

A REVIEW OF FOREST PATCH MODELS AND THEIR APPLICATION TO GLOBAL CHANGE RESEARCH

H. H. SHUGART and T. M. SMITH

Department of Environmental Sciences, University of Virginia, Charlottesville, VA 22903, U.S.A.

1. Introduction and Background

The term 'patch model' generally refers to models which examine vegetation dynamics at a spatial scale corresponding to the area occupied by a small number of mature individuals, approximately the size of a plot or quadrant used for vegetation sampling. Among the earliest patch models in ecology were individual-based models of forest succession based on the growth of the individual trees. These models were developed by quantitatively oriented foresters and were focused toward practical issues in production forestry (see Shugart et al., 1992).

There are several rather different modeling approaches that produce patch models. Indeed, many of the models developed for element cycling and carbon metabolism in ecosystems (notably the developments during the International Biological Programme of the 1960's and 1970's) were developed to duplicate experimental or observational results from a relatively small tract of land. The principal feature of patch models is their emphasis on the dynamics of ecosystems at relatively small spatial scales. The initial reasons for this emphasis lay with a need to model at the spatial scale at which data is collected, and with the necessity to assume a degree of spatial homogeneity in the model formulation. Recently, a recognition of the importance of treating phenomena that do not 'scale up' easily to larger spatial scales has reinforced an interest in patch modeling.

Computer models that simulate the dynamics of a forest by following the fates of each individual tree in a forest stand were developed initially in the mid-1960's. The earliest such model was developed by Newnham (1964) and this was followed by similar developments at several Schools of Forestry. The models predicted change in a small patch of forest using a digital computer to dynamically change a map of the sizes and positions of each tree in a forest. These early individual-tree based simulators took what was known from yield tables and other data sets and developed a more flexible, quantitative methodology for prediction. Some of the earliest attempts to apply such models were very successful and produced results of surprising detail.

An important sub-category of individual-organism-based patch models that have been widely used in ecology (as opposed to traditional forestry applications) are

the so-called 'gap' models (Shugart and West, 1980). The first such model was the JABOWA model (Botkin et al., 1972; Botkin, 1993) developed for forests in New England. Over the past twenty years, gap models have been developed for a wide variety of forest ecosystems, from boreal to tropical, and the general approach has been extended to nonforested ecosystems such as grasslands, shrublands and savannas (Figure 1).

The objective of this paper is to: (1) provide a description of the structure of patch (gap) models of vegetation dynamics, (2) examine some of the problems associated with the use of patch models to examine global change issues, (3) examine how recent model developments are attempting to overcome these limitations, and (4) suggest possible areas of future research.

2. General Structure of Gap Models

As is the case with many of the earlier individual-based models used in forestry, gap models simulate the establishment, diameter growth, and mortality of each tree in a given area. Calculations are on a weekly to annual time step. At least initially, gap models were developed for plot of a fixed size. Many of the models focus on a size unit (ca. 0.1 ha) approximately that of a forest canopy gap (Shugart and West, 1980).

Gap models feature relatively simple protocols for estimating the model parameters (Botkin et al., 1972; Shugart, 1984). For many of the more common temperate and boreal forest trees, there is a considerable body of information on the performance of individual trees (growth rates, establishment requirements, height/diameter relations) that can be used directly in estimating the parameters of such models. The models have simple rules for interactions among individuals (e.g., shading, competition for limiting resources, etc.) and equally simple rules for birth, death and growth of individuals. The simplicity of the functional relations in the models have positive and negative consequences. The positive aspects are largely involved in the ease of estimating model parameters for a large number of species; the negative aspects with a desire for more physiologically or empirically 'correct' functions.

The more recent gap models in many cases have functional relationships that are different from those used in the earlier gap models (e.g. JABOWA – Botkin et al. (1972) and FORET – Shugart and West, 1977). Gap models differ in their inclusion of processes which may be important in the dynamics of particular sites being simulated (e.g., hurricane disturbance, flooding, formation of permafrost, etc.), but share a common set of characteristics.

Each individual plant is simulated as an independent entity with respect to the processes of establishment, growth and mortality. This feature is common to most individual-tree based forest models. These features provide sufficient information to allow computation of species- and size-specific demographic effects.

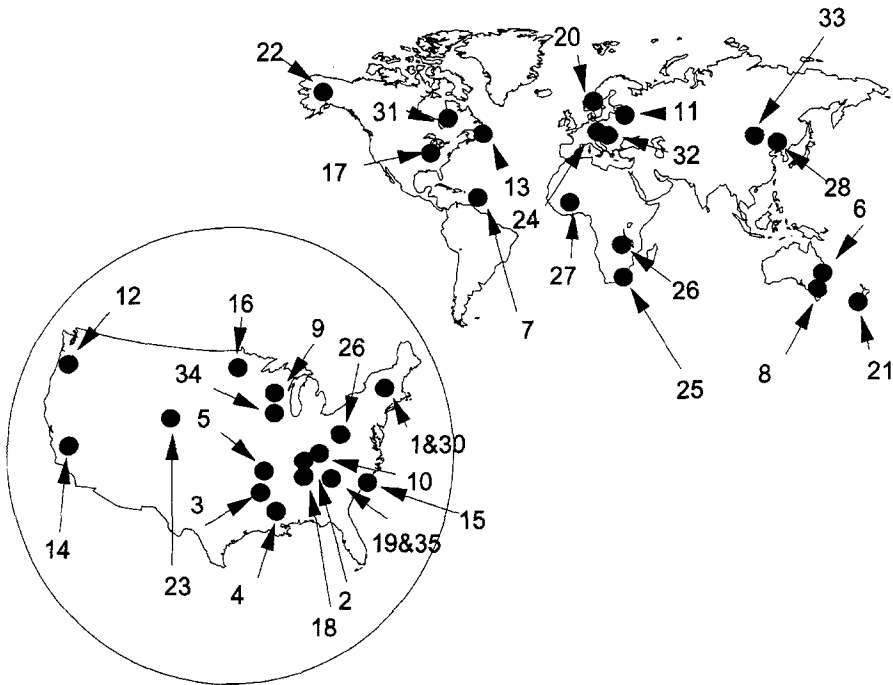


Figure 1. Individual-based gap models. Numbers correspond to the numbers on the map. Mnemonic for each model and reference citations are:

