explicitly instead of being related to diameter at breast height, which allows for a more realistic simulation of light competition.

In the approaches that link ecosystem structure and function (such as FIRE-BGC, HYBRID, and 4C), diameter at breast height is not used as a state variable at all. Instead, tree compartments that are important as carbon pools are used as state variables, including foliage biomass, sapwood, and fine roots, and the 'dimensional' variables tree height and bole height (for an example, cf. Figure 10). This adds considerable complexity to these models.

3.2.2. *Production*

Since most current gap models continue to use diameter at breast height as a state variable, annual net tree growth is predicted directly from the diameter increment
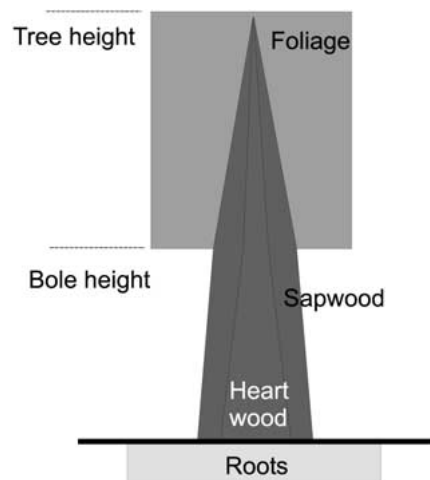
Figure 10. Tree geometry and associated state variables of the plant growth model in 4C (based on Bugmann et al., 1997). Diameter at breast height is replaced in physiology-based models by several state variables that represent different storage pools and functionally important tree organs.

equation (Equation (1)), or from a slightly modified variant of that equation (e.g., Moore, 1989; Bugmann, 1996; Lexer and Hönninger, 1998a).

The FORSKA family of gap models (Leemans and Prentice, 1989; Prentice et al., 1993; Price and Apps, 1995, 1996; Desanker, 1996; Lindner et al., 1996, 1997) is based on a phenomenological model of assimilation and respiration, which operates on an annual time step:

$$\frac{\Delta(D^2 H)}{\Delta t} = \int_B^H S_L(\gamma P_z - \delta z) dz \,, \tag{6}$$

where B is bole height, S_L is the vertical density of leaf area, γ is a species-specific growth scaling constant, P_z is the proportion of maximum possible annual net assimilation achieved by leaves at depth z in the canopy, and δ is a species-specific maintenance cost factor. This type of maximum growth equation incorporates the explicit conversion of sapwood to heartwood based on the pipe model theory (Shinozaki et al., 1964). As such, it also takes into account that the maintenance cost of the sapwood 'pipes' increases with tree height.

In the physiology-based approaches such as HYBRID (Friend et al., 1997), FIRE-BGC (Keane et al., 1996), and 4C (Bugmann et al., 1997), photosynthesis is typically modeled based on the equations by Farquhar et al. (1980). The calculation is sometimes simplified by assuming an optimum distribution of nitrogen within the canopy (Haxeltine and Prentice, 1996; Friend et al., 1997). The temperature dependency of respiration is taken into account through Q_{10} relationships that may or may not include a consideration of acclimation phenomena.

In all gap models except FIRE-BGC (Keane et al., 1996), the productivity of the forest stand is calculated by summing over the individual trees, cohorts, or age

classes. In FIRE-BGC, however, stand productivitiy is calculated first based on the FOREST-BGC approach (Waring and Running, 1998), and the fixed carbon is then distributed to the individual trees according to a priority scheme (cf. Korol et al., 1995).

3.2.3. *Allocation of Growth*

Even the simplest gap models such as JABOWA must incorporate assumptions regarding allocation of growth. Implicitly, JABOWA assumes that stemwood biomass is by far the largest tree compartment, so that all other compartments can be neglected (cf. Moore, 1989). Allocation to diameter and height growth of the stem is handled through an allometric relationship between height and diameter (cf. Section 2). Leaf biomass is predicted by another allometric relationship, and all other compartments such as coarse and fine roots, branches, and twigs are ignored. Most current gap models continue to use allometric relationships quite extensively to parameterize allocation processes. However, these relationships are used at fairly different levels of sophistication, as will be shown with two examples:

First, the simple exponential relationship between diameter at breast height and leaf area (or leaf weight) used in JABOWA (cf. Equation (4) and Figure 3b) was replaced for large diameters by a logarithmic function in CLIMACS (Dale and Hemstrom, 1984) and FORECE (Kienast, 1987). A significant problem is to find sufficient data to actually parameterize the function for large trees, which are rare in any real forest, and especially rare in managed forests.

Second, the parabolic relationship between diameter at breast height and tree height of JABOWA (cf. Figure 3a) was replaced by an asymptotic equation in the FORSKA model family (Leemans and Prentice, 1989; cf. Equation (7)), which relaxed the unrealistic assumption that diameter growth must cease when height growth stops:

$$H = 1.3 + (H_{\max} - 1.3) \cdot (1 - e^{-\frac{sD}{H_{\max} - 1.3}}) \,, \tag{7}$$

where s is a parameter that specifies the initial slope (at $D = 0$) of the height-diameter relationship.

In any real forest, not all the trees follow the same $H-D$ relationship, as is assumed in the parabolic Equation (3) as well as in the asymptotic Equation (7). In reality, allocation to height growth is strongly influenced by competition. Lindner et al. (1997) rewrote Equation (7) to

$$\frac{dH}{dD} = s \cdot \left(\frac{H - 1.3}{H_{\max} - 1.3} \right) \,. \tag{8}$$

Then, they introduced a light-dependence of parameter s such that under low light conditions, s increases because trees allocate more to height growth than to diameter growth. These developments are impressive in two respects: (1) Lindner et al. (1997) found that these modifications dramatically increase the realism of

the simulated stand structure when compared to long-term measured data; and (2) they showed that it is possible to introduce environmental influences in classical allometric relationships in an internally consistent way that does not disrupt the mass balance of the tree. It is likely that similar improvements could be made to gap models that would increase their realism and responsiveness to changing environmental conditions without having to take resort to full-fledged physiology-based approaches (cf. Norby et al., 2001).

In the models that link ecosystem structure and function, allocation is handled either through static schemes that apportion a constant fraction of the simulated NPP to specific tree compartments (e.g., Friend et al., 1997), without taking into account tree size or environmental influences, or, as in the 4C (Bugmann et al., 1997) and FIRE-BGC (Keane et al., 1996) models, dynamic allocation schemes are used that are based on principles such as the pipe model theory, the functional balance between root and leaf activity, and mass balance (cf. Mäkelä, 1986, 1990).

3.2.4. *Competition*

In spite of strongly simplifying assumptions that are made in many models with respect to crown geometry and other aspects of light competition (e.g., the lack of a seasonal course of light availability), competition for light is treated explicitly in all forest gap models, and they spend considerable effort on predicting light availability and light competition for tree growth. Note that gap models for low-stature vegetation, such as grasslands and alpine tundra (cf. Coffin and Lauenroth, 1990; Humphries et al., 1996), focus on competition for belowground resources instead of competition for light.

Competition for water and nutrients is not treated explicitly in forest gap models except in the physiology-based models, where transpiration is simulated mechanistically and it is assumed that water uptake is identical to transpiration, and nutrient uptake is proportional to nutrient availability and water uptake (cf. Friend et al., 1997; Bugmann et al., 1997). In all other forest gap models, species-specific parameters are used to limit the growth and distribution range of trees as a function of drought and nutrient-poor soils; these parameters implicitly embody competitive relationships. The lack of explicit competition for belowground resources in these models is based on the assumption that a good competitor for light is also a good competitor for water and nutrients, an assumption that may not be generally true.

In fact, many current gap models cannot explicitly simulate competition for belowground resources other than water because they do not include a consideration of soil carbon and nutrient turnover. The first gap model (FORTNITE) to include belowground C/N dynamics was developed by Aber et al. (1979) and Aber and Melillo (1982). It originated from a simple compartment model with constant turnover rates (Aber et al., 1978), and the only environmental influence on soil C/N processes (other than through the input of litter) was parameterized as an increase of the decomposition rates during the first decades after clearcutting (Aber et al., 1978), or under conditions of low leaf area (Aber et al., 1982). FORTNITE tracks

the decay of cohorts of as much as 19 litter types through time, and the lignin and nitrogen contents of the various litter types are used for predicting decay rates.

The LINKAGES model (Pastor and Post, 1985) carried these ideas a step further by making the turnover rates dependent on climate (i.e., actual evapotranspiration), based on the work by Meentemeyer (1978). In addition, LINKAGES included 72 North American species and thus could potentially be used throughout eastern North America, whereas FORTNITE was restricted in its applicability to forests in New England. Later gap models that are based on the LINKAGES C/N routine include EXE (Martin, 1992), SIMA (Kellomäki et al., 1992), and ForClim (Bugmann, 1994, 1996). As an alternative, HYBRID (Friend et al., 1997) adopts a modified version of the CENTURY model for predicting belowground C/N dynamics, and FIRE-BGC (Keane et al., 1996) is based on the FOREST-BGC approach for belowground C/N dynamics. These alternative approaches are considerably more mechanistic than the highly aggregated formulation used in LINKAGES.

3.2.5. *Environmental Influences*

In models that are based on a maximum diameter increment equation (e.g., Equation (1)) and an annual time step, the environmental scalars that modify tree growth must take into account the seasonal course of environmental factors. Already in JABOWA, climate-dependent factors such as annual actual evapotranspiration and the annual degree-day sum were calculated on a monthly time step. In any case, scaling from a sub-annual time step is required to derive scalars at the annual time step. In addition, the different scalars must be combined in an appropriate manner to yield the realized growth rate. Below, formulations that have been used for the effects of light, nitrogen, temperature, moisture, and CO_2 will be evaluated.

Regarding the influence of light on tree growth, the vast majority of current gap models continue to use the JABOWA approach (cf. Figure 3d) in spite of its shortcomings and scaling problems (cf. Bugmann et al., 2000). The models of the FORSKA family are based on a more sophisticated light response function that is used to predict net assimilation; however, this approach is also confronted with the problem of scaling from instantaneous net assimilation to the annual assimilation sum, P_z (cf. Equation (6)).

Although nitrogen typically is the most limiting nutrient in many terrestrial ecosystems, its influence on tree growth has not received much systematic attention in most gap models except LINKAGES (Pastor and Post, 1985) and its successors (see above). The approach by Aber et al. (1979) is commonly used to scale average nitrogen availability to annual tree growth rates.

