Individual-based simulation models for forest succession and management

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Abstract

Individual-based forest models simulate forest dynamics on the basis of establishment, growth and death of individual trees. This paper attempts to review and compare two major types of individual-based forest models: growth–yield and gap models. Although the two types of models share some similar features, they differ in model structure and data requirements and play several complementary roles. Growth–yield models are used by foresters to assist timber production and evaluate growth and yield of one to several commercial timber species in managed forests, while gap models are generally developed by ecologists to explore ecological mechanisms and patterns of structure and functional dynamics in natural forest ecosystems. Site-specific environmental and species information is necessary for constructing growth–yield models while gap models require species-specific biological information of individual trees and site-specific environmental data. The growth–yield models are more diverse in terms of model structure. In contrast, gap models belong to the same genealogy and later gap models are ultimately derived from the earliest one although they may vary in detail. In the future, we expect to see more individual-based hybrid models which integrate gap models with growth–yield models and ecophysiological models. As computer technology advances explosively, individual-based models could be much more efficient and user-friendly. There have existed disproportionately few individual-based models for biodiverse forests such as evergreen tropical rain forests. Development of individual-based models for tropical rain forests is more challenging and is being stimulated by new international conservation efforts.

Keywords: Forest succession; Forest management; Individual-based model; Gap model; Growth–yield model; Simulation

1. Introduction

To understand and project forest dynamics, modeling has proven to be a useful tool and numerous models have been published. Munro (1974) classified forest models into two major

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categories: stand models and individual-based models. Stand models are those constructed on the information at stand level such as tree density and total basal area (Clutter, 1963; Vanclay, 1989; Borders et al., 1990). Individual-based models simulate each individual tree as a unique entity in respect to establishment, growth and death (Huston et al., 1988; Huston, 1992; DeAngelis and Gross, 1992).

In this paper, we concentrate on individual-based models. Individual trees are the basic units

of a forest. They are usually different from each other in location, size, and behavior such as response to environmental stress, growth and reproduction patterns. The impacts of each individual tree on its neighbors and the effects of the neighbors on a focal individual tree vary (Huston et al., 1988). Individual-based models track species- and size-specific demographic behaviors and have become a major means to mimicking forest dynamics (DeAngelis and Gross, 1992).

Since Newnham (1964) published the first individual-based model, hundreds of models have been developed, tested, and applied to forest research and management (Munro, 1974; Shugart, 1984). We attempt to review the individual-based growth–yield and gap models. Growth–yield models provide managers with information about growth and yield of timber trees (Monserud, 1990), while gap models help ecologists understand forest successional patterns and processes (Shugart, 1984). A forest gap is an area created either by the fall of a tree or by clearing (Botkin et al., 1972a; Shugart, 1984). Gap models—the individualistic models simulating forest dynamics in a gap area—are the major succession models. Readers who are interested in other succession models such as Markov models can refer to Horn (1975, 1981). Examples of other individual-based models include a spatially explicit density-dependent model by Hubbell et al. (1991) and models which consider the assimilation and dissimilation processes of individual trees (McMurtrie and Wolf, 1983; Valentine, 1985; Bossel and Schafer, 1989; Bossel et al., 1991).

In 1974, Munro wrote a classic review on growth–yield models. Shugart (1984) and Botkin (1993) provided detailed introductions to gap models. Short summaries on the history and structure of gap models can also be found in Shugart and West (1980, 1981) and Huston (1992). Little effort, however, has been made to compare these two types of models (but see Dale et al., 1985).

This paper identifies the differences and similarities between growth–yield and gap models. First, we compare general features of the models.

Then, we examine assumptions and equations for modelling establishment, growth, and death of individual trees and major environmental factors which affect forest dynamics. We also review methods of testing and the applicability of these models. Finally, we discuss future model development needs. It should be kept in mind that this review does not cover an exhaustive list of literature, because some references especially 'grey literature' such as internal reports are not readily available. We also exclude those models which might be individual-based but the author(s) did not state so explicitly. As a result, the comparative conclusions should be treated as a general trend, and it is likely that exceptions exist in other references. Also, in a general sense, growth–yield models include not only individual-based growth–yield models but also other types of growth–yield models such as those at stand level. In this paper, however, for the sake of convenience, we refer to individual-based growth–yield models as growth–yield models.

2. General comparisons

2.1. Purpose and history

As illustrated in Table 1, the objective of growth–yield models is to provide foresters and forest managers with accurate growth and yield information for better planning and managing commercial forests. The ultimate goal of these models is to maximize, or economically optimize, timber production. By knowing forest growth and yield of a specific site, forest managers can build hypotheses for optimizing silvicultural manipulation of forest stands.

Gap models are usually used to describe ecological patterns and processes of forest dynamics over a long period of time (i.e. forest succession) (Shugart, 1984). Because ecologists have traditionally been interested in natural systems which are undisturbed or rarely disturbed by human beings, most of the gap models are developed for natural forests.

The first gap model (JABOWA) was built by Botkin et al. (1972a,b) at the Yale School of Forestry and Environmental Sciences, nearly a

Table 1
General comparisons between individual-based growth–yield models and gap models

