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Individual-based Forest Succession Models
and the Theory of Plant Competition*

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ABSTRACT

One of the few types of individual-based models that address multi-species interactions and community- and ecosystem-level phenomena is the class of forest succession models known as JABOWA or FORET models. This paper briefly reviews the history and major features of these models, which are probably the most widely used individual-based computer simulation models. The assumptions and mechanisms underlying these models, which originated over 20 years ago, are virtually identical to those that have been developed in the context of theoretical plant competition and plant population models. Interest among theoretical ecologists in mechanistic models of plant growth and competition has led to the convergence of recently developed models with the assumptions, mechanisms, and structure of a model that has been in use by ecosystem scientists for over 20 years.

Key Words: simulation, tree, succession, competition, ecosystem, spatial, physiology, community

Introduction

In 1972, at the height of the ecosystem research efforts of the International Biological Program, a fundamentally new type of ecological model was described in a major journal and subsequently ignored by most ecologists. Perhaps is it not surprising that one new model did not attract much attention and was lost in the flood of ecosystem models produced by the developing field of ecosystem ecology. The unique features that distinguished the new "forest growth simulator" from its IBP siblings were difficult to decipher from the two publications that announced its development. Nonetheless, it differed radically from the pool and flux ("box and arrow") models for which the IBP is remembered. The new "ecosystem" model was actually an individual-based population model (specifically, an i-state configuration model, Metz and Diekmann, 1986) of a multi-species forest, based on the growth and competitive interactions of many individual trees.

The model in question was developed by computer scientists at IBM's Thomas J. Watson Research Center, in collaboration with ecologists from Yale University who were part of IBP's Hubbard Brook Ecosystem Study. It was first published in the *IBM Journal of Research and Development* and is known by the acronym "JABOWA" (Botkin et al. 1972 a and b). Although the JABOWA model played little further role in the Hubbard Brook study, its basic concepts (and much of the original FORTRAN code) have proliferated into a host of closely-related "forest succession" or "gap" models which have been applied to many different forest types (see Shugart 1984, 1990) and used to address many different issues of population, community, and ecosystem ecology.

The JABOWA model was one of the first individual-based computer simulation models and, through its offspring such as the FORET model (Shugart and West 1977), has become one of the most widely used and best known models of this type. Although a growing group of researchers interested in the mechanisms of plant competition, succession, nutrient cycling, and other ecosystem processes has been using and publishing the results of these individual-based forest succession models for over 20 years, the models remain poorly understood by the majority of ecologists. The basic hypotheses about plant growth and competitive interactions that were implemented in the original JABOWA forest simulation model are still controversial ideas that are undergoing conceptual development in the fields of plant population and community ecology. If the JABOWA model were reinvented in 1991, it might be hailed as a major new contribution to plant ecology.

The goal of this brief review is to examine the assumptions and mechanisms of JABOWA-type models in relation to the major issues and modeling approaches in the field of theoretical plant population modeling. Hopefully, this exercise will contribute to improved communication and understanding between scientists who are pursuing the same goals from different modeling and philosophical backgrounds.

Individual-based Forest Succession Models: JABOWA and FORET

Two primary constraints shaped the structure of the JABOWA model. First, its objective was to reproduce the behavior of the ***mixed-species, mixed-age*** forest of the Hubbard Brook Experimental Station. This objective can be contrasted with that of most theoretical plant competition and plant population models, which were designed to be applied to and tested in even-aged monocultures. A second constraint on the JABOWA model was to produce output that could be compared directly with data collected from the forest, which were the diameters and growth increments of many individual trees in forest inventory plots. Consequently, the model was designed to grow individual trees and produce size distributions of the populations of many different species. Although the model output was often summed and presented as the total biomass per species, it was also possible to follow the simulated growth of a single individual, and to observe how it responded to such changes in its environment as the death of a neighboring tree (Botkin et al. 1972a).

The ability to account for variation due to local spatial interactions is one of the primary rationales behind the individual-based modeling approach (Huston et al. 1988). However, the JABOWA model takes a very different approach to spatial interactions than that developed in most theoretical plant competition models. On first inspection, it appears that spatial location is not even considered in the JABOWA model, which does not keep track of the locations of any of the hundreds of individual trees in a single simulation. This contrasts with the experimental and modeling approach in plant population ecology, where positions on a regular lattice or explicit interplant distances are used to model variation in the intensity of interplant interactions (see Ford and Sorrensen, this volume).

