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Forest Succession Models

H. H. Shugart, Jr., and D. C. West

The study of all natural phenomena included under the term *succession* has preoccupied the attention of a large portion of ecologists during the last 100 years. Studies in succession attempt to determine the changes in species composition and other ecosystem attributes (e.g., biomass, diversity) expected over time. Because successional studies have been concentrated on forests that tend to have system dynamics over long time periods, the exact patterns of these ecosystem dynamics often are inferred rather than directly measured. The subjectivity of the inferred patterns has fueled considerable debate on the general nature of succession and has led to seemingly interminable confusion on the biological mechanisms involved in succession. Indeed, Gleason's 1926 statement—

American ecologists as well, discussing the fundamental nature, structure, and classification of plant associations, and their chronic inability to come to any general agreement on the matters, make it evident that the last word is not been said on the subject.

—is as valid today as it was 50 years ago.

Recently ecologists interested in studying succession began using mathematical models of forest dynamics. Models have the advantage of being formal descriptions of inferences about successional mechanisms, which can be analyzed to produce predictions about long-term ecosystem dynamics. By the early 1960s, forest biologists at several institutions were independently using digital computers to design mathematical models of changes in forest composition (Hool 1966, Odum 1960, Olson 1963, Ol-

son and Christofolini 1966). These and other forest simulators have been tested and applied as tools for studying forest behavior. Some of the more recent models are capable of simulating successional patterns and have been used in developing new insights into the nature of long-term forest dynamics and ecological succession.

Simulations in the early 1960s were primarily aimed at production budgets, element cycling in plant-soil systems, or trophic-level dynamics. But exploration of mathematical, theoretical, and computer applications in ecology had become a dominant theme in ecological research by the late 1960s (Patten 1971, 1972, 1974, 1975), and papers in several journals touted the future of systems ecology as the logical consequence of trends emphasizing quantitative ecology (Davidson and Clymer 1966, Garfinkel 1962, Watt 1966). The International Biological Programme Biome, for example, used ecosystem models as a central theme. Ecologists also had begun to reconsider the underlying mechanisms involved in ecological succession (Drury and Nesbit 1973, Odum 1969), which generated further interest in the long-term dynamics of ecosystems. This intellectual climate made the development of models of ecological succession a logical and needed step toward progress in the analysis of forest ecosystems.

At the same time, foresters also recognized the potential for computers in their field, and papers addressing the future importance of forest models appeared in trade and forestry research journals. Research foresters realized that yield tables, the mainstay of prediction of forest yields, were not flexible enough to be used if the environment changed, if the genetics of the planted trees were improved greatly, or if forests were fertilized. So they began exploring modeling techniques to achieve a more mechanistic approach to understanding tree growth and forest yield.

Exchange of information between ecologists and foresters on their forest models seems limited. For example, in

the proceedings of two recent workshops on modeling forest dynamics (Fries 1974 in forestry, Slatyer 1977 in ecology), there is only one common literature citation. This is due, in part, to the newness of the models and, in part, to the publication of many forestry models in what a nonforester would consider rather obscure places.

In this paper, then, we will review the models developed in forestry and ecology, with an emphasis on models of ecological succession.

TYPES OF FOREST SIMULATIONS

There are three basic organizational categories of forest simulation models (see Table 1):

- *Tree models* take the individual tree as the basic unit of a forest simulator. The degree of complexity ranges from simple tabulation of the probabilities of an individual tree of one kind being replaced by an individual of another kind, to extremely detailed models that include three-dimensional geometry of different species at different sizes.

- *Gap models* dynamically simulate particular attributes of each individual tree on a prescribed spatial unit of relatively small size—usually either a gap in the forest canopy or a sample quadrat.

- *Forest models* consider the forest as the focal point of the simulation model. Forestry yield tables constitute a highly data-dependent subset of forest models.

In general, the model type used is based on the problem under consideration, the data available, and the desire to develop a flexible model. The tree and forest model categories correspond to the tree and stand model categories used in Munro's (1974) review of forestry models. In our review, we recognize gap models (which might be considered as a special case of tree models) as a category developed exclusively for use in studying ecological succession. In about one-half of the models we have considered, the authors have included features that allow simulations of long time

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periods (e.g., 200 years), in which case we have categorized them as being applicable to studying succession.

Tree Models

Monospecies spatial tree models (two categories in Table 1)—whether or not they consider even-age or mixed-age stands—are used almost exclusively in sophisticated evaluations of planting, spacing, and harvesting schemes in commercial forests. The information they produce is communicated to large governmental or industrial land managers usually by direct means (e.g., internal reports), rather than through the scientific literature. The models that we have listed in these categories in Table 1 are probably only a subsample of the ones actually in use.