	Growth–yield models	Gap models
Purpose	Management for timber production	Ecological studies of forest dynamics
Forest types	Mainly managed forests or plantations	Mainly natural forests
The first model	Newnham, 1964	Botkin et al., 1972a, b
Modeling spatial relations among trees	Vertical: function of tree size Horizontal: distance-dependent, distance-independent	Vertical: light extinction function Horizontal: generally distance-independent
Data requirement	Site-specific tree and environmental data	Site-specific environmental data and species-specific tree data
Measure of environmental factors	Site index	Multiplication of effects of single factors
Number of species simulated	One to several commercial (timber) species	A few to dozens (or even more than 100) ecologically important species
Simulation area	Large (hundred of hectares or larger)	Small (a gap size, usually 0.01–0.1 ha)

decade after the first growth–yield model (Newnham, 1964). Development of the JABOWA model was influenced by growth–yield models. As a matter of fact, Mitchell's (1969) growth–yield model, also developed at the Yale School of Forestry and Environmental Sciences, was cited in Botkin et al. (1972a). All other gap models were ultimately derived from the JABOWA model and the FORET model (Shugart and West, 1977; Shugart, 1984) which was in turn designed based upon the JABOWA model. Fig. 1 shows a genealogical tree of gap models, indicating their inherent relationships and the years when the models were published. Although Daniel B. Botkin and two computer experts at the IBM Thomas J. Watson Research Center pioneered gap model development, both groups of ecologists at Oak Ridge National Laboratory and the University of Virginia led by Hank H. Shugart have been playing a critical role in advancing and popularizing gap models (e.g. Shugart and West, 1977; Shugart and West, 1980; Shugart et al., 1981; Shugart, 1984; Smith and Urban, 1988; Bonan and Korzuhin, 1989; Bonan,

1989a,b; Urban et al., 1991). All gap models have the same rationale and basic structure, although to satisfy specific conditions they vary. For example, the FORET model by Shugart and West (1977) eliminated several subroutines of the JABOWA model (Botkin et al., 1972a,b) and added two new subroutines.

The first highly comprehensive and spatially explicit growth–yield model was developed by Newnham (a Ph.D. student at the University of British Columbia) for his dissertation in 1964, eight years earlier than the first gap model. Subsequently, a series of dissertations focused on the development of individual-based growth–yield models (Lee, 1967; Lin, 1969; Mitchell, 1969; Bella, 1970; Hatch, 1971; Arney, 1972). Encouraged by these early models, growth–yield models have been developing rapidly during the past three decades. Compared with gap models, growth–yield models are more diverse. Although they are constructed from the growth record of multiple measurements of individual trees using regression techniques, growth–yield models differ in regression functions and variables. This is
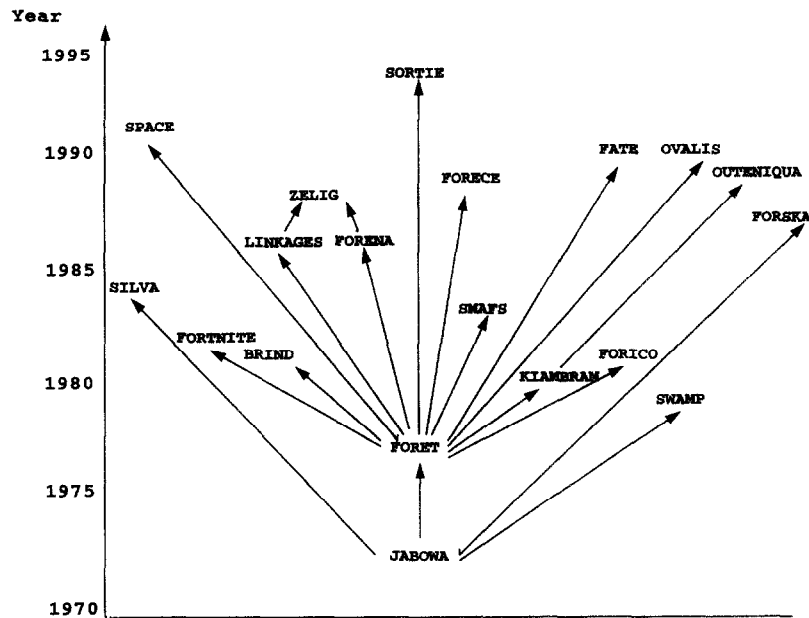
Fig. 1. A genealogical tree of gap models. All other gap models were ultimately derived from JABOWA. Author(s) and time of publication for each model are: JABOWA (Botkin et al., 1972a,b), FORET (Shugart and West, 1977), SWAMP (Phipps, 1979), KIAMBRAM (Shugart et al., 1980), FORICO (Doyle, 1981), BRIND (Shugart and Noble, 1981), FORTNITE (Aber and Melillo, 1982), SMAFS (El-Bayoumi et al., 1984), SILVA (Kercher and Axelrod, 1984), FORENA (Solomon, 1986), LINK-AGES (Pastor and Post, 1986), FORSKA (Leemans and Prentice, 1987), ZELIG (Smith and Urban, 1988), FORECE (Kienast and Kuhn, 1989), OUTENIQUA (Van Daalen and Shugart, 1989), FATE (Moore and Noble, 1990), OVALIS (Harrison and Shugart, 1990), SPACE (Busing, 1991), and SORTIE (Pacala et al., 1993).

not to say that no growth–yield models are related in their structures and functions. Some growth–yield models are in fact modified versions of others. For example, by extending Arney's (1972) model, Hegyi (1974) developed a model for jack pine (*Pinus banksiana*).

2.2. Modeling spatial relationships among individual trees

Spatial relationships among trees include vertical and horizontal dimensions. Growth–yield models consider the vertical relationship as a function of tree size (usually total height or diameter at breast height) (Ek and Monserud, 1974). Some growth–yield models consider the effects of distances among trees and these models are distance-dependent models in the terminology of Munro (1974). The first and probably best known distance-dependent model was built by Newnham (1964). Following his lead, numer-

ous models were developed (Lee, 1967; Lin, 1969; Mitchell, 1969; Bella, 1970; Hatch, 1971; Arney, 1972; Ek and Monserud, 1974; Fries, 1974; Hegyi, 1974; Larocque and Marshall, 1988; Wensel, 1990; Wensel and Biging, 1990). This modelling approach requires that each tree be placed at a point on a spatial coordinate plane. The basic assumption is that competition among individuals is determined by factors such as inter-tree distances and the size as measured by diameter at breast height (DBH).

Growth–yield models which do not consider the effects of inter-tree distances are distance-independent (Munro, 1974). They do not need information about the distances among individual trees and the location of each individual, although the basic simulation unit is still a single tree (Dress, 1970; Goulding, 1972; Teck and Hilt, 1991).