The parabolic response function that was used in JABOWA to scale the annual sum of degree-days to tree growth (Figure 4b) has received a lot of attention since the early 1990s (e.g., Bonan and Sirois, 1992; Pacala and Hurtt, 1993; Loehle and LeBlanc, 1996; Schenk, 1996). Two aspects were pointed out: (1) the functional form of the equation predicts nearly zero growth at the warm range limit of every species, which contradicts empirical studies that found high if not highest growth
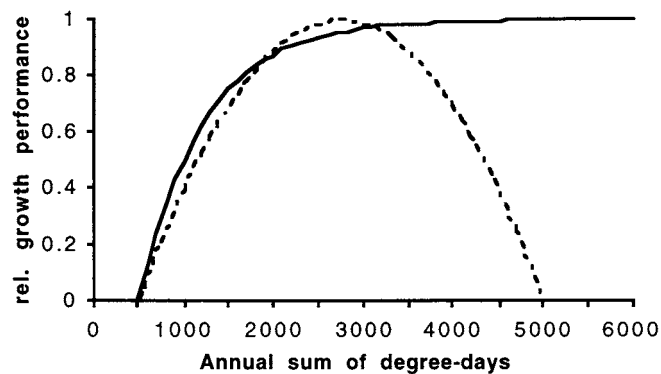
Figure 11. Comparison of the parabolic degree-day response function (g_3 [DD], Equation (2)) used in JABOWA and several other models (dashed line) with the asymptotic response function that was developed in ForClim V2.9 (solid line). Adapted from Bugmann and Solomon (2000).

rates at the warm range limit in the absence of drought (e.g., Korzhukin et al., 1989); (2) the parameter estimation procedure is based on the current distribution ranges and thus on the current realized niche of the species, which is inadequate for use in a competition model that should be based on the autecological requirements (i.e., the fundamental niches) of the species.

While the parabolic response function continues to be used in some models, several approaches have been developed to replace it, particularly asymptotic functions that maintain high growth rates with increasing temperature as long as drought does not become limiting (e.g., Lexer and Hönninger, 1998a; Miller and Urban, 1999; Talkkari et al., 1999; Bugmann and Solomon, 2000; cf. Figure 11). The FORSKA approach, which involves a parabolic response function to *daily* mean temperature – as opposed to the *annual* sum of degree-days that was used in JABOWA – is not prone to the criticisms discussed above.

Bugmann (1999) systematically analysed the effects of the removal of the parabolic temperature response function in the ForClim model. This study revealed that there is little impact on the simulated distribution and abundance of the species under current (i.e., *equilibrium*) climate if an asymptotic response function is used. Hence, the simulated absence of cold-tolerant species in warm climates is due to competition and not due to the parabolic response function, which is encouraging. However, the change in model structure had significant effects on the simulated *transient* model behavior under conditions of climatic change at some sites, whereas it proved to have no discernible effect at other sites (cf. Figure 12). Thus, earlier studies that addressed the impacts of climatic change on forest dynamics and included a parabolic temperature response function (e.g., Solomon, 1986; Pastor and Post, 1988; Kienast, 1991) should be scrutinized as to whether their predictions, specifically those regarding forest dieback events, are subject to the artifact evident from Figure 12 (site Bever).
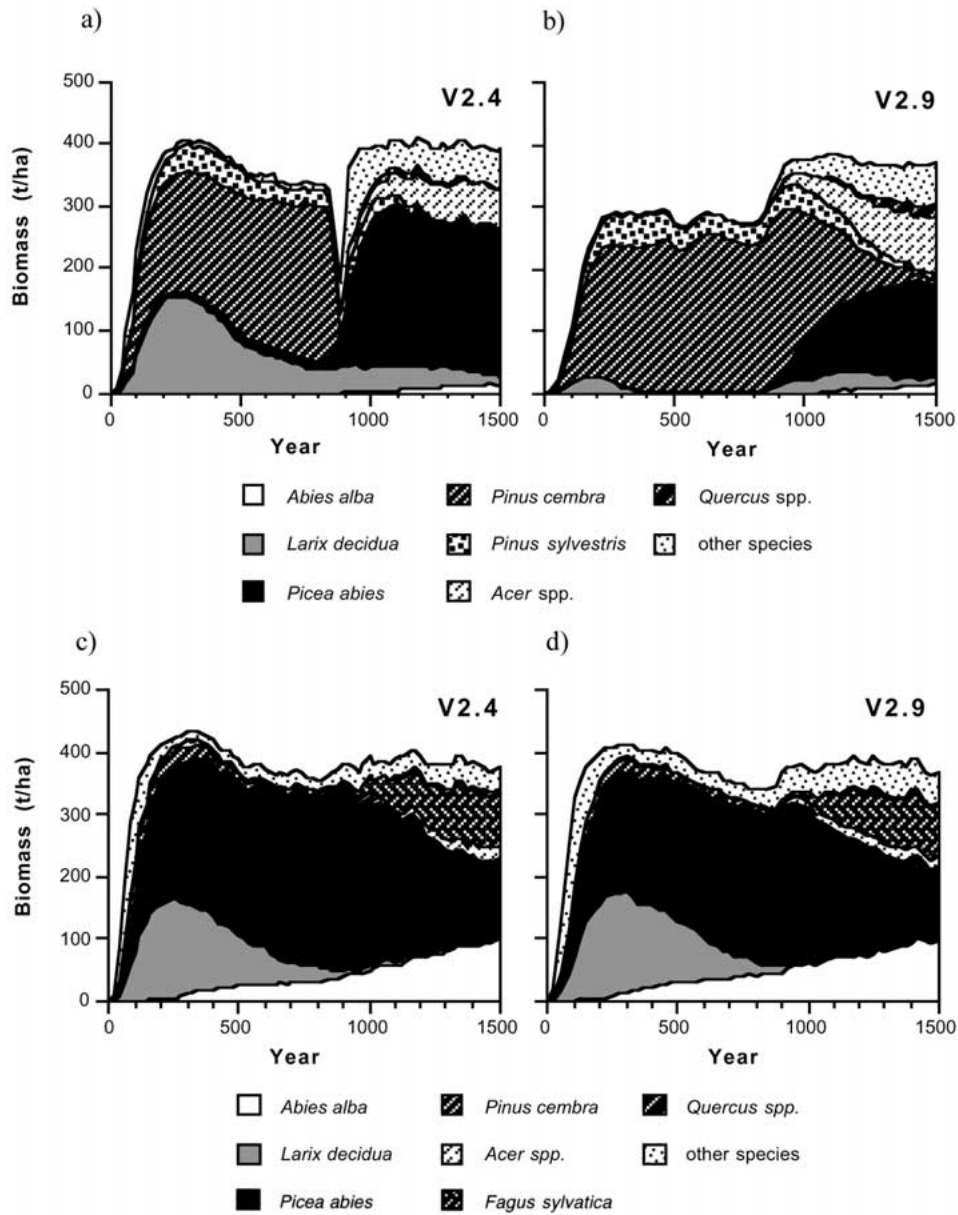
Figure 12. Comparison of the behavior of two versions of ForClim under current climate (years 0–800) and under conditions of climatic change (years 800–900) and under a hypothetical future constant climate (years 900–1500) at two sites in the European Alps, Bever (a, b) and Davos (c, d). Model version 2.4 (a, c) has a parabolic temperature response function for tree growth (like JABOWA, Figure 11), whereas model version 2.9 (b, d) features an asymptotic response function (Figure 11). Adapted from Bugmann (1999).
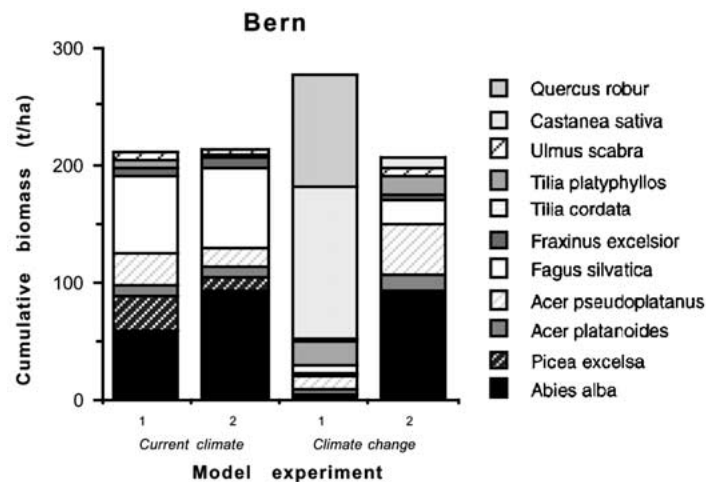
Figure 13. Comparison of the behavior of two versions of a forest gap model that differ mainly in the parameterization of environmental influences on tree growth and specifically the formulation of the drought index. Model variant 1 uses the number of days where soil moisture is below the wilting point as a drought index, whereas model variant 2 uses (1 – AET/PET) to express the severity of drought. The two model variants behave very similar under current climate, and very differently under a changed climate. Adapted from Fischlin et al. (1995).

A wide variety of approaches for treating soil moisture is being used in forest gap models, ranging from the simple Thornthwaite and Mather (1957) scheme in JABOWA that is still widespread in gap models (e.g., Pastor and Post, 1985; Kienast, 1987; Kellomäki et al., 1992; and many others), across modified versions of that model (e.g., Bugmann and Cramer, 1998) to more sophisticated Priestley–Taylor formulations (e.g., Prentice et al., 1993) and complete energy balance approaches based on the Penman–Monteith algorithm (e.g., Martin, 1992). In addition, many different indices of drought occurrence and drought stress have been used to link growing-season soil moisture conditions to annual tree growth. These include the number of days where soil moisture is below the wilting point (Pastor and Post, 1985; Solomon, 1986) as well as various measures of the evapotranspiration deficit (e.g., Prentice et al., 1993; Bugmann, 1996; Bugmann and Solomon, 2000). Several studies have shown that different formulations of the soil water submodel (e.g., Martin, 1992) or the drought index (Fischlin et al., 1995) can have profound effects on the simulated forest under a changed climate even if the predictions under current climate at a large number of sites are reasonably similar (for an example, cf. Figure 13).

The effects of the increasing atmospheric CO_2 concentration on long-term forest dynamics are difficult to incorporate into gap models that are based on an annual diameter increment equation. In such models, it is virtually impossible to incorporate our knowledge of the multiple effects and feedbacks that CO_2 has on tree physiology (cf. Amthor, 1995; Mooney et al., 1999). For example, an increase in

the *G* parameter of a JABOWA-type growth equation (Botkin et al., 1973; Shugart and Emanuel, 1985; Kienast, 1991) reflects the hypothesis that CO_2 increases net annual growth by a certain amount, and that it has no effect on water use efficiency. The former is, at least for the long term, not certain, and the latter is most likely wrong. Therefore, gap model studies that are based on tree diameter as the main state variable and address the CO_2 issue should be viewed as coarse sensitivity studies rather than predictions, although they can be quite informative (e.g., Shugart and Emanuel, 1985). In physiology-based models, the effects of CO_2 are more easily handled because the processes that are affected by increased CO_2, such as photosynthesis, transpiration, and respiration, are resolved explicitly (cf. Friend et al., 1997).