	Mnemonic	Citation	Ecological system simulated
1	FORTNITE	Aber and Melillo (1982)	Wisconsin mixed wood forest.
2	LOKI	Bonan (1989)	North American spruce-fir forest.
3	JABOWA	Botkin et al. (1972)	Northern hardwood forest.
4	JABOWA II	Botkin (1993)	Northern hardwood forest.
5	FORCLIM	Bugmann (1994)	Swiss Montane forest.
6	FORANAK	Busing and Clebsch (1987)	Appalachian spruce/fir forest.
7	STEPPE	Coffin et al. (1989a, b)	North American short-grass prairie.
8	CLIMACS	Dale and Hemstrom (1984)	Pacific Northwest coniferous forest.
9		Desanker and Prentice (1993)	Miombo woodland.
10	FORENZ	Develice (1988)	New Zealand forest.
11	FORICO	Doyle (1981)	Puerto Rican montane rain forest.
12	SMAFS	El Bayoumi et al. (1984)	Eastern Canadian mixed wood forest.
13	OVALIS	Harrison and Shugart (1990)	Appalachian oak-hickory forest.
14	SILVA	Kercher and Axelrod (1984)	Mixed conifer forest.
15	FORECE	Kienast and Kuhn (1989)	Central European forest.
16	FORSKA	Leemans and Prentice (1987)	Scandinavian forest.
17	EXE	Martin (1992)	Temperate/boreal forest transition.
18		Menaut et al. (1990)	West African humid savanna.
19	FORAR	Mielke et al. (1978)	Arkansas pine/oak forest.
20	SJABO	Oja (1983)	Estonian conifer forest.

Figure 1. (Continued)

	Mnemonic	Citation	Ecological system simulated
21	SORTIE	Pacala et al. (1993)	Northern hardwood forest.
22	LINKAGES	Pastor and Post (1986)	Temperate/boreal forest transition.
23	FORFLO	Pearlstine et al. (1985)	Southern USA floodplain forest.
24	SWAMP	Phipps (1979)	Arkansas floodplain forest.
25	SUCSIM	Reed (1980)	Douglas-fir forests.
26	KOPIDE	Shao (1991), Shao et al. (1991)	Chinese mixed pine/deciduous forest.
27	KIAMBRAM	Shugart et al. (1980)	Australian subtropical rain forest.
28	BOFORS	Shugart et al. (1992)	Boreal forest of Eurasia and North America.
29	BRIND	Shugart and Noble (1981)	Australian eucalyptus forest.
30	FORET	Shugart and West (1977)	Southern Appalachian deciduous forest.
31		Sirois et al. (1994)	Boreal forest/tundra transition.
32	FORENA	Solomon (1986)	Forests of eastern North America.
33	FORMIS	Tharp (1978)	Mississippi river floodplain forest.
34	OUTENQUA	Van Daalen and Shugart (1989)	South African temperate rain forest.
35	FORCAT	Waldrop et al. (1986)	Southern oak/hickory forest.
36	FORNUT	Weinstein et al. (1982)	Southern Appalachian deciduous forest.
37		Yan (this issue)	Chinese mixed pine/deciduous forest.

The model structure emphasizes two features important to a dynamic description of vegetation pattern: (1) the response of the individual plant to the prevailing environmental conditions, and (2) how the individual modifies those environmental conditions. The model is hierarchical in that the higher-level patterns observed (i.e., population, community, and ecosystem) are the integration of plant responses to the environmental constraints defined at the level of the individual.

2.1. GROWTH

In the original formulation of gap models, the growth of an individual is calculated using a function that is species-specific and predicts, under optimal conditions, an expected diameter increment given a tree's current diameter (Figure 2). This optimum increment is then modified to reflect the prevailing environmental conditions and the realized increment, an annual ring, is added to the tree.

The central assumption in formulating the diameter increment equation is that growth in trees is the consequence of two opposite processes. The positive part of rate of volume accumulation is assumed under optimal conditions to increase as a linear function of the leaf area of the tree. The magnitude of this positive growth rate depends on the net photosynthetic rate of the tree per unit of leaves. Contrary to this positive rate is a negative rate that is associated with the energetic cost of

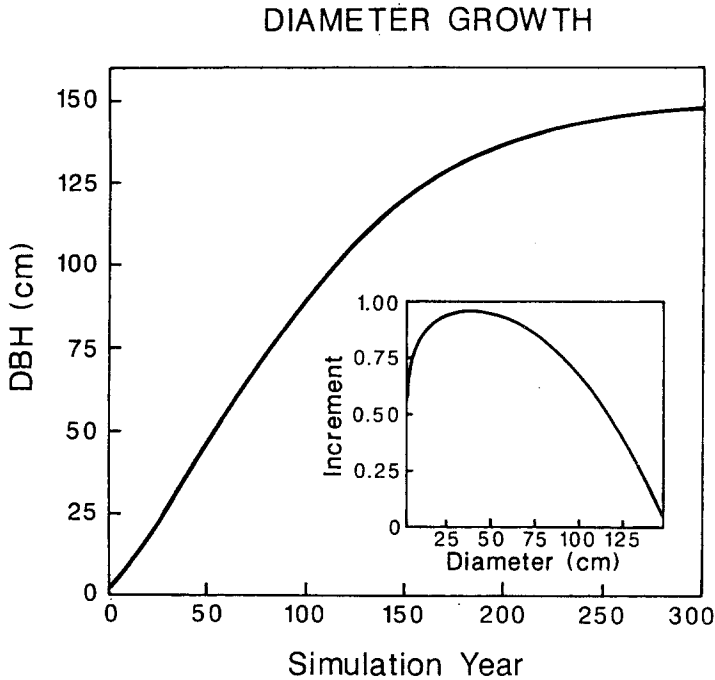


Figure 2. Optimal growth curve describing (a) growth (diameter at breast height) as a function of time (yrs), and (b) annual diameter increment as a function of diameter.

maintaining a given volume of living tissue. Presumably, as a tree increases in size, these negative costs increase until they begin to approach the positive growth in magnitude, and the rate of growth of the tree slows and stops.