Traditional gap models assume vertical differences in light utilization. Shorter trees receive less

light because taller individuals intercept light from the canopy. Conventionally, gap models consider a plot to be homogeneous and do not explicitly take account of spatial relationships on a horizontal dimension. Recently, however, attention has been paid to horizontal differences and interactions (Smith and Urban, 1988; Busing, 1991; Pacala et al., 1993). In the ZELIG model (Smith and Urban, 1988), horizontal homogeneity at the plot scale (10 m) is assumed. Each individual is assigned to a grid cell, but the location of an individual is still not specified. One of the major differences between the ZELIG model and conventional gap models is that in ZELIG adjacent cells (or plots) interact with each other by shading and seed dispersal, while plots in conventional models operate independently. The SPACE model developed by Busing (1991) uses a much finer spatial scale (0.5 m grid) than ZELIG. An individual occupies one or more grid cells depending on the size of an individual tree. In this sense, SPACE has higher flexibility than ZELIG and can deal with both fine- and coarse-scale problems. Pacala et al. (1993) adopted the approach of distance-dependent growth–yield models and placed all the trees on a plane according to their x and y coordinates.

2.3. Data requirements

Development of a forest simulation model demands two categories of data: tree information and local environmental information. Growth–yield models require site-specific knowledge about individual trees and environmental conditions. The data usually come from periodic growth–yield censuses of marked individual trees in a large number of plots. For example, Beck (1974) used data from 49 permanent 1/4-acre sample plots. Individual tree information from more than 2000 permanent plots was available for the model by Hilt and Teck (1988).

In gap models, information about species' ecological characteristics can be obtained in study plots and/or from the literature (Shugart, 1984). However, data about environmental conditions (e.g. soil moisture, light, temperature, frost, ele-

vation, aspects, altitude, nutrients) should be site-specific.

2.4. Simulations

Growth–yield models have usually been employed to simulate one or a few timber species. Most gap models take a few to several dozen or even more than 100 ecologically important species into account. For example, both the FORET model (Shugart and West, 1977) and the FORAR model (Mielke et al., 1978) studied 33 species. Shugart et al. (1981) simulated the dynamics of 125 species in a diverse subtropical forest in Australia.

Growth–yield models simulate the dynamics of a combination of stands within a forest which may be as large as hundreds or thousands of hectares in size. A large number of sample plots are customarily set up in a forest but each plot is small (usually less than 1 hectare). For example, Adlard (1974) constructed his model from the record of approximately 1200 plots with several remeasurements in a majority of the plots.

Gap models simulate forest dynamics taking place in an area of gap. Simulated areas usually vary from 0.01 to 0.1 ha. For example, Botkin et al. (1972a) did simulations on 10 m×10 m sample plots (0.01 ha each). Using the FORET model Shugart and West (1977) simulated forest dynamics in an area of 0.08 ha.

3. Model structure

The life of a tree goes through three processes: establishment, growth, and death (Fig. 2). These processes are influenced by both biotic and abiotic environmental factors, such as competition for limited resources with neighboring individuals, reproduction, pest attacks, and silvicultural practices such as harvesting, thinning, prescribed fires, and application of fertilizers. This section discusses the differences and similarities in the three processes and factors influencing these processes as circumscribed by the growth–yield and gap models.
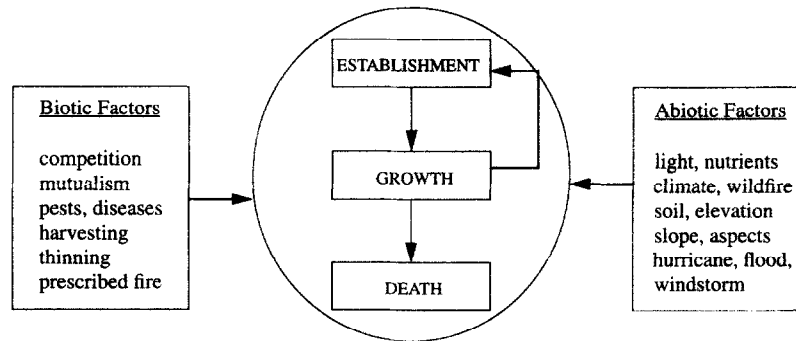
Fig. 2. Three processes (establishment, growth and death) of an individual tree and the environmental factors which affect the processes.

3.1. Establishment

Trees can be established in two ways: by natural regeneration and by plantation. The former relies on seed production and dispersal in forests. Some refer to the establishment process as regeneration (Shugart, 1984), while others recruitment (Pacala et al., 1993).

Since growth–yield models are generally developed for management of plantations, the establishment process is usually not modeled because the seedlings and saplings are planted either by hand or machine (but see Ek and Monserud, 1974), because the forests are usually cut before canopy gaps form and mature stands are initiated, and/or because natural regeneration is largely eliminated in the process of site preparation and plantation. There are exceptions, however. As an example, in Ek and Monserud (1974), establishment was generated by seed and sprout production of the overstory rather than plantation.

Gap models conventionally introduce new individuals to a modelled plot from an external seed source (Shugart et al., 1981; Shugart, 1984). The success of these seeds depends on site conditions and species-specific factors such as seed phenology, seed longevity, dormancy periods, seed dispersal mechanisms, the amounts of viable seed produced, and shade tolerance (Doyle, 1981; Shugart, 1984; Van Daalen and Shugart, 1989). In gap models, a general assumption about the establishment of a species is that the

climatic conditions are within the degree-day range of the species (Shugart and Noble, 1981). The species selected to initiate succession in the model and their juvenile numbers are stochastically chosen from a specified external source. The size of each juvenile introduced into the model is randomly determined and varies around a mean of approximately 2 cm in diameter. Some recent descendants of gap models such as ZELIG (Smith and Urban, 1988; Urban, 1990) allow plants to produce seeds inside the modelled plots and permit recruits from one parent to disperse across grid cells although a seed bank also randomly provides seeds to the plot. Pacala et al. (1993) assumed that the density of seedlings produced by a seed tree inside the plot was a function of the size (DBH) and the distance from the seed tree. When above-ground parts are lost or after the main stem dies, there is possibility of sprouting from the stem base or roots (Shugart and Noble, 1981; Kienast and Kuhn, 1989). Further, the sprouts are assumed to be more vigorous than seedlings and are given larger diameters than the seedlings when introduced into the models.