Finally, the different growth-reducing factors reviewed above must be considerd simultaneously to derive realized tree growth from maximum tree growth (cf. Equation (1)). In JABOWA and many subsequent models, a multiplicative approach was used for deriving the environmental scalar $f(e)$ (cf. Equation (2)): The fundamental problem with this approach is that it produces artificially low values especially when more than two factors are considered. For example, $f(0.8, 0.6, 0.4, 0.2) = 0.04$; in other words, if a multiplicative approach is used, maximum growth (Equation (1)) must be parameterized to be much higher than anything that can be measured and achieved in nature, or the approach will yield realized growth rates that are far too low. In view of these limitations, in a large number of models it was decided to use only the smallest of all the growth factors (often referred to as 'Liebig's Law of the Minimum'):

$$f(e) = \text{MIN}(g_1, g_2, \ldots, g_n). \tag{9}$$

While Equation (9) does not produce artificially low growth rates, it is also unrealistic in that it assumes that during any given year one single environmental factor explains all the variability of tree growth. Over the past years, several alternative approaches have been developed, some of which are rather *ad hoc* (e.g., Bugmann, 1996), whereas others are based on theoretical considerations regarding which resources can compensate for which others (e.g., Lexer and Hönninger, 1998b). Unfortunately, a systematic evaluation of the effects of the various formulations on the behavior of gap models is lacking.

The problem of modeling the environmental effects on tree growth is less pronounced in the physiology-based gap models because (1) they operate on a daily or even sub-daily time step (cf. Section 3.1.6), and (2) the different physiological processes are resolved more explicitly than in diameter-based gap models. Therefore, physiology-based gap models require fewer scaling assumptions, and environmental influences such as temperature, soil moisture, or nitrogen availability can be taken into account at the temporal resolution and for the process where they are effective. How environmental influences are handled in the growth routine of this type of models will not be discussed here because it is relatively straightforward.

3.3. ESTABLISHMENT SUBMODEL

The assumption of unlimited seed availability built into most gap models since
JABOWA has 'two opposing (offsetting?) consequences for species diversity: arti-
ficially high diversity due to continuous seed supply and artificially low diversity
due to lack of sites where good competitors with restricted dispersal should be
absent' (Clark and Yi, 1995). Specifically, with respect to assessments of the effects
of global change on forests, the assumption tends to exaggerate the response of
forests because it ignores any migration lags (cf. Davis, 1989). Several alternatives
to the assumption of unlimited seed availability have been sought over the years,
and they come in two steps:

In the first step, a feedback from the canopy trees on the patch itself was in-
troduced (e.g., Kienast, 1987; Keane et al., 1990; Bossel and Krieger, 1994; Lexer
and Hönninger, 1998b), so that there continues to be a constant influx of seeds from
all species, but the availability of seeds from species that have mature trees on the
patch is increased. The problem with this approach is that the balance between local
seed production and influx is critical for determining system behavior: With in-
creasing weight of local seed production, the system flips into a state of artificially
low diversity with, in the worst case, only one species surviving. Reliable data to
parameterize the relative importance of local production and influx are rare, giving
this approach aspects of a sophisticated tuning exercise, which is not desirable.

In the second step, the horizontal relationships between individual patches were
taken into account for determining seed availability at any given spot as a function
of the presence of mature trees in the landscape and their effective seeding dis-
tances (e.g., Keane et al., 1996; Lexer and Hönninger, 1998b). Besides providing
a more realistic description of seed availability under current environmental con-
ditions, this approach has the potential to allow for the study of migration rates
under conditions of environmental change, if the gap model that is used is efficient
enough for the simulation of many thousand patches that are arranged spatially
(cf. Lischke et al., 1998). Alternatively, a hierarchical scheme might be sought for
migration modeling, where long-range dispersal is handled by a model of relatively
coarse resolution that is coupled to a more detailed forest gap model.

There is a large number of processes operating in nature between seed avail-
ability and the establishment of saplings that are 2–3 m high. The latter continues
to be used as the initial condition for simulating tree growth and survival in most
gap models. As noted earlier (e.g., Shugart, 1984), these processes are difficult to
develop mechanistically in a forest succession model because of the sheer number
of individuals that are concerned and the lack of a mechanistic understanding of
the associated processes. The vast majority of gap models thus continues to use
so-called 'filters', i.e. simple functions that determine whether current environ-
mental conditions would allow for the establishment of a given species. If they do,
establishment usually takes place in a small fraction of the years when it would
theoretically be possible; this is to take into account the many factors that reduce

establishment probability but that are not modeled explicitly. Often, some or all of the establishment filters are defined in analogy to the growth-limiting factors discussed above. Usually only the occurrence of establishment is modeled as a boolean variable, whereas the number of saplings to be established is determined separately and independently of the environmental conditions as a property of the species.

Environmental filters for tree establishment that are used in gap models can be classified into three broad categories: (1) bioclimatic constraints; (2) biotic constraints; and (3) other limitations. These groups will be discussed in turn, and the model that first introduced a certain limitation will be referred to.

The set of bioclimatic filters that are used to determine establishment rates in gap models typically include the following:

- The annual sum of degree-days (JABOWA; Botkin et al., 1972b), which prevents species from establishing if it is too cold (or too warm, if the maximum degree-day constraint is used as well; cf. Figure 11) for them to grow.

- The lack of adequate soil moisture (FORENA; Solomon, 1986). In the many gap models that have a single-layer ('bucket') soil water submodel, this constraint is usually not set up to reflect the moisture conditions in the topsoil, but those throughout the soil profile, so that the drought filter tends to be less effective than it might need to be.

- The occurrence of freezing events below a threshold temperature in winter, which may kill flower buds and thus prevent seed production. A problem here is that such short-term weather events are not predictable by models that operate on a monthly time step for capturing bioclimatic influences on ecological processes. Prentice et al. (1992), however, showed that there is an excellent long-term correlation between absolute minimum temperature and monthly mean temperature, so that monthly mean temperature can be used as a proxy for the occurrence of extreme cold events (FORENA; Solomon, 1986).

- The lack of chilling (i.e., cold) temperatures in winter may delay or prevent bud break in the following year. The process was first introduced in FORSKA (Prentice et al., 1993), and a variety of approaches have been used for its simulation. FORSKA also includes a minimum temperature of the *warmest* month to limit tree establishment.

- The occurrence of frost events in spring that may kill flower buds. As with winter freezing, the correlation between absolute minimum and monthly mean temperature is used to predict this kind of damage relative to the hardiness of the species, which is parameterized as different threshold temperatures for different months in spring (FORECE; Kienast, 1987).

Biotic filters used in gap models include the following:

- Light availability at the forest floor or a proxy thereof is used in almost all gap models to exclude recruitment of shade-intolerant species when it is too dark (JABOWA; Botkin et al., 1972b). An important aspect here is that this allows one to differentiate the light requirements (i.e., shade tolerance) of saplings vs. older (adult) trees, which is important for at least some tree species.
- Differential browsing rates by domesticated mammals and game are taken into account through a simple parameterization in many models (FORET; Shugart and West, 1977); Kienast et al. (1999) and especially Jorritsma et al. (1999) developed the modeling of ungulate influences on long-term forest dynamics much further.

Finally, some models are using additional establishment limitations that are neither bioclimatic nor biotic. For example, in the FIRE-BGC model (Keane et al., 1996) the time since the last disturbance is used to exclude the establishment of late successional species in the pioneer phase. This should be viewed as a proxy for environmentally driven processes that are not modeled directly, but such approaches are somewhat unreliable if the model is used to study the effects of environmental change on successional processes.

The above filters are used in various combinations and at various levels of sophistication in most gap models that are based on an annual diameter increment equation (cf. Equation (1)). It is noteworthy that most physiology-based gap models treat establishment at a significantly less detailed level than most traditional gap models. A more detailed review of establishment processes in forest gap models, including recommendations for further research, can be found in Price et al. (2001).

3.4. MORTALITY SUBMODEL

As in the original JABOWA model, most gap models to date differentiate an age-independent mortality that is constant across a tree's life time and a stress-related mortality. In addition, many current models include an extrinsically caused mortality that is due to disturbances beyond the spatial scale of a single forest patch.

Traditionally, the age-independent mortality is scaled to 'maximum tree age', and only a small fraction (typically 1 or 2%) of the trees are allowed to reach that age in the absence of any other causes of mortality. The difficulty of adequately defining maximum tree age led Leemans and Prentice (1989) to formulate the age-independent mortality probility as a function of shade tolerance, and this approach is used in the FORSKA family of models. Shaded tolerance in turn is related to maximum tree age because shade-tolerant trees usually are longer-lived than shade-intolerant ones; hence the FORSKA formulation is not generically different from the JABOWA approach, although it has the advantage of not requiring the specification of maximum tree age.

Stress-related mortality functions are present in all gap models, but the definition of stress is based on widely different criteria. Some models have retained the JABOWA stress definition through an absolute diameter increment, but in

most models more sophisticated approaches have been adopted, often based on FORENA (Solomon, 1986) where a minimum relative diameter increment (10%) is used to define stress; note that because maximum diameter increment is species-specific, the requirement of a minimum relative increment makes the stress-related mortality criterion species-specific, too. In some models, the two approaches have been combined (Kienast, 1987; Bugmann, 1996), whereas the FORSKA family of models uses growth efficiency as a stress indicator, i.e., the stemwood increment relative to leaf area, which constitutes a well-established index of tree vigor (Waring and Schlesinger, 1985). The physiology-based gap models such as HYBRID (Friend et al., 1997) or 4C (Bugmann et al., 1997) use the whole-tree carbon balance to determine the presence of stress, and HYBRID also uses the occurrence of xylem cavitation as a proxy for stress.

Mortality that is induced by extrinsic disturbances is taken into account in a variety of models. In the FORSKA model (Prentice et al., 1993), a disturbance regime was implemented where the hazard increases with stand age, and the occurrence of the disturbance kills all the trees on the patch. This is a generic formulation that is broadly applicable to many disturbance agents, including timber harvesting, windthrow, and forest fires, but obviously it lacks a differentiation of the effects of the various disturbance agents. To take into account the detailed effects of some disturbances, several gap models contain submodels for specific disturbance agents, including fire (e.g., Shugart and Noble, 1981; Kercher and Axelrod, 1984; Keane et al., 1996) and pathogens such as bark beetles (e.g., Keane et al., 1996; Lexer and Hönninger, 1998a).

In view of this wide variety of formulations that are being used for modelling mortality in forest gap models, it is somewhat surprising to see that the sensitivity of the models to differences in these formulations has received almost no attention. As Figure 14 shows, there are cases where the simulated aboveground biomass and species composition depend strongly on the exact assumptions that are used for modeling tree mortality. Thus, mortality formulations in gap models should receive more attention in the future. These considerations are reviewed in more detail by Keane et al. (2001).