Local spatial interactions are handled in the JABOWA model simply by limiting the size of the simulated plot to an area small enough to be considered a "neighborhood." The original JABOWA model was designed to model trees growing on a 10 x 10 m plot. However, further work with the model demonstrated that the size of the plot had a critical effect on the model's behavior (Shugart and West 1977). Specifically, when the plot size was scaled to the canopy size of a full-grown individual of the largest species, the model reproduced the phenemenon known as "gap dynamics," that is, the establishment and growth of large numbers of saplings in the high light levels in the "gap" created by the death of a large tree. This practical definition of the competitive neighborhood as the crown area of a single large tree allowed the model to ignore the exact spatial locations of individual trees (most of which died as a result of simulated shading, anyway), while preserving the essential features of forest dynamics.

The most important aspect of the way in which spatial structure is modeled in JABOWA is the vertical dimension. Most theoretical plant competition and population models have focused on the "nearest-neighbor" distance, which is used as a two-dimensional index of the intensity of competition between neighboring plants. Analytical models of this type (e.g., Mead 1968; Diggle 1976; Gates 1978) included the assumption that competition between plants was "one-sided," that is, large plants had a negative effect on small plants, but small plants had little or no effect on large plants. Ford and Diggle (1981) developed an index based on the angle between the tops of neighboring trees that was used to determine whether one tree fell within the "cone of influence" of a larger tree. More recently, "neighborhood" models have attempted to parameterize the effect of competition on plant growth and reproduction in detailed spacing models (Pacala and Silander 1985, 1990).

The approach taken in the JABOWA model was not to calculate an index of competition, but to model the mechanism of competition directly. On the assumption that competition for light was the primary interaction between trees, the creators of JABOWA explicitly modeled the height growth of each individual tree, summed the leaf areas of all individuals of a given height class, and used a simple Beer-Lambert extinction equation to calculate the amount of light available at each height in the forest stand. Thus, the growth of each individual was determined by the light available at the top of its canopy, and each individual reduced the light available to shorter individuals. Although light availability was indexed in the original model in proportion to full sunlight at the top of the canopy, Botkin et al. (1972a) clearly intended that the model could be modified to use quantitative calculations of quantum flux.

The JABOWA model ignored most of the details of crown structure and growth plasticity that have played a major role in some plant competition models, in which interactions between trees have been modeled at the level of branches and foliage (Hamilton 1969; Mitchell 1975; Sorrensen et al., in review). Much of the theoretical interest in the growth form of competing trees relates to the attempt to explain the phenomenon known as the 3/2 thinning rule (Yoda et al. 1963) which describes the relation between mean plant size and plant density as the size of plants increases through time. This "rule" is a consequence of the geometric relationship between plant mass or volume (a cubic function of linear size) and the area on which the mass is located (a square function of linear size) and has turned out to be more flexible than originally supposed (cf. Weller 1987a and b; Zeide 1987; Norberg 1988). The 3/2 thinning rule is a phenomenon of even-aged, monospecific stands rather than the complex forests for which JABOWA was designed, and, not surprisingly, the JABOWA/FORET model does not produce this phenomenon even when monospecific stands are simulated (D. Weller, personal communication).

Some versions of JABOWA/FORET have been developed that do include horizontal spatial locations as well as height (e.g., Doyle 1990; Busing 1990), and these models could be expected to approximate the 3/2 thinning phenomenon.

One population-level phenomenon that has been of continuing interest in plant competition theory and modeling is size bimodality, which develops from initially unimodal size distributions under some conditions (Ford 1975; Gates 1978; Hara 1984; Huston 1986; Huston and DeAngelis 1987; Weiner and Thomas 1986). While bimodality can result from many different mechanisms (Huston and DeAngelis 1987), one important me
populations is dominance and suppression resulting from
light. JABOWA/FORET models can produce bimodal size dist
monospecific populations.

that

A key feature of any individual-based model is the
the individual organism. Given the current interest in the development of "mechanistic" and "process-based" models of plant populations, communities, and ecosystems (Schoener 1986, Tilman 1987), it is interesting to examine the mechanisms of plant growth incorporated in the original JABOWA model. "The model consists of a basic growth-rate equation tha~~n~~t may be taken to represent the growth of a tree with optimal site quality and no competition from other trees. ...this growth rate is decreased by factors that take into account shading and shade tolerance, soil quality, and average climate as measured by the number of growing degree-days... The equation states that the change in volume (D^2H) of a tree over a period of one year is proportional to the amount of sunlight the tree receives, derated by a factor ($1 - DH/D_{max}H_{max}$), which takes some account of the energy required to maintain the living tissue" (Botkin et al. 1972). Thus the model incorporates a simple

description of net carbon uptake proportional to leaf area, as well as allocation of carbon to aboveground growth versus respiration.