Botkin et al. (1972) included these effects in the initial JABOWA model using the following derivation. The volume of a tree is roughly that of a cone with the appropriate diameter and height:

$$V \propto D^2H \quad (1)$$

where:

- V is a tree's volume
- D is a tree's diameter
- H is a tree's height.

A function that approximates the relation between diameter and height (Ker and Smith, 1955) is:

$$H = 137 + b_2D - b_3D^2 \quad (2)$$

The 137 in the equation refers to the fact that tree diameters are usually measured at 'breast height' or 137 cm. Equation (2) is for a parabola. If the maximum height

of a tree is obtained when it reaches its maximum diameter ($dH/dD = 0$, when $H = H_{\max}$, and $D = D_{\max}$), then

$$b_2 = 2 \left(\frac{H_{\max} - 137}{D_{\max}} \right) \quad (3)$$

and

$$b_3 = \left(\frac{H_{\max} - 137}{D_{\max}^2} \right) \quad (4)$$

Assume that the growth of volume of a tree has a response much like that in the logistic equation, so that the change in volume increases with the photosynthetic production of the leaves but that this rate of increase is slowed as the volume increases (reflecting the costs of respiring tissue and other losses in the plant). This can be expressed as

$$\frac{dD^2H}{dt} = rL_a \left(1 - \frac{DH}{D_{\max}H_{\max}} \right) \quad (5)$$

where:

L_a is the leaf area and
 r is a rate parameter.

If one assumes (following Whittaker and Marks, 1975) that

$$L_a \approx cD^2 \quad (6)$$

Then one can substitute and perform the indicated operations on Equation (5) to find:

$$\begin{aligned} \frac{d[D^2H]}{dt} &= rL_a \left(1 - \frac{DH}{D_{\max}H_{\max}} \right) \\ \frac{d[D^2(137 + b_2D - b_3D^2)]}{dt} &= (rcD^2) \left(1 - \frac{DH}{D_{\max}H_{\max}} \right) \\ \frac{d[137D^2 + b_2D^3 - b_3D^4]}{dt} &= rcD^2 \left(1 - \frac{DH}{D_{\max}H_{\max}} \right) \\ \frac{dD}{dt} (274D + 3b_2D^2 - 4b_3D^3) &= rcD^2 \left(1 - \frac{DH}{D_{\max}H_{\max}} \right) \\ \frac{dD}{dt} &= \frac{GD \left(1 - \frac{DH}{D_{\max}H_{\max}} \right)}{(274 + 3b_2D - 4b_3D^2)} \end{aligned} \quad (7)$$

where:

G equals rc from earlier equations.

Clearly, this growth equation is designed to give an approximation of the growth rate and pattern of a species from a minimal amount of information. Several gap models are based on alternate growth equations (as well as other equations in the models). Some of these alternatives continue the appealing feature of ease of parameter estimation, but have improved functions in terms of better representing tree growth. A detailed discussion of these approaches is presented in Bugman et al. (1996).

As Bugman et al. (this issue) point out, the differences in growth-rate formulations in gap models are an expression of different views as to how to represent the growth process in trees. There has been relatively little intercomparison of model performance using different growth equations but since the parameter demands of the different formulations are similar this seems a logical exercise to be undertaken.

2.2. SPATIAL SCALE

The horizontal position of each individual on the plot is influenced by (and influences) the growth of all other individuals on the plot. The earlier models were constructed under an assumption of horizontal homogeneity within the simulated plot, and the size of the simulated plot is critical in these cases (Shugart and West, 1979). The spatial scale at which the earlier models operate is for an area corresponding to the zone of influence of single individuals of maximum size. This allows for an individual growing on the plot to achieve maximum size while at the same time allowing for the death of a large individual to significantly influence the light environment on the plot (Shugart and West, 1979).

Even in the early gap models, the vertical structure of the canopy is modeled explicitly. The sizes of individuals (height and leaf area predicted by regressions on each tree's diameter) are used to construct a vertical leaf-area profile. Using a light extinction equation, the vertical profile of available light is then calculated so that the light environment for each individual can be defined. More recent versions of the models compute the three-dimensional canopy interactions among trees and are much like the earlier forestry models (Smith and Urban, 1988; Busing, 1991; Weishampel et al., 1992).

2.3. ENVIRONMENTAL CONSTRAINTS AND RESOURCE COMPETITION AMONG TREES

All gap models simulate individual tree response to light availability at height intervals on the plot. Other resources are incorporated to varying degrees in different versions of the model; these other constraints include soil moisture, fertility (either fertility in a generic sense or nitrogen specifically), temperature, as well as disturbances such as fires, hurricanes, floods, and windthrow. In most of the

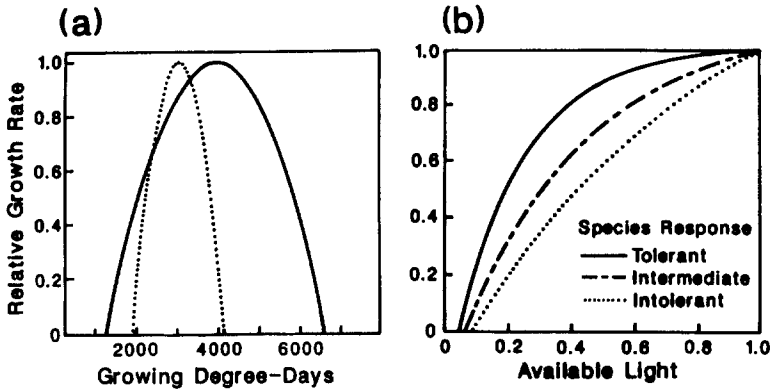


Figure 3. Environmental response functions relating proportion of optimal growth (see Figure 2) as a function of environmental conditions on the simulated plot. (a) Response functions for temperature for two different species. Each species is indicated by dashed and solid lines. (b) Response functions for available light for three species of differing tolerances.

models, the environmental responses are modeled via a 'constrained potential' paradigm. In this, a tree has a maximum potential behavior under optimal conditions (i.e., maximum diameter increment, survivorship, or establishment rate). This optimum is then reduced according to the environmental context of the plot (e.g., shading, drought), to yield the realized behavior under ambient conditions. The curves describing species response to environmental resources tend to be generic curves that scale between 0.0 and 1.0, and species are often categorized into a small number of functional types (Figure 3).