4. Simulation Methodology of Forest Gap Models

By definition, forest gap models consider tree population dynamics, which are inherently slow, on small patches of land. In addition, they are sensitive to climate variations on several time scales (cf. Bugmann and Pfister, 2000), and incorporate a significant amount of stochastic elements. These unique features of gap models (and forests) have strong implications for the methodology used when performing simulation experiments:

First, the stochastic dynamics simulated for a single patch (i.e., one realization of the stochastic process underlying any gap model) are of little interest *per se*,
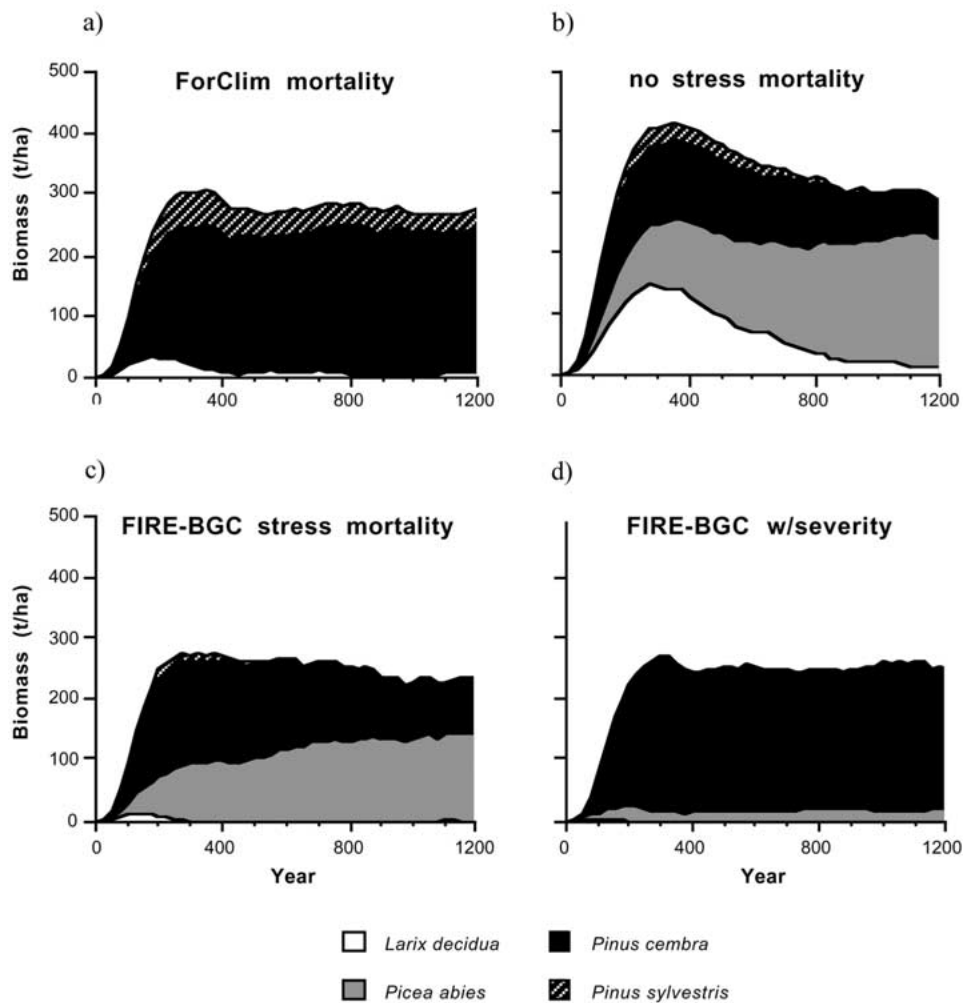
Figure 14. Behavior of the forest gap model ForClim (Bugmann and Solomon, 2000) at the central European mountain site Bever (Switzerland) under different assumptions for the formulation of the stress-related mortality function. (a): Stress mortality is induced after three consecutive years of diameter increment below 0.3 mm or below 10% of maximum diameter increment. (b): no stress-related mortality is simulated. (c): Stress mortality is formulated as in FIRE-BGC, where stress tolerance is tied to shade tolerance (Keane et al., 1996). (d): As an addition to the FIRE-BGC formulation, the severity of the stress is used to modify the mortality probabiliy. Data from Bugmann and Solomon (unpublished study).

because we cannot expect to find a real forest patch whose observed history corresponds exactly to the simulated dynamics. Hence, a statistical approach is required to analyze the simulation results, which is achieved by simulating the behavior of a forest across many patches; the simulation results are characterized by averages, medians, and higher-order statistical moments (standard deviation, kurtosis,

etc.) of variables such as species-specific biomass, stem numbers, etc. Historically, simulated variables typically were characterized by their averages (e.g., Figure 12), without paying full attention to their frequency distribution. Note that if we assume that a real forest can be described by an array of independent patches, the results from n simulated patches can be interpreted as representing the average properties of a real forest across the corresponding area. For example, for a patch size of $^1/_{12}$ ha and $n = 200$, this would correspond to an area of $200 \cdot ^1/_{12}$ ha $= 16.7$ ha.

Second, few data sources are available to initialize the state variables of forest gap models, mainly because the spatial extent of most measured records is much smaller than the sum of the n patches that are required to statistically characterize the stochastic process. As a consequence, it is a standard practice to initialize gap models from 'bare ground', which eliminates the need to estimate an initial state. Thus, gap models are typically used to simulate a secondary succession from bare ground to a steady state that results as an average across n patches after sufficiently long time. Note that the dynamics on a single patch never reach this steady state, but exhibit oscillatory behavior that is modulated by stochastic elements. From a systems theoretical point of view, the 'bare ground' scenario is particularly appealing because it allows us to explore the relaxation time in the transient phase and the development of the steady state.

Third, the slow nature of tree population dynamics and the climatic sensitivity of forest gap models imply that observed 'current climate' records, which typically span 30 to 100 years at most, are insufficient to explore the transient dynamics and the development of a steady-state during a secondary succession. The time scale required for this is on the order of 400–1200 years, depending on the longevity of the dominant tree species. Hence, for most gap model applications it is necessary to create a weather record that is based on a hypothetical 'current climate' that extends over several centuries. This is often achieved using one of three methods: (1) looping repeatedly through the measured weather series; (2) randomly selecting individual years from a measured weather series; or (3) using a weather generator to derive random series of weather data that are based on the statistical characteristics of the observed series. While each of these methods has limitations, the third approach is probably most desirable since it allows weather patterns to occur that are not contained in the measured record, including extreme events. However, the parameterization of a weather generator is a non-trivial task and, consequently, in many applications one of the former two methods is used.

Fourth, this methodology imposes limitations on the comparability between simulated and measured forest properties (e.g., model validation exercises). Given that virtually all gap model simulations are based on a synthetic time series of 'current climate' as described above, it is obvious that the real forest has not experienced the same weather and disturbance patterns as the simulated one. This inevitably must lead to differences between observed and simulated data, which makes it difficult to critically assess model validity (for a discussion, cf. Section 5.3). While forests are buffered to a certain extent against the impacts of ex-

treme events and climatic variations on shorter time scales (e.g., Davis and Botkin, 1985; Bugmann and Pfister, 2000), we cannot exclude that climatic changes in the more distant past (such as the Little Ice Age), extreme events or disturbances at specific times in the past decades have had a significant effect on the current structure and composition of a real forest (cf. Bugmann and Pfister, 2000).

In summary, for reasons that relate to the characteristic temporal and spatial scales of tree population dynamics, in most simulation studies with forest gap models (1) forest dynamics are simulated from bare ground to the establishment of a (hypothetical) steady-state; (2) the statistical properties of the simulated dynamics are evaluated across a large number of forest patches; and (3) a synthetic weather record representing 'current climate' is used that is much longer than the measured data. As in many other gap modeling studies, this simulation methodology is used in the model comparison exercises described by Badeck et al. (2001), Bugmann et al. (2001) and Shao et al. (2001).

5. Discussion

The above review of the basic structure and the variations in the formulation of forest gap models that have been developed over the past 30 years documents two things:

First, the concept behind forest gap models has been very appealing to a large number of forest ecologists who are faced with understanding and predicting long-term forest dynamics. In spite of all the criticisms that have been put forward in the recent past, there is no alternative approach available that would allow one to consider the effects of weather, intraspecific and interspecific competition on tree population dynamics as elegantly, intuitively and comprehensively as forest gap models do.

Second, although many formulations of the original JABOWA model continue to be used in many current forest gap models, there is a large variety of approaches that are being used to encapsulate the different ecological processes that are relevant for tree population dynamics. Thus, general statements about what factors are considered in gap models and what these models can and cannot do are generally inappropriate. Most gap models have evolved considerably from the original versions and contain far greater detail than is sometimes recognized.

5.1. INCREASED DETAIL ('PHYSIOLOGY'): DESIRABLE AND FEASIBLE?

It is tempting to demand that if gap models are to be used to project the impacts of global change on forest dynamics, they need to include the relevant processes (such as CO_2 assimilation, water use efficiency, and the impacts of climatic extremes and variability) in a mechanistic fashion instead of handling them through relatively simple parameterizations. While this would certainly be desirable, it is questionable whether fulfilling this requirement is feasible in all cases. There is a large

amount of ecophysiological knowledge on several key commercial tree species in a geographical region (e.g., *Picea abies*, *Pinus sylvestris*, and *Fagus sylvatica* as the main timber trees in Europe), but much less is known about the commercially less 'important' species. It should be kept in mind that the set of species that can potentially dominate forests includes 15–20 species in Europe (Prentice et al., 1993; Bugmann, 1996; Lexer and Hönninger, 1998a), 30–40 in eastern North America (Pastor and Post, 1985), 20–30 in western North America (Bugmann and Solomon, 2000), and around 20 in northeastern China (Shao et al., 1994; Yan and Zhao, 1995), to name just a few examples from the temperate zone of the Earth. In most forest gap models, more than this minimum set is included. Hence, the data base that would be required for implementing 'physiology-based' approaches in gap models often does not exist for such sets of species. As a consequence, models that include all the species that are relevant for forest succession must be based on approximate parameterizations.

At the same time, the structural complexity of even a simple forest gap model should not be underestimated. For example, the ForClim model (Bugmann, 1994) was initially developed by reducing the complexity of the FORECE model (Kienast, 1987) to the minimum set of equations and parameters that was required for reproducing (and sometimes even improving) the behavior of FORECE. Still, this 'simple' model in its present version (V2.9.2) includes 16 parameters for characterizing each tree species. For central European conditions, the model usually operates with 30 tree species, which results in 480 species-specific parameters that need to be known to run the model. In addition, there are ecotypes of some species that have significantly different characteristics, especially in species that have a wide distibution range (e.g., *Picea abies* and *Pinus sylvestris* in Europe).

The lack of precise data regarding all the life history traits of the set of tree species in gap models traditionally was circumvented by using functional types of trees, although this was not usually stated explicitly (Botkin et al., 1972b; Shugart, 1984). For example, tree species are typically assigned to one of a small number of categories regarding shade tolerance, nitrogen requirements, flooding tolerance, and so on. The known tolerances of well-researched species are used to 'anchor' the relationship, and the remaining tree species are assigned according to their tolerance relative to the known tolerances of the other species. As a consequence, the relative ranking of the species with respect to their behavior towards a limiting resource can be expected to be fairly robust, whereas the quantitative value of the functional response equation that is used in the model may be numerically wrong for most or even all species. In the context of a model that focuses on portraying the effects of competition, this probably is an acceptable compromise, whereas it may be more problematic in a model that aims at predicting functional aspects such as the fluxes of carbon and nitrogen between the land surface and the atmosphere.

This raises the general question whether the marriage between the traditional gap model approaches that emphasize forest structure and the more recent approaches that also consider functional aspects of forests (e.g., Friend et al., 1997;

Bugmann et al., 1997) is feasible without losing too much precision in the functional considerations while burdening the relatively elegant gap model structure with a large amount of often unknown physiological parameters. Hence, the question that ecologists who study long-term dynamics of forests and the implications of global change for these systems are facing has two facets: (1) 'How much physiology and detail is required in gap models?'; and, just as important, (2) 'How much physiology and detail is feasible in gap models?'. The papers by Norby et al. (2001), Wullschleger et al. (2001), Price et al. (2001) and Keane et al. (2001) focus on these topics in much more detail.