The authors note that "all growth curves tend to be sigmoid in shape and our final growth equation exhibits this overall property. We realize that some readers may feel that the equations ... are occasionally based on rather arbitrary assumptions, but we expect that they will concur with us that there is no unique model of forest growth and that many equations based on different assumptions could yield quite similar results" (Botkin et al. 1972). The essential features of the sigmiod growth curve, that is, low growth rates at small sizes, maximum growth rates at intermediate sizes, and a "leveling off" to low growth rates as the maximum size is approached, are common to nearly all growth models in biology, whether they are applied to cells, organs, individual organisms, or entire populations. The well-known logistic curve of the Lotka-Volterra competition and predation models is of this general form, as are the growth equations discussed by Aikman (this volume) and Clark (this volume).

The leaf area of a tree of a given size is calculated as a species-specific function of stem basal area, an assumption supported by later work on tree ecophysiology (Waring and Schlesinger 1985). The photosynthetic light response of trees is generalized into two types, representing either shade tolerant or shade intolerant species. Each type has an appropriate light compensation level and a light response curve that matches the classic generalizations of ecophysiology (cf. Larcher 1980, Ledig 1969). Growth suppression resulting from shading (or other factors) produces delayed mortality based on a mortality algorithm which states that a tree whose diameter increments fall below a specified minimum has a 0.368 probability of mortality in a given year (which results in a one percent probability of such a tree surviving for ten successive years).

Competition for belowground resources was modeled as a logistic decrease in the growth of all species as total basal area on the plot approaches a maximum that is related to site quality. "...the function S is a crude expression of the competition for soil moisture and nutrients on the plot" (Botkin et al. 1972a). Although there were no species-specific differences in competition for belowground resources in the original JABOWA, subsequent versions of the model did incorporate species-specific differences in nutrient uptake and response to soil nutrients (Aber and Melillo 1982; Pastor and Post 1985 and 1986; Weinstein et al. 1982; Bonan 1989).

Discussion

The recent interest in "mechanistic" ecological models as the next step toward a better theoretical understanding of communities and ecosystems (Schoener 1986; Tilman 1987) was presaged by the individual-based forest succession model developed over 20 years ago. The JABOWA model and its descendents have been modified to apply to many different forest ecosystems (Shugart 1984), as well as grasslands (Coffin and Lauenroth, 1990), mixed herbaceous and woody vegetation (Prentice et al. 1989), and even phytoplankton (Lehman et al. 1975). The models have been modified to incorporate ecosystem processes such as decomposition (Aber and Melillo 1982, Weinstein et al. 1982, Pastor and Post 1985, 1986), hydrology (Mann and Post 1980, Pastor and Post 1985; Bonan 1989) and soil thermodynamics (Bonan 1989, 1990a). Notwithstanding the evolution of the model to incorporate improved understanding of plant growth and ecosystem processes, the original model incorporated the basic concepts and assumptions that have been redeveloped over the past twenty years in the field of theoretical plant population and community modeling.

Perhaps the ecosystem orientation of the model, and its use to address "applied" problems such as forest yield (Aber et al. 1979, 1982, Shugart et al. 1981), response to fire (Mielke et al. 1977, 1978, Shugart and Noble 1981, Overpeck et al. 1990), and climate change (Solomon et al. 1981, Davis and Botkin 1985, Solomon 1986, Pastor and Post 1988, Dale and Franklin 1989, Urban and Shugart 1989, Overpeck et al. 1990, Shugart 1990, Bonan et al. 1990), have served to isolate it from those ecologists interested primarily in theory and theoretical models. Nonetheless, there has been some use of JABOWA/FORET models to address such theoretical issues as size bimodality (Huston and DeAngelis 1987), life history strategies and plant succession (Huston and Smith 1987, Smith and Huston 1989) and spatial pattern in forests and landscapes (Smith and Urban 1988, Smith and Huston 1989, Urban et al. 1991). It is interesting that some recent models developed in theoretical plant community ecology (e.g., ALLOCATE, Tilman 1988) show a remarkable convergence with the JABOWA/FORET models.