The limitation effects of resource shortages in the models were initially computed in a multiplicative fashion (Botkin et al., 1972; Shugart, 1984; Botkin, 1993). Later models in some cases use other approaches, notably assigning the growth reduction to that of the most limiting factor (Pastor and Post, 1986).

Competition in the model depends on the relative performance of different trees under the environmental conditions on the model plot. These environmental conditions may be influenced by the trees themselves (e.g., a tree's leaf area influences light available beneath it), or may be modeled as extrinsic and not influenced by the trees (e.g., temperature).

Competition may operate in two modes. Competition for light is asymmetric and exploitative: a tree at a given height absorbs light and reduces the resource available to trees at lower positions in the canopy. In most gap models, competition for below-ground resources (water and nutrients) is symmetric. Each tree experiences a resource level common to the plot. This approach to modeling the competition process has the result that competitive ability depends strictly on the context of the modeled gap.

The tree that has the best performance, relative only to other trees on the plot, is the most successful. Competitive success depends on the environmental conditions

on the plot, which species are present, and the relative sizes of the trees. Each of these varies through time in the model.

2.4. MORTALITY

The mortality of plants, general, and certainly of trees is a relatively poorly known aspect in plant ecology and the formulations in many of the gap models reflect the state of knowledge. The tendency in most of the existing gap models has been to use relatively straight-forward descriptions of mortality in the anticipation of additional information.

The death of individuals is modeled as a stochastic process. Most gap models have two components of mortality: age-related and stress-induced. The age-related component applies equally to all individuals of a species and depends on the maximum expected longevity for the species; this age is typically on the order of 300 years, yielding an annual survivorship rate of around 1–2%. The probability of mortality of each individual tree is determined as a stochastic function. Each tree is assumed to have an intrinsic mortality rate such that, under normal conditions, 1% of the individuals in a cohort could be expected to live long enough (a parameter called AGEMX) to attain their maximum height and diameter. Thus, the probability of mortality is:

$$P_m = 1 - e^{\frac{-4.605}{AGEMX}} \quad (8)$$

where:

P_m is the intrinsic probability of mortality.

AGEMX is the age at which one would expect 1% of a cohort to be alive and, by assumption, the age at which one might expect an individual to reach its maximum size.

Trees that are growing slowly have an increased probability of death. In the earlier gap models, trees with a minimum diameter increment of only 1.00 mm per year are subjected to additional mortality, $P_s = 0.368$, where P_s is the probability of survival of a tree suppressed (due to shade or other factors). This has the effect of allowing only 1% of a suppressed cohort to survive 10 years. In more recent gap models, stressed trees are defined with respect to a minimal relative diameter increment (typically 10% of optimum growth for a given size of tree). This latter modification reflects the tendency for trees with reduced rates of growth to suffer to higher mortality rates due to reduced vigor (Franklin et al., 1987). With either an absolute or relative minimum growth rate, individuals failing to meet the minimal condition are subjected to an elevated mortality rate (Equation (8)).

2.5. ESTABLISHMENT

Several authors (van der Pijl, 1972; Whitmore, 1975; Grubb, 1977; Bazzaz and Pickett, 1980) have discussed species attributes that are important in differentiat-

ing the regeneration success of various trees. The complexity of the regeneration process in trees and its stochastic nature makes it nearly impossible to predict the success of a given tree seedling. Most gap models are designed to treat regeneration in trees from a pragmatic view that the factors influencing the establishment of seedlings can be usefully grouped in broad classes (Kozlowski, 1971a, b; van der Pijl, 1972; Grubb, 1977; Denslow, 1980). In the model, tree establishment and regeneration are largely stochastic, with maximum potential establishment rates constrained by the same environmental factors that modify tree growth. Each simulation year, a pool of potential recruits is filtered through the environmental context of the plot, and a few new individuals are established.

2.6. APPLICATION OF PATCH MODELS TO GLOBAL CHANGE ISSUES: LIMITATIONS AND RECENT ADVANCES

The scientific questions relating to the potential response of terrestrial vegetation to global environmental change pose new problems for the development and application of patch models of vegetation dynamics. The original development and application of gap models discussed above focused on examining the temporal (e.g., successional) dynamics of vegetation at a given site or along simple environmental gradients (e.g., elevation) (see Table I). Many of the simplifying assumptions that have been made for ease in characterizing basic plant processes and patterns may no longer hold under changing environmental conditions. In this section we wish to examine some of the limitations of the basic gap model structure presented above for addressing global change issues, namely the response of terrestrial vegetation to changing atmospheric concentrations of CO₂ and possible associated changes in the global climate system. Many of the limitations that are discussed below have been addressed with new model developments, a number of which are presented in the following contributions to this volume.