3.2. Growth

A tree grows in diameter, height, basal area, and crown size. Most models are developed for simulating diameter growth, because it is much easier to measure than other variables and because height and basal area information can be

derived from functions which describe diameter–height and diameter–basal area relationships of individual species (Ker and Smith, 1957; Hilt and Teck, 1988).

Growth rates are greatly influenced by site conditions and interactions among individual trees. The major type of interactions is competition, a process which occurs when resources such as light and nutrients are in short supply. Growth–yield models and gap models differ dramatically as to how these environmental factors are modelled.

3.2.1. Gap models

Gap models usually consider the single factors separately and then multiply their effects. They further assume that individual trees grow in a sigmoid function under ideal conditions. The function may be modified because of competition for limited resources with neighboring individuals.

The initial gap model developed by Botkin et al. (1972a,b) assumes (1) that the diameter of a tree increases at a maximum rate under optimal conditions and is constrained by life history characteristics such as maximum age, maximum diameter, and maximum height, and (2) that tree growth is modified by its site-specific abiotic and biotic environment. Specifically, diameter increment is the product of a potential growth function and several modifiers which take into account the impacts of light, temperature, soil moisture and nutrients (Table 2). The modifier values range from 0 (no growth at all) to 1 (no growth reduction). The potential (or optimal) growth equation is a function of diameter at breast height, maximum diameter, height, maximum height, and a growth parameter. The light modifier considers shading relations among trees. Available radiation for a given individual tree is reduced by the summed shading effects of all the taller trees. Temperature effects on growth reduction in temperate forests have been simulated by means of the growing degree-day heat sum, which is the annual accumulation of daily differences of temperature above a 40°F (approximately 4°C) baseline. The soil modifier uses maximum basal area and existing basal area

in a plot to estimate the effects of competition for both nutrients and moisture. When the existing basal area equals the maximum basal area, the soil modifier becomes zero.

Although the basic rationale in other gap models is the same as that in JABOWA, some newer modifiers have more explicit consideration of ecosystem and ecophysiological processes. For example, Weinstein et al. (1982) reduced diameter growth rate because of nutrient limitations by using a polynomial function in which relative nutrient availability was an independent variable. Aber and Melillo (1982) also used relative nutrient availability to modify growth rate and simulate decomposition processes in order to calculate annual dynamics of nutrient reserves in the plot. In Pacala et al. (1993), the availability of local light was expressed as a 'general light index' (Canham, 1988), which incorporates the information of direct and diffuse beam radiation, spatial patterns of canopy openness, and diurnal and seasonal movement of the sun (Pacala et al., 1993). Without completing the estimation of the parameters relevant to soil nutrients and water, Pacala et al. (1993) regressed radial growth only against diameter and a general light index (Table 2).

Another type of deviation of later gap models from earlier ones can be found in the SWAMP model (Table 2). Phipps (1979) assumed that the three-dimensional shape of mature tree trunks is basically paraboloidal. Thus, he simulated radius increment by modifying a paraboloid model of tree geometry (Phipps, 1967). He assumed that trunks of juveniles were more conical than paraboloidal, and an adjustment was therefore made to reduce the width of center rings in calculations of volume increment derived from mature stems to allow juvenile stages to better fit the model. In his model, climatic variations, crowding effects, and moisture were the factors which caused additional annual variations in ring width.

3.2.2. Growth–yield models

Growth–yield models usually describe growth rate as a regression function of variables such as site-index, basal area, and tree density. Site-in-