5.2. ON THE BALANCE BETWEEN PROCESSES

Ecophysiology is mainly concerned with quantifying the effects of environmental factors on growth performance (e.g., Larcher, 1995), and much less on the implications of environmental factors for mortality and recruitment. Gap models that include physiological considerations at a high level of detail do so mainly with respect to growth processes. As a matter of fact, the mortality and recruitment formulations of 'mechanistic' gap models such as HYBRID are not significantly more sophisticated than their 'traditional' counterparts, and in some respects they are even coarser than what was conceptualized in JABOWA. Similarly, during several years of model development for 4C (Bugmann et al., 1997), a fairly sophisticated growth submodel has been produced, whereas recuitment and mortality processes are still treated fairly superficially.

The emphasis that is placed on tree growth in the more mechanistic gap models relative to the effort that goes into the modeling of mortality and recruitment certainly reflects our knowledge about the different processes. In other words, we emphasize and model what we know best. It is not obvious, however, that this emphasis reflects the real sensitivity of forest structure and composition to global change. It could well be that the major impacts of global change on long-term processes in forests are mediated though mortality and recruitment instead of tree growth. To a certain extent, mortality is a function of tree growth, but knowing the growth performance of a tree alone is insufficient to predict its mortality probability. Thus, research on recruitment and mortality processes of forest trees is a high priority area for further research that is indispensable if we are to increase our predictive understanding of long-term forest dynamics.

5.3. 'VALIDATION' OF FOREST GAP MODELS

There is no theory available for evaluating the validity of a model's predictions from its structure, and the same applies for the validity of a formulation of a specific process and the interactions between the different processes that are modeled. Quantitative methods for model 'validation' (although I would prefer the term 'evaluation'; Oreskes et al., 1994) are needed in addition to theoretical evaluations of models and model formulations (cf. Shugart, 1984, 1998).

At first sight, it may seem obvious that the behavior of models of long-term forest dynamics should be tested against time series data of biological observations. However, due to the scarcity of data sets on long-term changes of forest biomass, species composition, and size structure, the bulk of gap model evaluation efforts have focused on comparing model simulations against measured (or hypothesized, see below) data that refer to a single point in time. Therefore, I divide the discussion of model validation issues into those evaluation methods that deal with a single point in time, and those that deal with time series data.

5.3.1. *Single-Point Approaches*

When measured data are being used that refer to a specific sampling point in time and space, it is necessary to know the age of the stand to compare data from an appropriate point in time of the simulation with measured data. Alternatively, the assumption can be made that the measured data are from an 'equilibrium' ecosystem so that the empirical data can be compared to the simulated equilibrium values that result in the model after several centuries (e.g., Figure 14). Single-point approaches that have been used to evaluate forest gap models include the following:

- Since these models often are used to simulate succession in the absence of management regimes, it is a natural step to compare their projections in the equilibrium state between vegetation and climate with expert assessments on what constitutes the 'potential natural vegetation' (PNV) of an area (e.g., Küchler (1975) for North America, or Ellenberg (1986) for central Europe). While this approach can be useful for determining whether the right species are simulated to occur in a certain place, there are two major disadvantages with the concept of the PNV: (1) although based on field data, the PNV is a model construct itself, and the comparison thus essentially is a model-model comparison, and not a model-data comparison; and (2) most descriptions of the PNV are qualitative in nature and do not allow us to quantify the species-specific proportions of biomass, basal area, or other variables that are simulated by gap models; hence, the comparison is qualitative and, inevitably, 'fuzzy'. However, as a first test of the plausbility of the simulation results, comparisons to descriptions of the PNV are certainly useful, and there is hardly a gap model application where the concept of the PNW was not used to evaluate the 'realism' and 'plausibility' of model results.

- In some cases, measured DBH structure, species composition, or biomass has been compared quantitatively to gap model output. This has been achieved by using the estimated age of the stand to be simulated as a proxy for the simulation year used for the model-data comparison. An implicit assumption in this procedure is that the real stand originated from bare ground, which is not necessarily the case. Other problems involved in this approach are (1) the measured data usually are from small stands relative to the simulated average in gap models (for example, 100 replicate plots of $^1/_{12}$ ha each correspond to

an area of 8.3 ha, a stand size not often sampled in the real world), raising the question whether the measured data represent 'average' conditions; instead of comparing the average simulation results to the measured data, it may be more appropriate to evaluate the frequency distribution of the variables simulated for many patches against measured data; (2) any real forest stand was subject to a specific history in terms of weather events, natural disturbances, and most often also management regimes, even if the current forest is unmanaged; the simulated data, however, result from a random time series of weather (because the measured weather records often do not cover the entire life span of the stand), a random natural disturbance regime, and no human interventions. This complicates model comparisons against measured data considerably.

Evidently, these approaches can be useful and may even be necessary, but they are insufficient for a conclusive evaluation of the behavior of forest gap models. Additional methods are required, and those that rely on time series of measured data are especially powerful.

5.3.2. *Time Series Approaches*
At least three different sources of time series data have been used in the past to evaluate process formulations in gap models or the successional behavior of the models as a whole:

- Pollen data from mires and lakes have been used to evaluate model behavior on the time scale of millennia. This approach was pioneered by Solomon et al. (1980) and Solomon and Webb (1985), followed by several other authors (e.g., Davis and Botkin, 1985; Lotter and Kienast, 1992; Lischke et al., 1998). The advantage of the method is that it allows one to assess forest dynamics on very long time scales, but pollen data usually have a low temporal resolution, making it nearly impossible to determine the rates of change that occur on time scales faster than ≈100 yr. Note also that palynological data yield the relative frequency of pollen grains in a certain layer, whereas the simulation results typically refer to basal area or biomass, and transfer functions between the variables are uncertain.
- Tree rings represent a data source that is characterized by long records with annual or even sub-annual resolution. Ring width corresponds directly to diameter increment, the main state variable of many gap models, and thus is well suited for evaluating the simulated growth patterns. Tree-ring chronologies can be derived from the simulated growth of several trees analogous to dendrochronological procedures (e.g., growth trend removal). Only a few studies have attempted to use tree-ring data for the evaluation of gap models in the past (e.g., Keane et al., 1997; Bugmann and Pfister, 2000), and there is a large potential for further exploration of this method. Because precise input data are required for driving a gap model in this mode of application, the comparison will not usually cover more than 100–150 years at best, but

even such relatively short time series can be useful for evaluating simulated patterns with respect to the interannual variability of growth as well as decadal trends.

- Measured data from long-term forest trials extending over several decades to ≈100 yr have been used in a few approaches to estimate the initial state of the forest model and simulate its development across time (e.g., Lindner et al., 1997; Yaussy, 2000; Mäkelä et al., 2000). This is a potentially powerful approach for testing the growth submodels at the stand level; the other submodels cannot usually be tested with such data because establishment in forest trials is usually nil, and mortality is governed mainly by the thinning regime that was applied (cf. Lindner et al., 1997). It is unfortunate that this method has been exploited only marginally so far, which may be a consequence of the limited communication between the ecological research community, where the gap models are developed, and forestry research, where the trial experiments are maintained and documented.

While growth simulated at the tree and stand level can be tested from various angles (e.g., using forest trial data and tree-ring records), this is more difficult with tree mortality, where few approaches and experiences exist (cf. Pederson, 1998, 1999; Villalba and Veblen, 1998), and it is very difficult to evaluate tree establishment formulations; we are lacking both experience and reliable long-term data sets.

It is evident from the above considerations that there is a certain mismatch between the resolution and wealth of output variables provided by gap models and the availability and reliability of measured data. Hence, there is no single data source available that can be used to evaluate gap models. Rather, we should strive to combine several data sources for evaluating individual process formulations as well as the overall successional patterns that are simulated. A careful combination of sensitivity analyses, qualitative examinations of process formulations, and quantitative tests of gap models or selected submodels against various kinds of empirical data can serve to evaluate the usefulness of these models for assessing the impacts of global change on long-term forest dynamics, although it is impossible to devise a single model test that could 'validate' or falsify a gap model. The complexity of forest ecosystems is reflected to a certain extent in the much simpler, but still complex gap models, which in turn require complex protocols and procedures for model evaluation.

Lastly, the value of ecological models, including gap models, is not that they would be able to 'predict' the future; rather, it is that they can help us to understand processes and patterns in nature by allowing us to explore the consequences of a set of explicitly (i.e., mathematically) stated assumptions that are too complex to explore by other methods.

This does not imply that gap models could not be applied to study global change issues (cf. Smith, 1996), or for informing the policy-making process. However, the results of such modeling studies must not be taken at face value, but should

always be interpreted with respect to the model assumptions and the uncertainties in our knowledge. While this is true for all models, which represent deliberate simplifications of reality, it is crucial for complex models that are built to study long-term processes in complex ecosystems such as forests.

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References

Aber, J. D. and Melillo, J. M.: 1982, *FORTNITE: A Computer Model of Organic Matter and Nitrogen Dynamics in Forest Ecosystems*, Univ. of Wisconsin Res. Bulletin R3130.

Aber, J. D., Botkin, D. B., and Melillo, J. M.: 1978, 'Predicting the Effects of Different Harvesting Regimes on Forest Floor Dynamics in Northern Hardwoods', *Can. J. For. Res.*, **8**, 306-315.

Aber, J. D., Botkin, D. B. and Melillo, J. M.: 1979, 'Predicting the effects of different harvesting regimes on productivity and yield in northern hardwoods', *Can. J. Forest Res.* **9**, 10–14.

Aber, J. D., Melillo, J. M., and Federer, C. A.: 1982, 'Predicting the Effects of Rotation Length, Harvest Intensity, and Fertilization on Fiber Yield from Northern Hardwood Forests in New England', *Forest Sci.* **28**, 31–45.

Acevedo, M. F., Urban, D. L., and Ablan, M.: 1995, 'Transition and Gap Models of Forest Dynamics', *Ecol. Appl.* **5**, 1040–1055.

Allen, C. D. and Breshears, D. D.: 1998, 'Drought-Induced Shift of a Forest-Woodland Ecotone: Rapid Landscape Response to Climate Variation', *Proc. Nat. Acad. Sci. U.S.A.* **95**, 14839–14842.

Amthor, J. S.: 1995, 'Terrestrial Higher-Plant Response to Increasing Atmospheric [CO_2] in Relation to the Global Carbon Cycle', *Global Change Biol.* **1**, 243–274.

Andrzejczyk, T. and Brzeziecki, B.: 1995, 'The Structure and Dynamics of Old-Growth *Pinus sylvestris* (L.) Stands in the Wigry National Park, North-Eastern Poland', *Vegetatio* **117**, 81–94.

Aubréville, A.: 1938, 'La forêt coloniale: Les forêts de l'Afrique occidentale française', *Ann. Acad. Sci. Colon. Paris* **9**, 1–245.