2.7. CHARACTERIZATION OF ENVIRONMENTAL RESPONSES

2.7.1. *Temperature*

Although ecological theory suggests that the geographic distribution of a species is a function of both physiological tolerances (absolute limits or 'fundamental niche') and competition with other species (realized distribution or 'realized niche'), in the absence of a mechanistic understanding of the relative importance of these two processes, the environmental response functions characterizing growth, establishment and survival have typically been parameterized based on distributional data. For example, the function describing the growth response of a species to temperature (see Figure 4) has typically been characterized as a parabola. The minimum and maximum temperature tolerances (e.g., growing degree days) for a species are assumed to be the values observed at the boundaries of its geographic distribution (Figure 4). Although a questionable assumption, in the absence of empirical data on the response of various processes to temperature, the approach ensured that the

Table I
Examples of model tests on gap models

Type of model test	Example case	Other analogous cases
With a priori parameter estimation for species predict forest-level features (total biomass, leaf area, stem density, average tree diameter, etc.).	Prediction of biomass for floodplain forests (Phipps, 1979; Pearlstine et al., 1985). Predict effects of timber harvest on nutrient regimes in northern (USA) hardwood forests (Aber et al., 1978).	Similar predictions for a diverse array of systems: Estonian Conifer forest (Oja, 1983), New Zealand southern beech forests (Develice, 1988), Pacific Coast Douglas-fir forests (Dale and Hemstrom, 1984), West African Savannah (Menaut et al., 1990), etc. Most of the cases shown in Figure 1 have been inspected <i>vis-à-vis</i> this test.
Run model for a long period of time, test results against mature forests preserved in a region.	Predict structure and composition of relic mature forests in Sweden (Leemans and Prentice, 1987).	Predict old growth forest in montane spruce-fire zone in southern Appalachians (Busing and Clebsch, 1987), in Mississippi River floodplain (Tharp, 1978), upland forests in Arkansas (Mielke, 1977), and in Chinese mixed forest (Shao, 1991). This is a frequently used evaluation for most of the models found in Figure 1.
Calibrate model on stands of a given age, predict stand structure on stands of a different age.	Using a model that predicts the structure and composition of old-growth forests in the Great Smoky Mountains National Park (USA), test by independently predicting composition and structure of forest clear cut 40 and 70 years before (Busing and Clebsch, 1987).	Predictions of the composition and structure of Canadian forests (El Bayoumi et al., 1984), diameter structure of Puerto Rican rain forests stands of different ages (Doyle, 1981), Australian rain forest at different ages after harvest (Shugart et al., 1980).
Use introduction of disease or change in conditions (e.g., fire frequency, etc.) as a 'natural' experiment.	Predict the composition of mature forests in East Tennessee (USA) before the introduced chestnut blight eliminated one of the major tree species (Shugart and West, 1977).	Predict composition or structure of forest at different fire frequencies in mixed conifer forests (Kercher and Axelrod, 1984), for Puerto Rican montane rain forests under different hurricane conditions (Doyle, 1981; O'Brien et al., 1992).
Predict independent tree diameter increment data.	Predict the growth and diameter increment by species and diameters for subtropical rain forest (Van Daalen and Shugart, 1989).	Predict diameter frequency distributions for Puerto Rican montane rain plots of different ages (Doyle, 1981).
Predict forestry yield tables.	Test model on its ability to reproduce Swedish yield tables (Leemans and Prentice, 1987).	Predict Eucalyptus yield tables for montane Australian forests (Shugart and Noble, 1981), for Loblolly pine (Mielke et al., 1977), for Swiss forests (Kienast and Kuhn, 1989), for Chinese mixed forest (Shao, 1991).

Table I
(Continued)

Type of model test	Example case	Other analogous cases
Predict forest composition change to single environmental gradients.	Predict change from deciduous to coniferous forest in the mountains of New England (Botkin et al., 1972).	Predict changes in forest composition as a function of flood frequency (Tharp, 1978; Pearlstine et al., 1985), at a range of locations (Bonan, 1989) in the boreal zone, along altitudinal gradients in China (Shao et al., 1991). This test and more complex variants are often applied to gap models.
Predict forest composition response to multiple environmental gradients	Predict composition and structure of boreal forests on north and south facing slopes and for different ages since wildfire in Fairbanks, Alaska region (Bonan, 1989).	Tests again fire and altitude variables in mountains of California (Kercher and Axelrod, 1984) and Australia (Shugart and Noble, 1981). Tests in complex terrain (Slopes, altitudes, soils) in Switzerland (Kienast and Kuhn, 1989).
Reconstruct composition of vegetation under past climates (paleo-reconstruction)	Reproduce 16,000 year record of forest change based on fossil pollen chronology from East Tennessee (Solomon et al., 1980)	Reproduce forest composition under full glacial and other conditions (Solomon et al., 1981; Solomon and Shugart, 1984; Solomon and Webb, 1985; Bonan and Hayden, 1990). There have also been several applications of the models in this mode.

predictions of the models were broadly consistent with observed latitudinal and altitudinal ranges – the models were constrained from simulating the occurrence of species outside their known environmental domains. However, this simple temperature response function hides the direct response of many processes, such as photosynthesis and respiration and flowering, to temperature. It also masks the responses to extreme events such as drought or frost. Under a climate change, the balance of these phenomena may change, and thus better estimates of the thermal response of plants are needed.

Because the models treat the performance of each of the individual plants of each species, the ability to incorporate species-specific and size-specific environmental responses of tree establishment, growth, reproduction and survival is not an inherent problem of the patch models; rather it is a problem of available data. Recent work has focused on replacing this simple approach of modeling annual growth with physiologically detailed models of individual plant growth that explicitly consider the processes of photosynthesis, respiration and carbon allocation. These models typically simulate net photosynthesis on an hourly or daily basis, with calculations of net primary production and carbon allocation on an annual basis. One such example is the HYBRID model (Friend et al., 1992). HYBRID substitutes a detailed model of photosynthesis and transpiration (Friend, 1991) for the simple