Table 2
Examples of diameter growth functions in individual-based forest models

Model type	Source	Equation
Gap models	Botkin et al. (1972a,b)	$dD/dt = PG \times r(AL) \times T(DEGD) \times S(BAR)$ dD/dt, diameter increment PG, potential diameter growth: $PG = [G \times (1 - D \times H/D_{max} \times H_{max})] / [274 + 3b_2D - 4b_3D^2]$ D, diameter at breast height of an individual tree; D_{max}, maximum D for a species; H, tree height; H_{max}, maximum tree height for a species; b_2 and b_3, parameters defining tree forms which can be estimated by D_{max} and H_{max}; G, growth parameter which can be estimated according to maximum age, D_{max} and H_{max} $r(AL)$, light modifier: $r(AL) = 1 - \exp(a_1(AL - a_2))$ AL, available light; a_1, a_2, parameters for a given species $T(DEGD)$, temperature modifier: $T(DEGD) = 4(DEGD - DEGD_{min})(DEGD_{max} - DEGD)/(DEGD_{max} - DEGD_{min})^2$ DEGD, number of growing degree-days per year at the base of 40°F for a specific species in a study site; $DEGD_{max}$, maximum number of growing degree-days that a species can resist; $DEGD_{min}$, minimum number of growing degree-days that a species can resist $S(BAR)$, soil modifier: $S(BAR) = 1 - BAR/SOILQ$ $S(BAR)$, measurement of competition for soil nutrients and moisture on the plot; BAR, total basal area on the plot; SOILQ, maximum basal area under optimum growing conditions on the plot
	Phipps, 1979	$i_n = A_n\{[r_{n-1}/P][r_{n-1}^2 + G \times H)^{1/2} - r_{n-1}]\}$ i_n, width of the nth ring increment; A_n, climatic multiplier for the nth ring increment; r_{n-1}, radius length of the $(n-1)$th ring; P, radius length at the inflection point where ring shape changes from conical to paraboloidal; G, crowing multiplier; H, moisture modifier
	Pacala et al., 1993	$w = r[(P_1GLI)/(P_1/P_2 + GLI)] + a$ w, ring width; r, radius; GLI, general light index; P_1, asymptotic relative growth rate (w/r); P_2, slope of the relative growth rate at zero light; a, normally distributed random variable
Growth–yield models	Wan Razali and Rustagi, 1988	$\delta D = a + b \times D + c \times D^2 + e \times LDG + f \times BAT + g \times LBAG + h \times LTBAG + i \times D/RS$ δD, annual diameter growth (cm year^{-1}); D, tree diameter; LDG, tree diameter growth rate during the previous measurement period (cm year^{-1}); BAT, total plot basal area (cm^2 plot^{-1}); LBAG, annual tree basal area growth rate during the previous measurement period (cm^2 year^{-1}); LTBAG, total annual basal area growth of all species per plot during the previous measurement period (cm^2 year^{-1}); RS, ratio of species group basal area to the total plot basal area; $a - i$, estimated constants
	Wykoff and Monserud, 1988	$DDS = POT \times MOD$ DDS, squared diameter; POT, potential DDS: $POT = c_0 + \exp(c_1 + c_2 \ln(DBH + c_3 DBH^{c4})$ $c_0 - c_4$, site index dependent parameters MOD, modifier for the potential growth $MOD = c_5/[1.0 + \exp(c_6 + c_7 DBH + c_8 BAL + c_9 CR)]$ $c_5 - c_9$, regression coefficients
	Wykoff and Monserud, 1988	$\ln(DDS) = HAB + LOC + b_1 \ln(DBH) + b_2 DBH^2 + b_3 BAL + b_4 BAL/\ln(DBH + 1)$ $+ b_5 CR + b_6 CR_2 + b_7 CCF + b_8 SL \times \cos(ASP) + b_9 SL \times \sin(ASP) + b_{10} SL$ $+ b_{11} SL^2 + b_{12} EL + b_{13} EL^2$ DDS, squared diameter; DBH, diameter at breast height; CR, crown ratio; SL, slope; ASP, aspect; CCF, crown competition factor; EL, elevation; LOC, intercept dependent on plot location; HAB, intercept dependent on habitat type; BAL, estimate of stand basal area represented in trees that are larger than the subject tree; $b_1 - b_{13}$, regression coefficients

Model type	Source	Equation
	Hilt ad Teck, 1988	DGROW = $[(c \times DBH^2 + POTBAG \times MOD)/c]^{1/2} - DBH$
		DGROW, diameter growth rate; c, constant; DBH, diameter at breast height; POTBAG, potential basal area growth; MOD, modifier of basal area growth
		POTBAG = $b_1 \times SI \times [1.0 - exp(-b_2 DBH)]$
		SI, site index; DBH, diameter at breast height; b_1–b_2, regression coefficients
		MOD = $exp(-b_3 BAL)$
		BAL, basal area; b_3, regression coefficient
	Zeide, 1989	$D = D_m \times [1 - exp(-at)]^b$ (Chapman–Richards equation)
		$D = D_m \times exp[-a \times exp(-bt)]$ (Gompertz equation)
		$D = D_m / [1 + a \times exp(-bt)]$ (Logistic equation)
		$D = D_m \times exp[-a/(b-1)] \times t^{1-b}$ (Power decline equation)
		$D = D_m \times [1 - exp(-at)^b]$ (Weibull equation)
		D, diameter at breast height at age t; D_m, maximum diameter (or asymptotic diameter); a, b, parameters specific for each equation

dex is a measurement of site quality and is generally expressed as the expected height of dominant and/or codominant trees at a specified age (Clutter et al., 1983). The primary assumption is that the factors influencing forest growth can properly be integrated as a single site index (Meldahl et al., 1988), which is the outcome of interactions among different environmental factors such as nutrient and water contents rather than the environmental factors themselves. In most growth–yield models, site index is used to determine the growth potential or maximum growth rate. The maximum growth is then reduced (or modified) by incorporating other effects caused by tree size and density.

Besides site-index, competition among neighboring individual trees also influences growth rate significantly. Many growth–yield models have used competition indices to measure the competitive impact by adjacent trees and incorporate these competition indices into predictive models to estimate individual tree growth. Competition measures are very diverse depending on research objectives and constraints. Many competition indices take account of tree DBH, stem position, total basal area, basal area of trees larger than the subject tree (Monserud, 1975), and crown closure (Wensel and Biging, 1988). A majority of competition indices are based on the concept of 'influence zone' which was first employed by Newnham (1964) although it was originally developed by Staebler in the early

1950s (Larocque and Marshall, 1988). The philosophy behind the competition indices is that they can reasonably reflect the impacts of the amount of resources that a subject tree cannot obtain because of the competitive effects from neighboring individuals, and that tree growth is directly influenced by the degree of competition (Daniels et al., 1986). For example, Newnham (1964) assumed that (1) a tree grows at maximum rate if there is no competition for resources, and (2) reduction of growth increment depends upon competition levels.

The growth functions vary in terms of types of functions and variables in the functions. For example, in Hilt and Teck (1988), basal area was selected to establish a predictive model for diameter growth (Table 2). The potential basal-area growth model is a modified version of the Chapman–Richards function (Richards, 1959). Potential basal area increases linearly with the site index for a given DBH of the top 10% of the fastest growing trees. The actual basal area estimate is the product of the potential basal area and a modifier (a negative exponential function of basal area).

Meldahl et al. (1988) adopted different approaches to simulating growth of different diameter sizes. For trees that had diameters of less than 5 in. (12.7 cm), a linear model was used, whereas for trees whose diameters were equal to or greater than 12.7 cm, a potential growth function was first developed and actual growth was

predicted by modifying potential growth. Because there was a lack of open grown trees, the fastest growing trees and those trees which were growing with very little competition were used for constructing nonlinear potential growth functions. The potential growth functions were non-linear functions and the inverse of DBH was used as an independent variable. The modifier functions were usually linear models which incorporated many variables such as site index, DBH, tree density, and crown ratio.