These models function by periodically incrementing individual trees (usually tree diameter, crown volume, and various form and shape parameters)—usually in 1- to 5-year time steps. For example, Mitchell's (1969) model of white spruce (*Picea glauca*) uses branch-pruning of trees that overlap to determine competition interaction.

The models contain equations that explicitly express the crowding of trees and can be easily adapted to either even- or mixed-age stands. In fact, Hegyi's (1974) mixed-age model, and Mitchell's (1969, 1975) models are modified in the converse manner. Designed for commercial forestry operations, the models do not include phenomena that ecologists would expect in a succession simulator. They generally ignore establishment of invading seedlings and often use functions for geometry of trees that could only be expected to hold in young, vigorously growing trees. The models sometimes use thinning or harvest as a surrogate for mortality.

Because of the level of detail needed, these models synthesize great amounts of autecological data that are usually only available for commercial species, so it is difficult to extend the models to mixed-species forests. There is a distinct bias toward using this modeling approach with tree species that are commercially important in the Pacific Northwest of the United States and in British Columbia. Many of the papers cite C. S. Holling's works (e.g., Holling 1966, 1971) as a source of inspiration in terms of the approaches used.

Even-age, monospecies, nonspatial tree models, also useful in commercial forestry, are logical nonspatial alterna-

TABLE 1. Categories of forest dynamic models and examples of each type of model. Succession models (indicated by rectangles) are able to simulate forest dynamics over time scales exceeding the life spans of the species considered.

CATEGORY	AGE-STRUCTURE	DIVERSITY	SPACE	REFERENCE	SUCCESSION MODELS	SPECIES OR FOREST TYPE
TREE	even-aged	mono-species	spatial	Newham 1964*		<i>Pseudotsuga menziesii</i>
				Lee 1967*		<i>Pinus contorta</i>
		mixed-species	nonspatial	Mitchell 1969*		<i>Picea glauca</i>
				Lin 1970*		<i>Thuja heterophylla</i>
				Bello 1971*		<i>Populus tremuloides</i>
	mixed-aged	mono-species	spatial	Haich 1971*		<i>Pinus resinosa</i>
				Hegyi 1974		<i>Pinus banksiana</i>
		mixed-species	nonspatial	Lin 1974		<i>Pseudotsuga menziesii</i> <i>Thuja heterophylla</i>
				Clutter 1963		<i>Pinus laevis</i>
				Curtis 1967		<i>Pseudotsuga menziesii</i>
GAP	mixed-aged	mono-species	spatial	Dress 1970*		<i>Pseudotsuga menziesii</i>
				Gauding 1972*		<i>Pinus laevis</i>
		mixed-species	nonspatial	Sullivan & Clutter 1972		<i>Pinus laevis</i>
				Burkhardt & Strub 1974		<i>Pinus radiata</i>
				Clutter 1974		<i>Pinus sylvestris</i>
	even-aged	mono-species	spatial	Elfvig 1974		Northern Hardwood Forest
				Salomon 1974		<i>Pinus patula</i> , <i>Cupressus spp.</i>
		mixed-species	nonspatial	Adlard 1974		<i>Pseudotsuga menziesii</i>
				Arney 1974		<i>Pseudotsuga menziesii</i>
				Mitchell 1975		
FOREST	mixed-aged	mono-species	spatial	Basch 1971		<i>Sequoia sempervirens</i>
				Hansburg & Roberts 1974		<i>Sequoia sempervirens</i>
		mixed-species	nonspatial	Suzuki & Umemura 1974		<i>Chamaecyparis spp.</i>
				Leak 1970		Northern Hardwood Forest
				Forcier 1973		Northern Hardwood Forest
	even-aged	mono-species	spatial	Hain 1976		Northern Hardwood Forest
				Noble & Slatyer 1980		Tasmanian Wet Sclerophyll Rainforest
		mixed-species	nonspatial	Ek & Monserud 1974		Northern Hardwood Forest
				Waggoner & Stephens 1970		Northern Hardwood Forest
				Bolton et al. 1972		Northern Hardwood Forest
FOREST	mixed-aged	mono-species	spatial	Shugart & West 1977		Northern Hardwood Forest
				Mielke et al. 1978*		Southern Appalachian Forest
		mixed-species	nonspatial	Tharp 1978*		Upland Pine-Oak Forest
				Shugart & Noble 1980		Mississippi Floodplain Forest
				Hoad 1986		Montane Eucalyptus Forest
	even-aged	mono-species	spatial	Olson & Christofolini, 1966		Tropical Rainforest
				Moser & Hall 1969		Northern Hardwood Forest
		mixed-species	nonspatial	Shugart et al. 1973		Southern Appalachian Forest
				Johnson & Sharpe 1976		Northern Hardwood Forest
				Wilkins 1977*		Forests in Upper Michigan
FOREST	mixed-aged	mono-species	spatial	Most yield tables used in forestry today		Forests in Georgia Piedmont
						Forests in Tasmania
		mixed-species	nonspatial			
	even-aged	mono-species	spatial			
		mixed-species	nonspatial			