Badeck, F.-W., Lischke, H., Bugmann, H., Hickler, T., Hönninger, K., Lasch, P., Lexer, M. J., Mouillot, F., Schaber, J., and Smith, B.: 2001, 'Tree Species Composition in European Pristine Forests. Comparison of Stand Data to Model Predictions', *Clim. Change* **51**, 307–347.

Belsky, A. J. and Canham, C. D.: 1994, 'Forest Gaps and Isolated Savanna Trees', *Bioscience* **44**, 77–84.

Bonan, G. B.: 1993, 'Do Biophysics and Physiology Matter in Ecosystem Models?', *Clim. Change* **24**, 281–285.

Bonan, G. B. and Sirois, L.: 1992, 'Air Temperature, Tree Growth, and the Northern and Southern Range Limits to *Picea mariana*', *J. Veg. Sci.* **3**, 495–506.

Bormann, F. H., Siccama, T. G., Likens, G. E., and Whittaker, R. H.: 1970, 'The Hubbard Brook Ecosystem Study: Composition and Dynamics of the Tree Stratum', *Ecol. Monogr.* **40**, 373–388.

Bossel, H. and Krieger, H.: 1994, 'Simulation of Multi-Species Tropical Forest Dynamics Using a Vertically and Horizontally Structured Model', *For. Ecol. Manage.* **69**, 123–144.

Botkin, D. B.: 1993, *Forest Dynamics: An Ecological Model*, Oxford University Press, Oxford and New York, p. 309.

Botkin, D. B., Janak, J. F., and Wallis, J. R.: 1970, *A Simulator for Northeastern Forest Growth*, Research Report 3140, IBM Thomas J. Watson Research Center, Yorktown Heights, N.Y.

Botkin, D. B., Janak, J. F., and Wallis, J. R.: 1972a, 'Rationale, Limitations and Assumptions of a Northeastern Forest Growth Simulator', *IBM J. Res. Develop.* **16**, 101–116.

Botkin, D. B., Janak, J. F., and Wallis, J. R.: 1972b, 'Some Ecological Consequences of a Computer Model of Forest Growth', *J. Ecol.* **60**, 849–872.

Botkin, D. B., Janak, J. F., and Wallis, J. R.: 1973, 'Estimating the Effects of Carbon Fertilization on Forest Composition by Ecosystem Simulation', in Woodwell, G. M. and Pecan, E. V. (eds.), *Carbon and the Biosphere*, U.S. Department of Commerce, Washington D.C., pp. 328–344.

Bugmann, H.: 1994, *On the Ecology of Mountainous Forests in a Changing Climate: A Simulation Study*, Ph.D. Thesis No. 10638, Swiss Federal Institute of Technology Zurich, Switzerland, p. 258.

Bugmann, H.: 1996, 'A Simplified Forest Model to Study Species Composition along Climate Gradients', *Ecology* **77**, 2055–2074.

Bugmann, H.: 1999, 'Anthropogene Klimaveränderung, Sukzessionsprozesse und forstwirtschaftliche Optionen', *Schweiz. Z. Forstwesen* **150**, 275–287.

Bugmann, H. and Martin, P.: 1995, 'How Physics and Biology Matter in Forest Gap Models', *Clim. Change* **29**, 251–257.

Bugmann, H. and Cramer, W.: 1998, 'Improving the Behaviour of Forest Gap Models along Drought Gradients', *For. Ecol. Manage.* **103**, 247–263.

Bugmann, H. K. M. and Solomon, A. M.: 2000, 'Explaining Forest Biomass and Species Composition across Multiple Biogeographical Regions', *Ecol. Appl.* **10**, 95–114.

Bugmann, H. and Pfister, Ch.: 2000, 'Impacts of Interannual Climate Variability on Past and Future Forest Composition', *Regional Environ. Change* **1**, 112–125.

Bugmann, H. K. M., Yan Xiaodong, Sykes, M. T., Martin, Ph., Lindner, M., Desanker, P. V., and Cumming, S. G.: 1996, 'A Comparison of Forest Gap Models: Model Structure and Behaviour', *Clim. Change* **34**, 289–313.

Bugmann, H., Grote, R., Lasch, P., Lindner, M., and Suckow, F.: 1997, 'A New Forest Gap Model to Study the Effects of Environmental Change on Forest Structure and Functioning', in Mohren, G. M. J., Kramer, K., and Sabaté, S. (eds.), *Global Change Impacts on Tree Physiology and Forest Ecosystems*, Kluwer Academic Publishers, pp. 255–261.

Bugmann, H., Lindner, M., Lasch, P., Flechsig, M., Ebert, B., and Cramer, W.: 2000, 'Scaling Issues in Forest Succession Modelling', *Clim. Change* **44**, 265–289.

Bugmann, H. K. M., Wullschleger, S. D., Price, D. T., Ogle, K., Clark, D. F., and Solomon, A. M.: 2001, 'Comparing the Performance of Forest Gap Models in North America', *Clim. Change* **51**, 349–388.

Busing, R. T.: 1998, 'Composition, Structure and Diversity of Cove Forest Stands in the Great Smoky Mountains: A Patch Dynamics Perspective', *J. Veg. Sci.* **9**, 881–890.

Clark, J. S. and Ji, Y.: 1995, 'Fecundity and Dispersal in Plant-Populations – Implications for Structure and Diversity', *Amer. Nat.* **146**, 72–111.

Clements, F. E.: 1916, *Plant Succession: An Analysis of the Development of Vegetation*, Carnegie Inst. Pub., Washington, D.C., **242**, p. 512.

Coffin, D. P. and Lauenroth, W. K.: 1990, 'A Gap Dynamics Simulation Model of Succession in a Semiarid Grassland', *Ecol. Modelling* **49**, 229–236.

Cramer, W., Shugart, H. H., Noble, I. R., Woodward, F. I., Bugmann, H., Bondeau, A., Foley, J. A., Gardner, R. H., Lauenroth, W. K., Pitelka, L. F., Sala, O. E., and Sutherst, R. W.: 1999, 'Ecosystem Composition and Structure', in Walker, B. H., Steffen, W. L., Canadell, J., and Ingram, J. S. I. (eds.), *Global Change and the Terrestrial Biosphere: Implications for Natural and Managed Ecosystems. A Synthesis of GCTE and Related Research*, IGBP Book Series No. 4, Cambridge University Press, Cambridge, pp. 190–228.

Dale, V. H. and Hemstrøm, M.: 1984, *CLIMACS: A Computer Model of Forest Stand Development for Western Oregon and Washington*, Res. Paper PNW-327, Pacific Forest and Range Experiment Station, U.S. Department of Agriculture, Forest Service, p. 60.

Dale, V. H., Doyle, T. W., and Shugart, H. H.: 1985, 'A Comparison of Tree Growth Models', *Ecol. Modelling* **29**, 145–169.

Davis, M. B.: 1989, 'Lags in Vegetation Response to Greenhouse Warming', *Clim. Change* **15**, 75–82.

Davis, M. B. and Botkin, D. B.: 1985, 'Sensitivity of Cool-Temperate Forests and their Fossil Pollen Record to Rapid Temperature Change', *Quat. Res.* **23**, 327–340.

Desanker, P. V.: 1996, 'Development of a Miombo Woodland Dynamics Model in Zambezian Africa Using Malawi as a Case Study', *Clim. Change* **34**, 279–288.

Doyle, T. W.: 1981, 'The Role of Disturbance in the Gap Dynamics of a Montane Rain Forest: An Application of a Tropical Forest Succession Model', in West, D. C., Shugart, H. H., and Botkin, D. B. (eds.), *Forest Succession: Concepts and Application*, Springer, New York a.o., pp. 56–73.

Ellenberg, H.: 1986, *Vegetation Mitteleuropas mit den Alpen in ökologischer Sicht*, Verlag Eugen Ulmer, Stuttgart, 4th edn, p. 989.

Farquhar, G. D., von Caemmerer, S., and Berry, J. A.: 1980, 'A Biochemical Model of Photosynthetic CO_2 Assimilation in Leaves of C_3 Species', *Planta* **149**, 78–90.

Fischlin, A., Bugmann, H., and Gyalistras, D.: 1995, 'Sensitivity of a Forest Ecosystem Model to Climate Parametrization Schemes', *Environ. Pollut.* **87**, 267–282.

Frelich, L. E. and Lorimer, C. G.: 1991, 'Natural Disturbance Regimes in Hemlock-Hardwood Forests of the Upper Great Lakes Region', *Ecol. Monogr.* **61**, 145–164.

Friend, A. D., Shugart, H. H., and Running, S. W.: 1993, 'A Physiology-Based Gap Model of Forest Dynamics', *Ecology* **74**, 792–797.

Friend, A. D., Stevens, A. K., Knox, R. G., and Cannell, M. G. R.: 1997, 'A Process-Based, Terrestrial Biosphere Model of Ecosystem Dynamics (HYBRID v3.0)', *Ecol. Modelling* **95**, 249–287.

Fulton, M.: 1991, 'A Computationally Efficient Forest Succession Model: Design and Initial Tests', *For. Ecol. Manage.* **42**, 23–34.

Fulton, M. R.: 1993, 'Rapid Simulations of Vegetation Stand Dynamics with Mixed Life-Forms', in Solomon, A. M. and Shugart, H. H. (eds.), *Vegetation Dynamics and Global Change*, Chapman and Hall, New York a.o., pp. 251–271.

Gignoux, J., Noble, I., and Menaut, J. C.: 1995, 'Modelling Tree Community Dynamics in Savannas: Effects of Competition with Grasses and Impact of Disturbance', in Bellan-Santini, D., Bonin, G.,

and Emig, C. (eds.), *Functioning and Dynamics of Natural and Perturbed Ecosystems*, Lavoisier Publishing, Paris, pp. 219–230.

Gleason, H. A.: 1926, 'The Individualistic Concept of the Plant Association', *Bull. Torrey Bot. Club* **53**, 7–26.

Goff, F. G. and West, D.: 1975, 'Canopy-Understory Interaction Effects on Forest Population Structure', *Forest Sci.* **21**, 98–108.

Harcombe, P. A.: 1987, 'Tree Life Tables', *Bioscience* **37**, 557–568.

Haxeltine, A. and Prentice, I. C.: 1996, 'A General Model for the Light Use Efficiency of Primary Production by Terrestrial Ecosystems', *Func. Ecol.* **10**, 551–561.

Horn, H. S.: 1971, *The Adaptive Geometry of Trees*, Princeton University Press, Princeton, N.J.

Humphries, H. C., Coffin, D. P., and Lauenroth, W. K.: 1996, 'An Individual-Based Model of Alpine Plant Distributions', *Ecol. Modelling* **84**, 99–126.

Hurtt, G. C., Moorcroft, P. R., Pacala, S. W., and Levin, S. A.: 1998, 'Terrestrial Models and Global Change: Challenges for the Future', *Global Change Biol.* **4**, 581–590.

Huth, A., Ditzer, T., and Bossel, H.: 1998, *The Rain Forest Growth Model FORMIX3 – Model Description and Analysis of Forest Growth and Logging Scenarios for the Deramakot Forest Reserve (Malaysia)*, Erich Goltze Publishers, Göttingen.