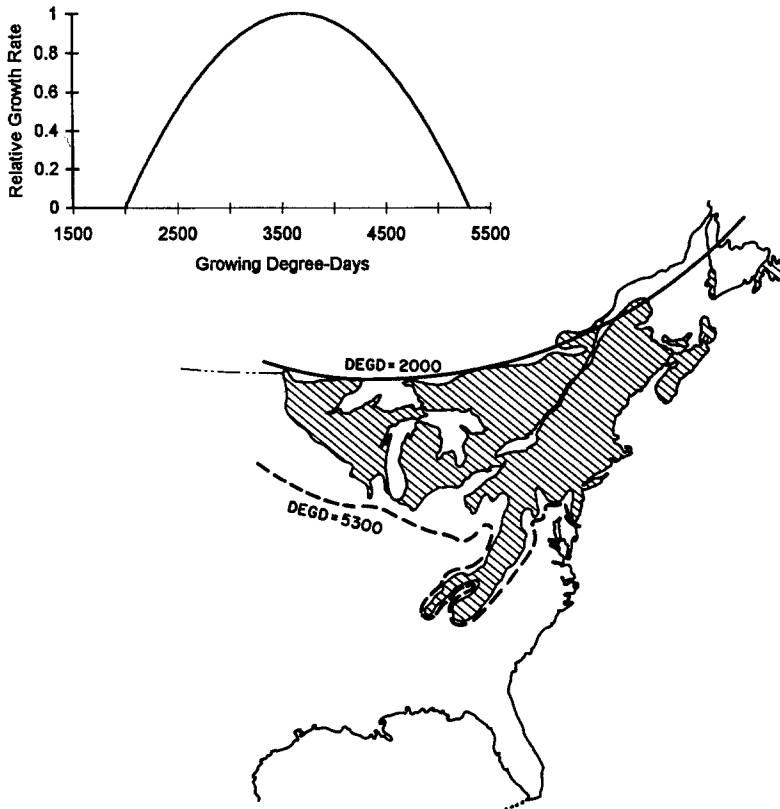


Figure 4. Example of the development of species' temperature response function. The area outlined on the map represents the geographic distribution of the species. The corresponding growing degree-day (DEGD) values at the northern and southern limits to its distribution are labelled. These values are used to define the minimum and maximum growing degree-days for the parabolic function describing the temperature response of the species.

growth equation(s) described earlier (see Description of Gap Models, Section 2.1, *Growth*). In this approach, the response of carbon balance to temperature, moisture and available nitrogen are modeled explicitly. Although this approach overcomes the inherent shortcoming in modeling species' environmental responses using distributional data, it is very data intensive in the characterization of basic parameters describing species' physiology.

The FORCLIM model (Bugman and Fischlin, this issue) uses an approach similar to that of HYBRID, explicitly modeling the environmental constraint on photosynthesis and respiration.

Other studies have examined temperature response on plant processes other than carbon gain. Recent regional studies have included specific temperature responses relating to chilling requirements or frost tolerance within patch models (see Cummings and Burton, this issue). These studies have shown the sensitivity of model predictions to these processes under climate change scenarios. The characteriza-

tion of species-specific environmental response functions to key plant processes is critical for advancing the ability of patch models to address global change issues related to climate change.

2.7.2. *Moisture*

Plant response to available moisture has been incorporated into the gap (patch) model framework using a number of approaches (see Bugman et al., this issue). As with temperature, the characterization of species' response to moisture has been largely based on data derived from geographical distributions. Typically, simplified models of evapotranspiration (e.g., Thornthwaite, 1931; Priestley and Taylor, 1972) are used to quantify the moisture environment at the arid extreme of a species distribution (see Shugart (1984) for detailed discussion). For example, Post and Pastor (this issue) use an index of drought-days. Drought-days is defined as the proportion of the growing season during which soil moisture is at or below wilting point. A species' tolerance to moisture deficit is defined as the drought-day value associated with the arid limit to its geographical distribution (see Figure 4). A square-root function is used to describe the species response, with optimal response (e.g., growth or establishment) occurring when the value of drought-days is zero. Although this approach provides a simple index of moisture stress, it may be inadequate to describe plant response to a climate change induced by rising atmospheric CO₂ concentrations. The simple representations of evapotranspiration used in most applications do not explicitly consider the interactions of temperature and water vapor pressure deficit, nor do they have an explicit treatment of foliage area and stomatal dynamics. The latter may be of greatest importance given the potential implications of increasing atmospheric CO₂ on stomatal conductance and subsequent water-use efficiency. Recently developed patch models using more physiologically-based representations of canopy processes (Martin, this issue; Kramer and Mohren, this issue) are a hopeful beginning to eliminating these limitations. However, questions still exist on the degree to which leaf-level responses can be scaled up to the canopy, stand or landscape levels without distortion (see Root and Schneider, 1995).

2.7.3. *CO₂ Response*

A very important environmental response in the context to global change issues is that of the direct effects of rising CO₂ concentrations on plant and ecosystem processes.

Information of the effects of CO₂ enrichment on plant species is virtually restricted to short-term studies of juvenile plants (see Bazzaz, 1990). Considerable uncertainty surrounds the extrapolation from juveniles to adults, including the tendency of some species to acclimate to enhanced CO₂. Moreover, there is a large degree of variation among species in the observed responses to CO₂. Just as is the case with more aggregated biome models, this diversity of response, both among species and with time present a problem with incorporating direct effects of

CO₂ enrichment into patch models. Gap models simulate the dynamics of species composition and vegetation structure, explicitly considering the variation among species in their life history and environmental responses.

The current limitation on including direct CO₂ effect into patch models is the lack of data on whole plant response at the species level, and a need to better characterize the relevant eco-system feedbacks. A number of studies based on the limited data for tree species which is available are currently under way (Steven Pacala, personal communication). It appears that the application of a simple scalars (e.g. ' β ' factors) applied equally to all species are inappropriate. Preliminary results suggest that in the case where there is variation among species in CO₂ response, the resulting changes in net primary productivity differ from corresponding estimates where a single response function (such as a β factor) is applied across species (also see Smith, 1996). Differential species responses to elevated CO₂ can change the relative abundance of species, thus dynamically altering the mixture of responses are assumed invariant in calculating a simple CO₂ response scalar for the ecosystem.