tives to monospecies spatial tree models. Used almost exclusively in pine (*Pinus* sp.) plantations, nonspatial models are usually in the form of differential equations with basal area, stocking density, and volume (biomass) of a forest stand changing with respect to time. Since these relationships are functions of the size of the average tree, the models contain parameters derived from the expected growth of trees. The even-age, monospecies character of the simulated forests allows the assumption that mathematical functions for the expected response of an average or typical tree are sufficient to express these relationships among volume, stocking, and basal area.

These models work best if the trees tend to be the same size, which explains their use in the genetically optimized, short-rotation, crop-like *Pinus* plantations. The underlying assumptions of the models limit their application to even-age stands, and the development of mixed-age models using this approach is difficult. Unlike spatial monospecies models, even-age, monospecies nonspatial tree models can be solved analytically in some cases and in all cases require only a moderate amount of computer time.

Solomon's (1974) even-age, mixed-species, nonspatial tree model is related to the present category and uses a typical tree at different ages in a system of dynamic equations solving for forest-level attributes of northern hardwood forest stands. Solomon's application does not

require the degree of exactness that some of the models considered are capable of providing, and his derivations, based on a typical-size tree in a mixed forest as a modeling unit, are probably reasonable. Suzuki and Umemura (1974) have attempted to include mixed-age effects in nonspatial tree models by solving for shape parameters of the underlying statistical frequency distribution of the diameters of all the trees in a modeled stand as dynamic variables.

Mixed-age, mixed- or monospecies, nonspatial tree models simulate ecological success in naturally regenerated forests. They emphasize birth-death processes affecting individual trees and greatly deemphasize the importance of tree growth and form. Because they are not particularly complex (i.e., birth and death of trees might be treated as simple stochastic processes; replacement of trees as a first-order Markov process), the authors frequently attempt to capture the salient aspects of succession with a minimal model representation. In this objective, the models are actually explorations into the consequences of theories and assumptions on the nature of ecological succession based on the attributes of the species involved (Drury and Nesbit 1973, Gleason 1926).

These models can provide considerable insight into patterns of ecosystem dynamics and can be solved analytically without resorting to digital computation. The Noble and Slatyer (1980) model, for example, uses the vital attributes of spe-

cies to determine the expected patterns of community successions generated by competition among the species. Vital attributes considered are the modes that a species uses to persist at a site, the modes for establishment, the availability of a method for persistence (e.g., seeds, vegetative sprouts) at different life stages of the plants (juvenile, mature, propagule, extinct), and longevity of individuals. Using these species attributes, they construct schematic diagrams of changes that can be compared with observational data from a given area.

Mixed-age, mixed-species, spatial tree models have only one representative in Table 1: FOREST (Ek and Monserud 1974). The mathematical functions in the model include form, seed supply, and exact location of each simulated tree above a certain diameter and height. The model can simulate a forest of any size, because the only limitation is the amount of data storage space available on the computer.

FOREST is the most complex and detailed model of forest succession we have considered. Because of its level of detail, the model requires many parameters (e.g., form equations, canopy-shape functions, density and pattern of seed rain associated with different individual trees). Developed for the forests of Wisconsin, it would require considerable effort to modify it for another forest system. The model produces output and predictions at a level of complexity unequaled in most forest inventories.

Gap Models

Gap models simulate succession by calculating the competitive interrelations among trees in a restricted spatial unit—either a gap created by the death and removal of a canopy tree or a sample quadrat. A nonspatial example (Waggoner and Stephens 1970) uses the probability that a forest inventory quadrat, classified as one type of forest, will at some later time have changed to the extent that it can be classified as some other type of forest. This model is of similar form mathematically to that of Horn (1976), except that it is applied to a change in stands and not to single-tree replacements.