Significant recent developments in JABOWA/FORET models include 1) a more physiologically explicit representation of plant growth, and 2) a more realistic representation of the light regime of trees in large heterogeneous areas. While the species-specific parameters used in the original JABOWA model implicitly incorporated tradeoffs in resource allocation for life history processes and physiological responses, recent efforts have been made to make both the consequences and the representation of these tradeoffs more explicit (Smith and Huston 1989, Luxmoore et al. 1990, Weinstein and Yanai, in review).

Huston and Smith (1987) demonstrated that the single mechanism of competition for light was able to produce a wide variety of successional patterns, depending on the correlation between life history and physiological traits such as maximum size and growth rate, reproductive rate, maximum age, and shade tolerance. While the model was able to reproduce the anomalous patterns of species replacement and coexistence that are often cited as exceptions to general models of succession, the "classical" successional sequence of one species replacing another was produced only by a specific set of inverse correlations among the traits. These inverse correlations, between traits such as maximum size and maximum growth rate, were hypothesized to be the result of tradeoffs resulting from basic energetic and physiological constraints that apply to all plants, and consequently explain the remarkable similarity in successional patterns found in all plant communities.

The effect of such basic physiological and energetic con
the linkage between CO_2 uptake and water loss, and the allocati
resources to the capture of aboveground versus belowground res
been incorporated into the description of individual tree grow
Huston 1989). This increase in physiological detail allows th
predict changes in species composition and canopy leaf area al
gradients, as well as to predict how successional patterns will be different at different positions along the gradient. The leaf area supported by a particular tree is a function of light available to that tree and its physiological status with regard to water, along with its size and species. This allows the model to predict not only the distribution of different

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species along resource gradients, but also the distribution of such aggregate ecosystem properties as leaf area. The connection between shade tolerance, drought tolerance, and leaf chemistry has major implications for decomposition and the nitrogen cycle (Post and Pastor 1990).

The treatment of light penetration through the forest canopy has become more sophisticated in versions of the model that consider diffuse as well as direct light, and calculate leaf area along paths parallel to the angle of direct beam penetration (Bonan 1989, Urban 1990). A model version known as ZELIG extends the basic concept of the individual-based gap model to a grid of interacting cells, each of which can potentially interact with neighboring cells (Smith and Urban 1988, Urban 1990, Urban et al. 1991). Shading interactions are calculated based on tree height and solar angle, while seed dispersal is calculated as a function of the size and number of mature trees, with an inverse-square decrease with distance from seed source (Urban 1990). This model, which is spatially explicit at the scale of large trees, reproduces large-scale spatial phenomena, such as gradients, variation in gap size, and wave phenomena. Versions of the model that are spatially explicit at the scale of individual trees within a plot reproduce smaller-scale phenomena that result from interactions between close neighbors.

Further improvement in the reliability of individual-based forest succession models depends not on an improvement of model structure or the representation of specific mechanisms, but on an improved understanding of the growth of individual trees. The regulation of the growth of large woody plants remains one of the major challenges in plant physiology, with major unknowns such as the regulation of stomatal opening and the control of resource allocation. "It is our conclusion that the population dynamics of forest trees can be simulated, that such simulation can be done from first principles, and that at present the improvement of simulation is prevented primarily by a lack of data that accurately describe the relation between tree growth and the environment" (Botkin et al. 1972a).

In summary, individual-based forest succession models, beginning with JABOWA (Botkin et al. 1972a and b), are based on the same five theorems that have been developed as a theory of plant competition (see Ford and Sorrensen, this volume). The parallel development of theoretical plant population biology and forest succession modeling has been driven by different motivations. Theoretical plant population and competition models have been designed to address experimentally tractable systems, and have consequently focused on monospecific populations, either herbs or even-aged forest stands. Forest succession models have been designed to address complex problems in the dynamics of natural and managed forests and the prediction of ecosystem response to disturbance and environmental change. The evolution of theoretical plant competition models toward a more mechanistic, process-based approach represents a convergence with the assumptions and structure of individual-based ecosystem models. From a theoretical perspective, the forest simulation models can be seen as tools to investigate the natural selection processes that determine which life history and resource allocation strategies are most successful under different environmental conditions of resource availability and disturbance (Huston and Smith 1987; Smith and Huston 1989).

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