The more recently developed gap models that include an explicit treatment of photosynthesis and transpiration are capable of incorporating our current understanding of the response of plants to elevated CO₂ at the leaf-level (Kramer and Mohren, this issue; Martin, this issue). However, care should be taken in the interpretation of the resulting predictions from these models. These models implicitly assume that the whole plant response to CO₂ follows directly from the integration of the leaf-level responses. This assumption has been shown to be false in many experimental studies that have examined whole-plant and/or ecosystem responses to elevated CO₂ (see Bazzaz, 1990, for a review). Root and Schneider (1995) discuss the problem of scaling such multiscale incorporation of phenomena in models and propose iteration between large and small scale studies (SCS, strategic cyclical scaling) as a research paradigm to better understand the behavior of complex environmental systems. The incorporation of detailed physiological mechanisms into gap models is a link in such a strategic procedure.

2.8. REPRESENTATION OF SOIL PROCESS

In general, patch models give little attention to soil processes. More recent models (e.g., LINKAGES – Pastor and Post, 1986; Post and Pastor, this issue) incorporate more complete models of the nutrient cycle to capture the complex nature of the feed back mechanisms between vegetation and soil dynamics. Decomposition rates and organic matter formation will both be affected by a changed climate, and the net result (C storage in soils) is therefore difficult to predict. Given the possibilities for feedbacks between changes in productivity/species composition and the rates of decomposition and nutrient cycling under changing environmental conditions, there is a need for explicit consideration of soil processes within the framework of patch models.

Even among those patch models that explicitly consider the processes of decomposition and nutrient cycling, none include or are constrained by mass balance of carbon or other nutrients. For many applications, such as addressing carbon storage issues, models must incorporate nutrient cycling and mass balance of carbon and nitrogen. However, it is probably not necessary that all patch models have this capability. Initial studies which have linked patch models with ecosystem models of carbon and nitrogen dynamics (e.g., CENTURY – Parton et al., 1988) which require mass balance have met with some difficulties related to the spatial scales at which the different processes are described (Lauenroth et al., 1993 and this issue). Most patch models operate at a spatial scale at which material-dynamics processes such as the building of biomass, the death of the dominant plant, subsequent regeneration and growth are in a state of quasi-cyclical disequilibrium. Most ecosystem models of nutrients and biomass using a mass-balance approach assume these same processes are operating in a relatively constant and equilibrium-seeking fashion. For patch models, such quasi-equilibrium behavior is found only at larger spatial scales (where the small scale dynamics are averaged and thus become more predictable). Spatially extensive forms of the patch model (e.g., ZELIG – Smith and Urban, 1989; STEPPE – Coffin and Lauenroth, 1989a, b, 1994; Coffin et al., 1993) may be necessary to dynamically simulate the larger-scale behavior of the non-equilibrium dynamics expressed in patch models and thus achieve more constant estimates of mass balance needed to ecosystem models.

2.9. SPATIAL CONTEXT FOR EVALUATING LANDSCAPE PROCESSES

In earlier versions of patch models recruitment was represented very simplistically (see Section 2.5, *Establishment*). All species from the area/region were assumed to be available for recruitment into the patch. Species which were inappropriate for the environmental conditions on the patch were filtered out via the environmental constraints on growth. Dispersal was largely ignored. Under conditions of environmental change, these assumptions (models) are inappropriate. Changes in species composition within an area or region will be related to rates of dispersal and species immigration. Explicit consideration of these processes require that the patch models (gap models) operate within some spatial context (e.g., spatial grid) and that they have ‘memory’ of whether or not seeds are available in the plots. Research on the development of spatially explicit patch models has progressed on two independent fronts; (1) explicit consideration of the position of each individual within a single patch, and (2) the linking of individual patches into a spatial network. Explicit consideration of the position of individuals within the patch (e.g., SORTIE – Pacala et al., 1993; Busing, 1991) has allowed for studies which examine small-scale patterns of species distribution within a forest stand resulting from feedbacks between canopy composition and patterns of recruitment. New model structures which place each patch being simulated into a spatial context (e.g., ZELIG – Smith and Urban, 1989; STEPPE – Coffin and Lauenroth, 1989, 1990,

1994) have allowed for patch models to be used to explore a range of questions relating to landscape processes and scale-related issues.

Current forms of the patch models which operate within a spatial framework (e.g., ZELIG – Smith and Urban, 1989; FORANAK – Busing and Clebsch, 1987; SORTIE – Pacala et al., 1993) are explicitly modeling the process of dispersal and linking recruitment to canopy composition. Data are needed to develop more specific models of early recruitment processes in a realistic manner, and models of dispersal (including long-distance dispersal) need to be developed and tested.

In addition to examining patterns of dispersal, providing a spatial context has allowed recent research to examine other landscape processes which involve spatially explicit interactions between patches such as catchment hydrology, fire and insect outbreaks.

2.10. EXPANSION OF GAP MODEL APPROACH TO MULTIPLE LIFE FORMS

The original development of patch models focused on forest ecosystems. Over the past decade, patch models have been developed for a wide variety of forested ecosystems, however, only in recent years has the patch model framework been applied to grassland (Coffin and Lauenroth, 1989a, b, 1990, 1994, this issue) and shrub and heathland (van Tongeren and Prentice, 1986) ecosystems. In addition to the smaller spatial scale at which these models operate ($< 1 \text{ m}^2$ as compared to 0.1–1.0 ha for forest patch models), the development of grassland patch models required a more detailed consideration of competition for below-ground resources.

Although patch models have been developed for grasslands, shrublands and forests, only recently have patch models been developed which are capable of simulating the dynamics of ecosystems in which multiple life forms are codominant (e.g., tropical/subtropical savannas). Two basic approaches are being taken. The first approach involves using a spatially explicit structure where the position of each individual within a patch is considered and interactions among individuals are spatially dependent (e.g., Menaut et al., 1990). The second approach involves the use of nested patches similar in concept to the approach of nested quadrats used in vegetation sampling. Smaller patches which simulate herbaceous and small woody plants are 'contained' within larger patches which are used to simulate larger woody plants. Larger patches define the environment for smaller patches while recruitment is handled as a statistical process from smaller to larger patches (e.g., VEGOMAT – Smith et al., 1989, Lauenroth et al., 1993).