Wan Razali and Rustagi (1988) used unweighted and weighted linear models and weighted nonlinear ones to predict annual diameter growth of mixed tropical forests in Peninsular Malaysia. The independent variables were tree diameter, ratio of species group basal area to total plot basal area, and species group basal area per plot. They reported that weighted linear regression models performed the best. Although all the regressors were significant, the R^2 values were very low. By adding past annual diameter growth rate and basal area, species group basal area and total basal area as logged variables, the prediction of tree diameter growth was notably improved (the R^2 value was doubled). The best-fitting model for dipterocarps is listed in Table 2. Wan Razali and Rustagi suggested that the previous diameter growth rate reflected the impact of site productivity and inter-tree competition quite well and was the best predictor of future diameter growth when site quality and species interactions were unknown.

Zeide (1989) tested five equations which used tree age and maximum diameter as independent variables for predicting growth of Norway spruce (*Picea abies*) (Table 2). He noticed that the power decline function was more accurate than other equations in describing diameter growth of the investigated data.

3.3. Death

Trees may die of aging, suppression, fires, diseases, or harvesting. Some researchers divide mortality into two major categories: regular and irregular (Lin, 1974). Regular mortality results from suppression or competition for limited re-

sources such as light, water, and nutrients. Irregular mortality occurs because of density-independent forces including insect and pathogen attack, and catastrophic factors such as hurricanes, windstorms, floods, and fires. Many methods have been developed to model regular mortality, while irregular mortality is usually treated as a stochastic process because it is very variable and difficult to predict. Compared with growth submodels, modelling mortality has greater sampling errors because mortality probability over similar time periods for a given tree is usually low and the number of dead trees in a forest is often relatively small.

3.3.1. Gap models

Gap models simulate mortality caused by suppression, random factors, harvesting and aging (Botkin et al., 1972a; Shugart, 1984) (Table 3). The probability of mortality because of suppression is set to a number between 0.0 and 1.0 for an individual tree if the growth rate of an individual is below a threshold (Botkin et al., 1972a,b). Pacala and his colleagues adopted a similar philosophy by using average ring width for the previous 5 years as an independent variable to estimate mortality probability because of limited resources (Pacala et al., 1993). In gap models, aging mortality for an individual over a given period of time (usually a year) is a function of the maximum age (longevity) of the species (Botkin et al., 1972a,b; Shugart, 1984, see Table 3).

In some gap models, the effects of silvicultural practices have been taken into account. For example, the KIAMBRAM model (Shugart et al., 1981) has a LUMBER routine which simulates the impacts of cutting trees based on the local practice adopted in the Wiangaree State Forest near Kyogle, New South Wales. For the year immediately after the harvest, the probability of mortality for each unharvested tree is set at 0.3 as a way of taking logging damage into account (Table 3).

A number of gap models have considered catastrophic disturbances such as hurricanes, fires (Doyle, 1981), and windthrow (Pacala et al., 1993). Wildfires and/or prescribed fires are im-

Table 3
Examples of mortality functions in individual-based forest models

Model type	Cause	Mortality functions	Source
Gap models	Suppression	$MP=0.38$ $(\Delta D<0.1$ cm year^{-1}) MP, annual mortality; ΔD, diameter increment	Shugart, 1984
	Random	$MP=0\sim0.1$ (hurricane damage)	Doyle, 1981
	Harvesting	$MPLD=0.30$ (logging damage)	Shugart et al., 1980
Senescence		$P_n=1-(1-MP)^n$ P_n, probability that a tree will die by year n; MP, annual mortality probability (if a tree dies in a probability of 98% and 99% before reaching maximum age, then $MP=4.0/$AGEMAX and 4.6/ AGEMAX, respectively, where AGEMAX is maximum age)	Shugart, 1984
		$M(g)=\exp(-U\times[\text{average ring width}]^V)$ U and V, constants estimated by regression from field data; average-ring width, arithmetic average of ring width for the previous 5 years	Pacala et al., 1993
Growth–yield models	Suppression	$MP=(1+\exp(a+b_1\text{DBH}+b_2\text{DGR})^{-1}$ MP, mortality; DBH, diameter at breath height; DGR, diameter growth rate; a, b_1, b_2, parameters	Chang, 1990
		$MP=1.0$ (RATIO$<$THOLD) RATIO$=\Delta D/D$ D, diameter; ΔD, average annual diameter increment; THOLD, a value derived from remeasurement data on dying trees	Ek and Monserud, 1974
	Random	$MP=0.20$ (of all the trees to be removed)	Hegyi, 1974
		MP varies to match the field data	Lin, 1974
	Harvesting	MP (degree of cutting) may be set by the user	Ek and Monserud, 1974
	Pests and diseases	$\delta(t;Z)=\delta_0(t)\exp(Z\times\beta)$ $\delta(t;Z)$, probability of dying at time t, given alive before t; δ_0, baseline hazard at time t; Z, covariate matrix; β, vector of regression coefficients	Reams, 1988

portant factors in influencing forest dynamics because fires can kill individual trees instantly or increase mortality probability in the future. Some models have simulated the effects of fire intensity and frequency (Kercher and Axelrod, 1984; Keane et al., 1990). For example, in the BRIND model developed for high-altitude eucalyptus forest of Australian Capital Territory, Shugart and Noble (1981) assumed that the wildfires occurred randomly with a fixed probability. Fire intensity was modeled as a function of fuel load

and climate. The FORICO model (Doyle, 1981) simulated the effects of hurricanes on forest dynamics. The model assumed that the probability of hurricane occurrence was 0.111 and that hurricanes caused damage amounting to 0–10% of the stand density (Table 3). The SWAMP model (Phipps, 1979) simulated the effects of flood frequency and duration on wetlands forest vegetation dynamics of the White River National Wildlife Refuge in southeastern Arkansas.