Jorritsma, I. T. M., van Hees, A. F. M., and Mohren, G. M. J.: 1999, 'Forest Development in Relation to Ungulate Grazing: A Modeling Approach', *For. Ecol. Manage.* **120**, 23–34.

Keane, R. E., Arno, S. F., Brown, J. K., and Tomback, D. F.: 1990, 'Modelling Stand Dynamics in Whitebark Pine (*Pinus albicaulis*) Forests', *Ecol. Modelling* **51**, 73–95.

Keane, R. E., Morgan, P., and Running, S. W.: 1996, *FIRE-BGC – A Mechanistic Ecological Process Model for Simulating Fire Succession on Coniferous Forest Landscapes of the Northern Rocky Mountains*, USDA Forest Service Research Paper INT-RP-484, p. 122.

Keane, R. E., Hardy, C. C., Ryan, K. C., and Finney, M. A.: 1997, 'Simulating Effects of Fire on Gaseous Emissions and Atmospheric Carbon Fluxes from Coniferous Forest Landscapes', *World Resource Rev.* **9**, 177–205.

Keane, R. E., Austin, M., Dahlman, R., Field, C., Huth, A., Lexer, M. J., Peters, D., Solomon, A., and Wyckoff, P.: 2001, 'Tree Mortality in Gap Models: Application to Climate Change', *Clim. Change* **51**, 509–540.

Kellomäki, S., Väisänen, H., Hänninen, H., Kolström, T., Lauhanen, R., Mattila, U., and Pajari, B.: 1992, 'SIMA: A Model for Forest Succession Based on the Carbon and Nitrogen Cycles with Application to Silvicultural Management of the Forest Ecosystem', *Silva Carelica* **22**, 91.

Ker, J. W. and Smith, J. H. G.: 1955, 'Advantages of the Parabolic Expression of Height-Diameter Relationships', *For. Chron.* **31**, 235–246.

Kercher, J. R. and Axelrod, M. C.: 1984, 'A Process Model of Fire Ecology and Succession in a Mixed-Conifer Forest', *Ecology* **65**, 1725–1742.

Kienast, F.: 1987, *FORECE – A Forest Succession Model for Southern Central Europe*, Oak Ridge National Laboratory, Oak Ridge, Tennessee, ORNL/TM-10575, p. 69.

Kienast, F.: 1991, 'Simulated Effects of Increasing CO_2 on the Successional Characteristics of Alpine Forest Ecosystems', *Landscape Ecol.* **5**, 225–238.

Kienast, F., Fritschi, J., Bissegger, M., and Abderhalden, W.: 1999, 'Modelling Successional Patterns of High-Elevation Forests under Changing Herbivore Pressure – Responses at the Landscape Level', *For. Ecol. Manage.* **120**, 35–46.

Körner, C.: 1996, 'The Response of Complex Multispecies Systems to Elevated CO_2', in Walker, B. and Steffen, W. (eds.), *Global Change and Terrestrial Ecosystems*, Cambridge University Press, Cambridge, pp. 20–42.

Kohyama, T.: 1993, 'Size-Structured Tree Populations in Gap-Dynamic Forest – the Forest Architecture Hypothesis for the Stable Coexistence of Species', *J. Ecol.* **81**, 131–143.

Kohyama, T.: 1994, 'Size-Structure-Based Models of Forest Dynamics to Interpret Population- and Community-Level Mechanisms', *J. Plant Res.* **107**, 107–116.

Kohyama, T. and Shigesada, N.: 1995, 'A Size-Distribution-Based Model of Forest Dynamics along a Latitudinal Environmental Gradient', *Vegetatio* **121**, 117–126.

Korol, R. L., Running, S. W., and Milner, K. S.: 1995, 'Incorporating Intertree Competition into an Ecosystem Model', *Can. J. Forest Res.* **25**, 413–424.

Korzukhin, M. D., Rubinina, A. E., Bonan, G. B., Solomon, A. M., and Antonovsky, M. Y.: 1989, *The Silvics of Some East European and Siberian Boreal Forest Tree Species,* WP-89-56, International Institute for Applied Systems Analysis, Laxenburg, Austria.

Küchler, A. W.: 1975, *Potential Natural Vegetation of the Conterminous United States 1:3,168,000*, Amer. Geogr. Soc. Spec. Publ. No. 36.

Larcher, W.: 1995, *Physiological Plant Ecology*, Springer, Berlin a.o., 3rd edn, p. 506.

Leemans, R.: 1992, 'The Biological Component of the Simulation Model for Boreal Forest Dynamics', in Shugart, H. H., Leemans, R., and Bonan, G. B. (eds.), *A Systems Analysis of the Global Boreal Forest*, Cambridge Univ. Press, Cambridge a.o., pp. 428–445.

Leemans, R. and Prentice, I. C.: 1989, *FORSKA, a General Forest Succession Model*, Institute of Ecological Botany, Uppsala, p. 70.

Lemée, G.: 1987, 'Dynamique de fermeture par régénération et évolution morphométrique du hêtre dans les vides d'une forêt non exploitée (Réserves biologiques de la fôret de Fontainebleau)', *Bull. Ecol.* **18**, 1–11.

Lertzman, K. P. and Krebs, C. J.: 1991, 'Gap-Phase Structure of a Subalpine Old-Growth Forest', *Can. J. Forest Res.* **21**, 1730–1741.

Lertzman, K. P., Sutherland, G. D., Inselberg, A., and Saunders, S. C.: 1996, 'Canopy Gaps and the Landscape Mosaic in a Coastal Temperate Rain Forest', *Ecology* **77**, 1254–1270.

Lexer, M. J. and Hönninger, K.: 1998a, 'Simulated Effects of Bark Beetle Infestations on Stand Dynamics in *Picea abies* Stands: Coupling a Patch Model and a Stand Risk Model', in Beniston, M. and Innes, J. L. (eds.), *The Impacts of Climate Variability on Forests*, Lecture Notes in Earth Sciences Vol. 74, Springer-Verlag, Berlin a.o., pp. 289–308.

Lexer, M. J. and Hönninger, K.: 1998b, *Computergestützte Simulation der Waldentwicklung*, Report, Institut für Waldbau, Universität für Bodenkultur Wien, p. 176.

Lindner, M., Lasch, P., and Cramer, W.: 1996, 'Application of a Forest Succession Model to a Continentality Gradient through Central Europe', *Clim. Change* **34**, 179–190.

Lindner, M., Sievänen, R., and Pretzsch, H.: 1997, 'Improving the Simulation of Stand Structure in a Forest Gap Model through a Flexible Height Growth Function', *For. Ecol. Manage.* **95**, 183–195.

Lischke, H., Löffler, T. J., and Fischlin, A.: 1998, 'Aggregation of Individual Trees and Patches in Forest Succession Models – Capturing Variability with Height Structured Random Dispersions', *Theor. Popul. Biol.* **54**, 213–226.

Lischke, H., Guisan, A., Fischlin, A., Williams, J., and Bugmann, H.: 1998, 'Vegetation Responses to Climate Change in the Alps: Modeling Studies', in Cebon, P., Dahinden, U., Davies, H., Imboden, D., and Jäger, C. (eds.), *A View from the Alps: Regional Perspectives on Climate Change*, MIT Press, Cambridge, Massachusetts, pp. 309–350.

Liu, J. and Ashton, P. S.: 1995, 'Individual-Based Simulation Models for Forest Succession and Management', *For. Ecol. Manage.* **73**, 157–175.

Löffler, T. J. and Lischke, H.: 2001, 'Incorporation and Influence of Variability in an Aggregated Forest Model', *Natural Resource Modeling* **14**, 103–137.

Loehle, C. and LeBlanc, D.: 1996, 'Model-Based Assessments of Climate Change Effects on Forests: A Critical Review', *Ecol. Modelling* **90**, 1–31.

Lotter, A. and Kienast, F.: 1992, 'Validation of a Forest Succession Model by Means of Annually Laminated Sediments', in Saarnisto, M. and Kahra, A. (eds.), *Proceedings of the INQUA Workshop on Laminated Sediments, June 4–6, 1990, Lammi, Finland*, Geological Survey of Finland, Special Paper Series, **14**, pp. 25–31.

Mäkelä, A.: 1986, 'Implications of the Pipe Model Theory on Dry Matter Partitioning and Height Growth in Trees', *J. Theor. Biol.* **123**, 103–120.

Mäkelä, A.: 1990, 'Modeling Structural-Functional Relationships in Whole-Tree Growth: Resource Allocation', in Dixon, R. K., Meldahl, R. S., Ruark, G. A., and Warren, W. G. (eds.), *Process Modeling of Forest Growth Responses to Environmental Stress*, Timber Press, Portland, Oregon, pp. 81–95.

Mäkelä, A., Sievänen, R., Lindner, M., and Lasch, P.: 2000, 'Application of Volume Growth and Survival Graphs in the Evaluation of Four Process-Based Forest Growth Models', *Tree Physiol.* **20**, 347–355.

Meentemeyer, V.: 1978, 'Macroclimate and Lignin Control of Litter Decomposition Rates', *Ecology* **59**, 465–472.

Miller, C. and Urban, D. L.: 1999, 'Forest Pattern, Fire, and Climatic Change in the Sierra Nevada', *Ecosystems* **2**, 76–87.

Mooney, H. A., Canadell, J., Chapin, F. S. III, Ehleringer, J. R., Körner, Ch., McMurtrie, R. E., Parton, W. J., Pitelka, L. F., and Shulze, E.-D.: 1999, 'Ecosystem Physiology Responses to Global Change', in Walker, B. H., Steffen, W. L., Canadell, J., and Ingram, J. S. I. (eds.), *Global Change and the Terrestrial Biosphere: Implications for Natural and Managed Ecosystems. A Synthesis of GCTE and Related Research*, IGBP Book Series No. 4, Cambridge University Press, Cambridge, pp. 141–189.

Moore, A. D.: 1989, 'On the Maximum Growth Equation Used in Forest Gap Simulation Models', *Ecol. Modelling* **45**, 63–67.

Munro, D. D.: 1974, 'Forest Growth Models: A Prognosis', in Fries, J. (ed.), *Growth Models for Tree and Stand Simulation*, Dept. of Forest Yield Research, Royal College of Forestry, Stockholm Res. Notes Vol. 30.

Newnham, R. M.: 1964, *The Development of a Stand Model for Douglas-Fir*, Ph.D. Thesis, Faculty of Forestry, University of British Columbia, Vancouver, p. 201.

Norby, R. J., Ogle, K., Curtis, P. S., Badeck, F.-W., Huth, A., Hurtt, G. C., Kohyama, T., and Peñuelas, J.: 2001, 'Aboveground Growth and Competition in Forest Patch Models: An Analysis for Studies of Climatic Change', *Clim. Change* **51**, 415–447.

Oreskes, N., Shrader-Frechette, K., and Belitz, K.: 1994, 'Verification, Validation, and Confirmation of Numerical Models in the Earth Sciences', *Science* **263**, 641–646.

Pacala, S. W. and Hurtt, G. C.: 1993, 'Terrestrial Vegetation and Climate Change: Integrating Models and Experiments', in Kareiva, P. M., Kingsolver, J. G., and Huey, R. B. (eds.), *Biotic Interactions and Global Change*, Sinauer Associates, Sunderland MA, pp. 57–74.