The development of patch models that can examine the dynamics of non-forest ecosystems will greatly expand the range of ecosystems represented by current patch-gap models. This step is essential for providing an understanding of global patterns of vegetation response to climate change.

3. Future Research

Although the research discussed above is making significant progress in resolving the current limitations of patch models in addressing the issues of global change, much research remains to be done. The research agenda outlined below focuses solely on questions related to global change. Although patch models have an important role to play in global change research, their utility as a research tool is not limited to global change issues. Patch models have a rich history in ecological research over the past two decades, in areas ranging from the development of ecological theory to applications in forest management and the conservation of biodiversity.

3.1. RECONCILIATION OF SCALING ISSUES

A major focus of research relating to global change is the attempt to understand how certain processes that operate at one spatial or temporal scale influence process and pattern at larger or longer spatial or temporal scales. For example, how do patterns of photosynthesis at the leaf-level relate to patterns of growth at the level of the whole plant, or how do population and community dynamics of species composition and population structure relate to ecosystem level processes of the cycling of water and nutrients at the ecosystem level? Individual-based patch models can help address many of these questions because they can simulate aspects of population community, ecosystem and landscape dynamics as a function of the response of individual plants interacting with the environment of the patch.

3.2. INCLUDE MULTIPLE DISTURBANCES AND HUMAN IMPACTS

Patch models have incorporated disturbances such as fire, hurricanes, herbivory and timber harvest into the model framework as agents of mortality. However, in the context of global change there is a need for a more mechanistic approach to modeling disturbance and an explicit consideration of human impacts related to landuse. To address many of these features/processes using patch models requires that a spatial approach be adopted such as the one discussed above for examining landscape level processes.

3.3. NEED TO CONSIDER MULTIPLE STRESSES WHERE POSSIBLE

In addition to increasing atmospheric concentrations of CO₂ and the associated potential for climate change, there are additional potential stresses on plant function related to anthropogenic causes, such as increased levels of ozone, UV radiation, acid precipitation, and fragmentation. Experimental studies have shown that there are significant interactions among these and other stress factors. These interactions may be a function of direct physiological effects on the plant or via indirect effects on ecosystem level processes such as decomposition and nutrient availability. The

nature of these interactions must be understood and incorporated into the framework of models of plant processes if we are to be able to predict more fully the response of ecosystems to changing environmental conditions relating to anthropogenic disturbance.

3.4. DEVELOPMENT OF A FUNCTIONAL CLASSIFICATION OF PLANTS FOR PARAMETERIZING REGIONAL TO GLOBAL-SCALE MODEL OF VEGETATION DYNAMICS

Patch models simulate the dynamics of species composition and stand structure using species-specific parameters describing life history and environmental response. Although this approach has proven feasible for modeling even species rich ecosystems such as tropical/subtropical rain forest, deriving parameters for even the dominant species at a continental to global scale appears unrealistic. To overcome this limitation, efforts are underway to develop a functional classification(s) of species based on similarities in characteristics (e.g., life history, environmental response) important to dominant ecosystem processes and environmental feedbacks (Smith et al., 1996). Patch models can, and should, play an important role in the theoretical and practical development of such classification systems. Patch models can be used to examine the consequences of aggregating species into groupings which are characterized by a single set of parameters, in contrast to predicted dynamics based on species-specific parameterizations.

3.4.1. *Provide Broader Geographic Coverage*

Patch models have been developed for a wide range of ecosystems around the world, however, there are many ecosystems (even biomes) for which models have not been developed. One obvious area for future model development is in the southern hemisphere, specifically in the tropical regions of Africa, South America and Asia. The development of mixed-life form models will provide for an expansion of the approach into tropical/subtropical savannas. This addition will allow the application of patch models to address potential long-term changes along the moisture gradient from grassland to forest. In addition, the recent development of patch models in herbaceous and shrub-dominated ecosystems should allow for the development of patch models for tundra ecosystems, providing the ability to address the important transition zone between tundra and boreal forests at the high northern latitudes.

3.5. DYNAMIC GLOBAL VEGETATION MODELS (DGVM)

One of the priority activities of International Geosphere Biosphere Programme (IGBP), Global Change and Terrestrial Ecosystems (GCTE) Focus 2 is the development of dynamic models of global vegetation (DGVM). Two approaches for model development have been discussed, the bottom-up and the top-down. The bottom-up approach involves the scaling-up of patch models using some statistical sampling procedure to provide continental and global coverage. This approach

would require a generalized patch model which is able to simulate the dynamics of all ecosystem types (e.g., boreal forest, tropical savanna, temperate grassland). This generalized patch model would use a functional classification of plants rather than addressing species composition. The development of such a modeling approach is dependent on future research and development of patch models relating to many of the activities outlined in this document.

The second approach, top-down, utilizes current 'equilibrium models' of global vegetation pattern. This class of models includes biogeographical models which relate the large scale patterns of climate and vegetation (e.g., Holdridge Life Zone Classification – Holdridge, 1967; BIOME – Prentice et al., 1992), and global models of net primary productivity (e.g., GEM – Melillo et al., 1993). Although capable of predicting changes in the state of vegetation following a climate change, these models do not address the time scale or processes associated with those changes; they do not represent the transient dynamics of vegetation involved in achieving these new equilibrium patterns. The top-down approach of DGVM development would modify these global vegetation models by defining functional types of vegetation which make up each of the ecosystems or biomes currently used to describe vegetation pattern/composition within global models. These functional plant types would then be assigned parameters relating to rates of growth, mortality, dispersal and other processes which influence the transient dynamics of vegetation in response to changing environmental conditions. Note that this iteration between spatial scales and attendant processes, is an analogue to the strategic cyclical scaling (Root and Schneider, 1995) mentioned in the earlier section on incorporating CO₂-effects into gap models.

Both approaches to the development of DGVMs will rely heavily on patch models, either directly in the case of the bottom-up approach, or indirectly in the development of parameters for the functional plant types in the case of the top-down approach.

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