3.3.2. Growth–yield models

Like gap models, growth–yield models also consider tree death caused by suppression, random factors, and harvesting. But growth–yield models usually do not explicitly simulate death due to aging or senescence possibly because there is no need to do so as the timber trees are usually harvested before the effects of senescence become significant. In growth–yield models, functions for mortality probability of trees are quite different. With respect to suppression mortality, Ek and Monserud's (1974) approach, similar to that in gap models, assumes that the death of a tree occurs when the diameter or height growth is below a threshold (Table 3). Hegyi (1974) assumed that 80% of the trees to be eliminated died of inter-tree competition. Trees with the highest competition indices were removed until a designated number of trees was reached. The remaining twenty percent were killed by random mortality. The percentage (80% and 20%) assigned to the two types of death was a preliminary estimate and could be changed as more field data are obtained (Hegyi, 1974).

Lin (1974) assumed that regular mortality rate changed with a growing space index, which is a quantitative measure of growing space available to an individual tree. The growing space index integrated competition effects of neighboring trees into one value. After the growing space index became zero, a probability of mortality was given. Irregular mortality rates were randomly assigned across the tree sizes. Lin used a 'trial and error' process to vary mortality probability until the simulation results were quite close to the field data.

Many researchers have used a logistic mortality function to predict mortality probability of individual trees (Monserud, 1976; Wan Razali and Rustagi, 1988; Meldahl et al., 1988; Chang, 1990). Ratio of dead to live trees is also calculated to fit the logistic equation. Because the number of live trees is usually much larger than that of dead trees, a simple random sampling method is used to select a certain number of live trees for parameterizing the model. The probability of mortality from the logistic mortality function is then compared with the mortality

threshold. If the calculated mortality of an individual tree is larger than the threshold, then the tree is assigned to death. Otherwise, the individual is considered still alive. The expected number of dead trees is the summation of those died in the simulated forest. Chang (1990) employed a maximum likelihood method to estimate the parameters in his mortality function (Table 3).

In addition to the influences of natural environments on mortality, human beings also play a large role through harvesting (Ek and Monserud, 1974). There are two harvesting methods: selective and clearcutting. Selecting harvesting eliminates some of the trees in a forest according to certain criteria such as tree sizes, while clearcutting harvests all the trees regardless of tree size and age. For selective harvesting, logging damage to residual trees is almost always present although mortality due to logging damage varies.

Mortality due to attack by insect pests is one of the most important factors which cause death of trees in managed forests. Reams (1988) used a nonparametric survival model to estimate annual individual mortality probability of balsam fir (*Abies balsamea*) and red spruce (*Picea rubens*) resulting from spruce budworm and blowdown. The use of proportional hazards models (see Table 3) allowed a greater refinement of estimating mortality probability than parametric models (Cox and Oakes, 1984).

4. Model testing and predictability

An important task in the development of simulation models for forest succession and management is to test model performances. Like many other computer models, there are two ways to test individual-based forest models: verification and validation. Verification is a process in which the simulation results are compared to the observations used in constructing the models and in estimating the parameters. Validation means that the simulation results are tested with data that are independent of structuring the models. According to Shugart (1984), model applications are special validations because they usually involve the prediction of future changes. Both gap

models and growth–yield models can be used as 'what-if' evaluators to assess the consequences of changes in environment and silvicultural practices if the future conditions are within the range of model extrapolation and interpolation (Post and Pastor, 1990; Kimmins et al., 1990).

Many gap models have been extensively tested (Shugart and West, 1981; Shugart, 1984; Mohren and Kienast, 1991). For example, in a summary table, Shugart (1984) listed seven examples of verification, seven examples of validation, and five applications of eight representative gap models. Gap models are usually employed to understand compositional structure and forest dynamics. At least one gap model (FORAR) for Arkansas mixed pine–oak forests was used to predict yield tables for loblolly pine (*Pinus taeda*) (Mielke et al., 1978) although the predictive accuracy has yet to be tested against that of growth–yield models.

Gap models have been applied to various forest types including temperate forests (Shugart, 1984), boreal forests (Bonan, 1989a,b), and tropical forests (Doyle, 1981; Shugart et al., 1981). Gap models were originally developed for forests, but they have recently been applied to grassland communities (Coffin and Lauenroth, 1989).

Like gap models, growth–yield models are commonly verified with the dataset used in constructing the models (Dale et al., 1985). It is relatively more difficult, however, to validate growth–yield models because of the demands for remeasurement data at frequent intervals (Dale et al., 1985; Hilt and Teck, 1988; Larocque and Marshall, 1988).

5. Future individual-based forest models

5.1. Hybrid models

In principle, it can be beneficial to combine growth–yield models with gap models because they have some complementary advantages and disadvantages. For example, growth–yield models have a series of comprehensive procedures to simulate the intensity and impact of in-

ter-tree competition. Distance-dependent growth–yield models simulate horizontal inter-tree relationships while gap models simulate vertical inter-tree relationships. In gap models, the results are sensitive to the size of the simulated area (Shugart, 1984). Although gap sizes vary dramatically because different canopies have different heights, conventional gap models assume that all gaps in a given simulation are equal in size. Some assumptions in gap models need further improvement. For instance, the impact of growth multipliers may not be simply additive or multiplicative; rather, compensatory effects may also take place. Take light for example. If light is critically limiting growth, a limited nutrient supply may have no particular importance in determining growth, and vice versa. These phenomena usually are not satisfactorily treated by gap models. Because it is difficult to determine the site index in mixed-species and uneven-aged forests such as tropical rain forests, the traditional site index approach in growth–yield models has certain limitations (Meldahl et al., 1988).

It is quite encouraging to see that a number of hybrid individual-based forest models have already been published. For example, although the SORTIE model developed by Pacala et al. (1993) is acknowledged as a descendant of the JABOWA–FORET gap models, it considers the spatial locations of individual trees in terms of x and y coordinates. In the terminology of Munro (1974), the SORTIE model shares spatial characteristics with distance-dependent growth–yield models.