Other gap models simulate year-to-year changes in the diameter of each tree. They do not account for the exact location of each tree but use tree diameters to determine tree height, and then use simulated leaf area profiles to devise competition relationships due to shading. These models are spatial in the verti-

cal, not the horizontal, dimension—a simplification that greatly reduces the cost in running them but also eliminates consideration of complex spatial patterns of trees (should this be important in a given application). The vertical gap models are probably best used in studies of successional dynamics of natural forests considered over long time spans.

Forest Models

Yield tables used in forestry management are, in fact, empirical models of expected responses of an even-age forest usually of a single species. In this context, a forest is taken at a larger spatial dimension than either single tree or gap models consider explicitly.

Comparable succession models have been developed through a variety of mathematical approaches. Most consider the landscape to be composed of a number of mosaic elements that change in response to successional processes. These changes may be viewed as probabilistic (e.g., Hool 1966, Wilkins 1977) or as continuous, depending on modeling assumptions relating to the actual size of the landscape considered (Shugart et al. 1973).

Forest models tend to be dependent on data on rates of change of the mosaic elements assumed to comprise the forests, and the actual mechanisms that cause the changes in the forests do not appear explicitly in the models. All of the forest models listed in Table 1 require little computer time and can be solved analytically in many cases.

TESTING SUCCESSION MODELS

The process of testing a model to determine how much credibility one should place in its predictions has been termed model “validation.” This is an unfortunate term, because testing does not make models “valid”; it simply gives one an idea about the reliability and, hence, the utility of a given model (Mankin et al. 1977). Succession models are particularly challenging to test because the phenomena they predict may take years (or even generations) to observe in nature. Further, the stochastic nature of many models requires large sample sizes in the test data sets. Thus, most succession model tests have to rely on inference rather than direct observation.

Model testing procedures take a variety of forms:

“*Brute force*” procedures compare model responses directly with field ob-

servations. Generally, logistic considerations in collecting samples limit the range of conditions over which the models can be tested (e.g., it is difficult to collect data that relate to assessing a change in climate). Many of the forestry-oriented models (Table 1) are used with specific prescribed conditions and can be tested directly with independent data sets.

In most applications, models are designed to save costs (via reduction in the need for large and expensive data collection programs); so the need to collect data to test a model must be optimized with the cost of collecting the data. Most models used in studies of succession (Table 1) make direct comparisons between model responses and field observations, but the logistics of collecting field data are a greater problem than in the short-term forestry applications.

Logical procedures appeal to underlying principles or model assumptions that, if true, would be taken as a logical basis to expect the model's predictions to be correct. For example, Horn (1976) assumed that probabilities of species transitions in succession are ergodic (constant over space and time); our own set of assumptions (Shugart et al. 1973) allowed succession to be modeled as a set of ordinary linear differential equations. Almost any model develops from a logical set of assumptions as an underlying basis, and more theoretical studies of succession may use logical procedures as a primary means of anticipating the applicability of model results.

Long-term projections constitute a natural test on a succession model, which agrees with extant data on forest dynamics. Since most of the vegetation considered by the models has been disturbed by human activities, this test uses the model to project the pattern of vegetation after a long period of time. The resultant predictions can then be tested for consistency with what is known—either from old records or from relict sites—about the undisturbed vegetation. Horn (1976) used such a test in comparing the species composition at equilibrium predicted by his Markovian simulator with that of a climax beech forest in the Princeton Woods. Of the models shown in Table 1, only those indicated as succession models could reasonably be expected to satisfy this sort of test.

In many instances, the long-term predictions of forest succession models can be used to develop a theoretical understanding of forest dynamics, which can be inspected as new data are collected. For example, Ranney et al. (1978) simu-