Pacala, S. W., Canham, C. D., and Silander Jr., J. A.: 1993, 'Forest Models Defined by Field Measurements: I. The Design of a Northeastern Forest Simulator', *Can. J. Forest Res.* **23**, 1980–1988.

Pacala, S. W., Canham, C. D., Saponara, J., Silander, J. A., Kobe, R. K., and Ribbens, E.: 1996, 'Forest Models Defined by Field Measurements: Estimation, Error Analysis and Dynamics', *Ecol. Monogr.* **66**, 1–43.

Pastor, J. and Post, W. M.: 1985, *Development of a Linked Forest Productivity-Soil Process Model*, U.S. Dept. of Energy, ORNL/TM-9519.

Pastor, J. and Post, W. M.: 1988, 'Response of Northern Forests to CO_2-Induced Climate Change', *Nature* **334**, 55–58.

Pedersen, B. S.: 1998, 'The Role of Stress in the Mortality of Midwestern Oaks as Indicated by Growth Prior to Death', *Ecology* **79**, 79–93.

Pedersen, B. S.: 1999, 'The Mortality of Midwestern Overstory Oaks as a Bioindicator of Environmental Stress', *Ecol. Appl.* **9**, 1017–1027.

Pickett, S. T. A. and White, P. S.: 1985, *The Ecology of Natural Disturbance and Patch Dynamics*, Academic Press, Orlando a.o., p. 472.

Prentice, I. C., Sykes, M. T., and Cramer, W.: 1993, 'A Simulation Model for the Transient Effects of Climate Change on Forest Landscapes', *Ecol. Modelling* **65**, 51–70.

Prentice, I. C., Cramer, W., Harrison, S. P., Leemans, R., Monserud, R. A., and Solomon, A. M.: 1992, 'A Global Biome Model Based on Plant Physiology and Dominance, Soil Properties and Climate', *J. Biogeogr.* **19**, 117–134.

Price, D. T. and Apps, M. J.: 1995, 'The Boreal Forest Transect Case Study: Global Change Effects on Ecosystem Processes and Carbon Dynamics in Boreal Canada', *Water Air Soil Pollut.* **82**, 203–214.

Price, D. T. and Apps, M. J.: 1996, 'Boreal Forest Responses to Climate-Change Scenarios along an Ecoclimatic Transect in Central Canada', *Clim. Change* **34**, 179–190.

Price, D. T., Zimmermann, N. E., van der Meer, P. J., Lexer, M. J., Leadley, P., Jorritsma, I. T. M., Schaber, J., Clark, D. F., Lasch, P., McNulty, S., Wu, J., and Smith, B.: 2001, 'Regeneration in Gap Models: Priority Issues for Studying Forest Response to Climate Change', *Clim. Change* **51**, 475–508.

Reynolds, J. F., Acock, B., and Whitney, R.: 1993, 'Linking CO_2 Experiments and Modeling', in Schulze, E.-D. and Mooney, H. A. (eds.), *Design and Execution of Experiments on CO_2 Enrichment*, Report No. 6, Ecosystems Research Series of Environmental Research Programme, Commission of the European Communities, Brussels, pp. 93–106.

Schenk, H. J.: 1996, 'Modeling the Effects of Temperature on Growth and Persistence of Tree Species: A Critical Review of Tree Population Models', *Ecol. Modelling* **92**, 1–32.

Schulze, E.-D., Fuchs, M., and Fuchs, M. I.: 1977, 'Spatial Distribution of Photosynthetic Capacity and Performance in a Mountain Spruce Forest of Northern Germany. I. Biomass Distribution and Daily CO_2 Uptake in Different Crown Layers', *Oecologia* **29**, 43–61.

Shao, G., Schall, P., and Weishampel, J. F.: 1994, 'Dynamic Simulations of Mixed Broadleaved *Pinus koraiensis* Forests in the Changbaishan Biosphere Reserve of China', *For. Ecol. Manage.* **70**, 169–181.

Shao, G., Shugart, H. H., and Smith, T. M.: 1995, 'A Role-Type Model (Rope) and its Application in Assessing Climate Change Impacts on Forest Landscapes', *Vegetatio* **121**, 135–146.

Shao, G., Bugmann, H., and Yan, X.: 2001, 'A Comparative Analysis of the Structure and Behavior of Three Gap Models at Sites in Northeastern China', *Clim. Change* **51**, 389–413.

Shinozaki, K., Yoda, K., Hozumi, K., and Kira, T.: 1964, 'A Quantitative Analysis of Plant Form – the Pipe Model Theory. I. Basic Analyses', *Jap. J. Ecol.* **14**, 97–105.

Shugart, H. H.: 1984, *A Theory of Forest Dynamics. The Ecological Implications of Forest Succession Models*, Springer, New York a.o., p. 278.

Shugart, H. H.: 1998, *Terrestrial Ecosystems in Changing Environments*, Cambridge Studies in Ecology, Cambridge University Press, Cambridge, p. 537.

Shugart, H. H. and West, D. C.: 1977, 'Development of an Appalachian Deciduous Forest Succession Model and its Application to Assessment of the Impact of the Chestnut Blight', *J. Environ. Manage.* **5**, 161–179.

Shugart, H. H. and West, D. C.: 1979, 'Size and Pattern of Simulated Forest Stands', *Forest Sci.* **25**, 120–122.

Shugart, H. H. and West, D. C.: 1980, 'Forest Succession Models', *Bioscience* **30**, 308–313.

Shugart, H. H. and Noble, I. R.: 1981, 'A Computer Model of Succession and Fire Response of the High-Altitude Eucalyptus Forest of the Brindabella Range, Australian Capital Territory', *Aust. J. Ecol.* **6**, 149–164.

Shugart, H. H. and Emanuel, W. R.: 1985, 'Carbon Dioxide Increase: The Implications at the Ecosystem Level', *Plant Cell Environ.* **8**, 381–386.

Shugart, H. H. and Smith, T. M.: 1996, 'A Review of Forest Patch Models and their Application to Global Change Research', *Clim. Change* **34**, 131–153.

Siccama, T. G., Botkin, D. B., Bormann, F. H., and Likens, G. E.: 1969, 'Computer Simulation of a Northern Hardwood Forest', *Bull. Ecol. Soc. Amer.* **50**, 93.

Smith, T. M. (ed.): 1996, 'The Application of Patch Models of Vegetation Dynamics to Global Change Issues', *Clim. Change* **34**, 131–313.

Solomon, A. M.: 1986, 'Transient Response of Forests to CO_2-Induced Climate Change: Simulation Modeling Experiments in Eastern North America', *Oecologia* **68**, 567–579.

Solomon, A. M. and Webb, T.: 1985, 'Computer-Aided Reconstruction of Late-Quaternary Landscape Dynamics', *Ann. Rev. Ecol. Syst.* **16**, 63–84.

Solomon, A. M., Delcourt, H. R., West, D. C., and Blasing, T. J.: 1980, 'Testing a Simulation Model for Reconstruction of Prehistoric Forest-Stand Dynamics', *Quat. Res.* **14**, 275–293.

Szwagrzyk, J.: 1992, 'Small-Scale Spatial Patterns of Trees in a Mixed *Pinus sylvestris-Fagus silvatica* Forest', *For. Ecol. Manage.* **51**, 301–315.

Talkkari, A., Kellomäki, S., and Peltola, H.: 1999, 'Bridging a Gap between a Gap Model and a Physiological Model for Calculating the Effect of Temperature on Forest Growth under Boreal Conditions', *For. Ecol. Manage.* **119**, 137–150.

Tansley, A. G.: 1935, 'The Use and Abuse of Vegetational Concepts and Terms', *Ecology* **16**, 284–307.

Thornthwaite, C. W. and Mather, J. R.: 1957, 'Instructions and Tables for Computing Potential Evapotranspiration and the Water Balance', *Publ. Climatol.* **10**, 183–311.

Urban, D. L.: 1990, *A Versatile Model to Simulate Forest Pattern: A User's Guide to Zelig 1.0*, Univ. of Virginia, Dept. of Environmental Sciences, Charlottesville, Virginia, p. 108.

Urban, D. L. and Shugart, H. H.: 1992, 'Individual-Based Models of Forest Succession', in Glenn-Lewin, D. C., Peet, R. K., and Veblen, T. T. (eds.), *Plant Succession: Theory and Prediction*, Chapman and Hall, London a.o., pp. 249–292.

Urban, D. L., Acevedo, M. F., and Garman, S. L.: 1999, 'Scaling Fine-Scale Processes to Large-Scale Patterns Using Models Derived from Models: Meta-Models', in Mladenoff, D. J. and Baker, W. L. (eds.), *Spatial Modeling of Forest Landscape Change*, Cambridge University Press, Cambridge, pp. 70–98.

Urban, D. L., Bonan, G. B., Smith, T. M., and Shugart, H. H.: 1991, 'Spatial Applications of Gap Models', *For. Ecol. Manage.* **42**, 95–110.

Villalba, R. and Veblen, T. T.: 1998, 'Influences of Large-Scale Climatic Variability on Episodic Tree Mortality in Northern Patagonia', *Ecology* **79**, 2624–2640.

Waring, R. H.: 1987, 'Characteristics of Trees Predisposed to Die', *Bioscience* **37**, 569–574.

Waring, R. H. and Schlesinger, W. H.: 1985, *Forest Ecosystems: Concepts and Management*, Academic Press, London a.o., p. 340.

Waring, R. H. and Running, S. W.: 1998, *Forest Ecosystems: Analysis at Multiple Scales*, Academic Press, San Diego a.o., p. 370.

Watt, A. S.: 1925, 'On the Ecology of British Beechwoods with Special Reference to their Regeneration', *J. Ecol.* **13**, 27–73.

Weishampel, J. F. and Urban, D. L.: 1996, 'Coupling a Spatially-Explicit Forest Gap Model with a 3-D Solar Routine to Simulate Latitudinal Effects', *Ecol. Modelling* **86**, 101–111.

Whittaker, R. H.: 1953, 'A Consideration of Climax Theory: The Climax as a Population and Pattern', *Ecol. Monogr.* **23**, 41–78.

Wullschleger, S. D., Jackson, R. B., Currie, W. S., Friend, A. D., Luo, Y., Mouillot, F., Pan, Y., and Shao, G.: 2001, 'Below-Ground Processes in Gap Models for Simulating Forest Response to Global Change', *Clim. Change* **51**, 449–473.

Yan, X. and Zhao, S.: 1995, 'Simulating the Carbon Storage Dynamics of Temperate Broad-Leaved Coniferous Mixed Forest Ecosystems: I. Dynamics of the Tree Layer of Broad-Leaved Korean Pine Forests in Changbai Mountain', *Chinese J. Ecol.* **14**, 6–12.

Yaussy, D. A., 2000, 'Comparison of an Empirical Forest Growth and Yield Simulator and a Forest Gap Simulator Using Actual 30-Year Growth from Two Even-Aged Forests in Kentucky', *For. Ecol. Manage.* **126**, 385–398.