Although growth–yield models conventionally use site index as a single integrative measure of site quality, a few growth–yield models have used environmental factors such as elevation, slope, aspect and location as separate variables (Wykoff et al., 1982; Wykoff, 1986; Wykoff and Monserud, 1988). These variables were incorporated as a multiple linear function. Wykoff and Monserud (1988) employed two methods to reflect site quality in predicting diameter growth (Table 2). The first method was to use site index as a predictive variable and the second method was to incorporate various factors into the pre-

dictive function. Interestingly, Wykoff and Monserud (1988) reported that the performances of the growth models for Douglas fir (*Pseudotsuga menziesii* var. *glauca*) using the two disparate approaches were similar and the variation in diameter increment explained by these models was approximately the same.

Both gap models and growth–yield models have begun to integrate with rapidly-emerging physiology-based or tree process models whose dynamics are mostly determined by the physiological processes (McMurtrie et al., 1990; Bossel, 1991). For example, the HYBRID model by Friend et al. (1993) is derived from a forest gap model, an ecosystem process model, and a photosynthesis model. The growth equations of gap models are replaced with more realistic equations and processes for carbon fixation and partitioning. Prentice et al. (1993) also expanded a gap model by considering carbon fertilizations and other biophysical factors such as foliage net assimilation and sapwood respiration. This new hybridization allows multiscale studies, that is, to predict the responses at larger scales (individual, population, species, and landscape) based on physiology of different parts of a tree. One application of this new breed is to predict the impact of climatic changes on ecosystems by linking global climatic change models (e.g. Schneider, 1987) with gap models (Shugart, 1990).

Sievanen et al. (1988) presented one hybrid model which combined some features of growth–yield models with those of physiology-based ones. The model of Sievanen et al. (1988) predicted biomass and basal area of even-aged stands of red-pine (*Pinus resinosa* Ait.) by considering photosynthesis and respiration relationships, stems per unit area, site index and other information from yield tables.

In the future, we expect to see hybrid models which integrate gap models, growth–yield models, and physiology-based models. These highly interbred models may provide more accurate and powerful prediction of forest dynamics, but they also require extra efforts to deal with data availability and scale-dependent phenomena.

5.2. Efficient and user-friendly individual-based models

Computer technology has made it possible to develop so many forest simulation models. There is no doubt that future individual-based models will continue to evolve with explosively advancing computer techniques. Workstations and high-end personal computers are now readily available. Today forest modelers can access supercomputers with massively parallel processors and scalable architecture. Computational barriers can be overcome and high-speed computers allow foresters and ecologists to see the results of large-scale simulations instantly.

In additional to computer hardware, computer software also is important in shaping forest models. Most existing models were developed using procedural or structural languages such as FORTRAN (e.g. Trimble and Shriner, 1981) and C (e.g. Pacala et al., 1993). Applications of the most advanced computer languages like object-oriented C++ (e.g. Liu, 1993) can enhance flexibility, effectiveness and efficiency of forest simulation models.

A majority of previously published models were developed for modelers themselves; they are intractable for people who lack advanced computer skills. Future models should have a graphical user interface and be run in a 'game' atmosphere so that they can be easy for novices to learn, use, and modify.

5.3. Individual-based models for tropical forests

Forests in temperate, subtropical, and tropical zones account for 40.7%, 7.8% and 51.5% of the earth's forested area, respectively (Borota, 1991). Hundreds of individual-based models have been developed in temperate regions (Shugart, 1984; Ek et al., 1988) and boreal regions (Leemans and Prentice, 1987; Bonan, 1989a; Bonan and Korzuhin, 1989; Bonan et al., 1990; Kellomaki and Vaisanen, 1991), but only a few individual-based models have been developed for tropical and subtropical forests (Doyle, 1981; Shugart and Noble, 1981; Shugart et al., 1981; Wan Razali and Rustagi, 1988; Van Daalen and

Shugart, 1989; Hubbell et al., 1991). There are at least two reasons for the relative scarcity of individual-based models for tropical forests. First, most forest research was conducted in temperate and boreal regions. Thus, there are more data available for developing individual-based models for temperate and boreal forests than for tropical ones. World-wide attention to tropical forests has become serious only recently, as scientists and governments realize that large-scale loss of biodiversity and timber harvests in the tropics are accelerating (Hubbell and Foster, 1986; Panayotou and Ashton, 1992). Second, most tropical forests are in developing countries which have fewer researchers to develop forest models.

The existing tropical forest models are mainly based on the models developed for temperate or boreal forests (Shugart et al., 1981; Bonan et al., 1989a,b). Many modelling strategies applied in temperate and boreal forests are inappropriate to tropical forest systems (Adlard et al., 1989) because of data availability and significant differences in forest structures. Tropical forests are much more complicated and diverse than temperate ones (Whitmore, 1984; Ashton, 1992a,b). For instance, in a 50-ha experimental plot of Pasoh forest reserve in Malaysia, there exist more than 800 species (Manokaran et al., 1990). An important variable in both growth–yield models and gap models is tree age. Age information may be readily available based on plantation history or tree growth rings. Estimation of diameter increment is easy for species which produce growth rings (Rai, 1989). Annual growth rings are usually apparent in temperate forests, but it has been very difficult, if not impossible, thus far to reliably distinguish annual wood growth in trees in tropical forests because tropical forests are evergreen and individual tree growth may be quite intermittent, but not necessarily seasonal.

6. Conclusion

It has been approximately three and two decades, respectively, since the publication of the first individual-based growth–yield model (Newnham, 1964) and the first gap model (Bot-

kin et al., 1972). During this period of time, hundreds of individual-based models have been developed and tested (Munro, 1974; Trimble and Shriner, 1981; Shugart, 1984). Gap and growth–yield models share some characteristics, although they have differences in model structure and functions. Interbreeding these two types of models, in addition to integrating several new features, is necessary to develop a new generation of individual-based models for biodiversity conservation and timber production (Wilcove, 1989).

As Huston et al. (1988) pointed out, the individual-based modelling approach has a great potential to be explored. It is expected that during the coming years individual-based forest simulation models will become an even more important tool for understanding mechanisms of forest dynamics and for managing forests sustainably.

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