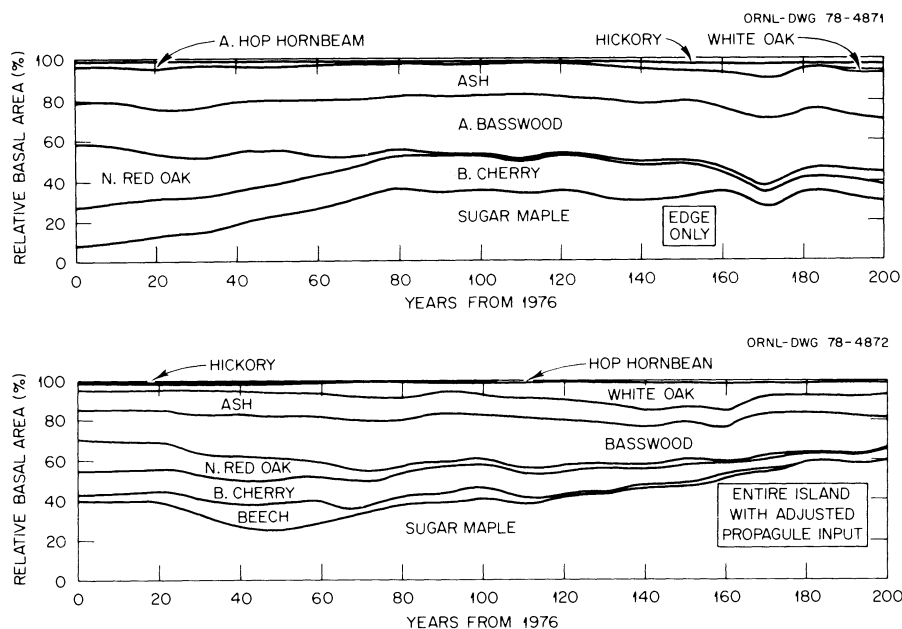


Figure 1. Top: Simulated edge development for forest islands of 1 to 2 ha showing expected composition of the forest edge for 200 years from measurements made in 1976 (year 0 on graph). Bottom: Simulated composition for entire forest island including edge and interior. These simulations are based on the FOREST model (Ek and Monserud 1974) and are taken from Ranney et al. (1978).

lated the expected dynamics of forest islands—namely, small relic patches of forest in a matrix of farm or urban land uses—in Wisconsin using Ek and Monserud's (1974) FOREST model. They predicted the expected equilibrium composition and structure of forest islands of different sizes. Further, because the FOREST model explicitly considers the location and spatial interactions of each simulated tree, they could predict differences in different parts of each forest island. Figure 1 shows a 200-year projection of a forest island's floristic composition starting from actual data collected in 1976 and contrasts the overall island composition with that of the island's edge. Certain species (e.g., northern red oak) disappear from the edge with time, and the compositions of edges and interiors of the forests are clearly different.

Since forest islands are to a great degree a consequence of man's land use, they are a new type of natural system for which we have a limited data base enabling us to infer the long-term system behavior. Models represent a valuable adjunct to studies on the fundamental nature of such ecosystems.

Predicting gradient responses involves running the model under a set of differing conditions that approximate some naturally occurring ecological gradient. If the model can predict patterns of vegetation along this gradient, it has then passed a rather severe test of the range of conditions over which it can be expected to produce reasonable results.

This is particularly true in instances in which the patterns predicted are a product of higher order (e.g., competitive) interactions and not simply a consequence of the physiological ranges of the species considered. For example, Botkin et al. (1972) predicted the location of the deciduous/coniferous forest transition; Tharp (1978) tested her model of a flood-plain forest with a similar test using a gradient of flood frequency; Shugart and Noble (1980) used a combination of altitude changes and different wildfire frequencies to test their model's ability to simulate gradients in the vegetation in the Brindabella Range in the Australian Alps.

In a model experiment inspecting the forest response to a slowly changing climate, we (Shugart et al. 1980) noted a hysteretic response in the composition of the simulated forest (Figure 2). In this simulation, the composition of forests at particular sites could be expected to differ depending upon whether the region had been under warming or cooling climatic conditions over the previous thousands of years. Such hysteretic responses have been noted for years, manifested as differences in the locations of community boundaries in mountains or following disturbances (Griggs 1946, Marie-Victorin 1929, Polunin 1937), but the actual mechanisms involved in such responses are not amenable to direct experimentation because of the long time-scales involved. With model experiments, one possible mechanism for such

responses is in the structure (e.g., diameter distribution) of the forests. One obvious advantage of the use of models in succession research is in exploring such cases, which are not open to direct experimentation with well-tested simulation models.

Hindcast procedures involve using past events as if they were natural experiments to test the model's ability to predict them. For example, we (Shugart and West 1977) used the chestnut blight as a perturbation to test our model on its ability to predict the species composition of forests not subjected to the chestnut blight, based on historical data. Other events that might be used for such hindcast tests include other diseases, climate changes expressed in pollen records, the advent of Europeans, or introduction or extinction of species.

Accidents can also serve as tests. Occasionally, while the computer program of a model is being tested or while a documented model is being used, the model may predict a correct response in the face of a program error. For example, a model that we developed for the southern Appalachian Forest (Shugart and West 1977) was predicting forests that, to the best of our knowledge, should occur in the Georgia Piedmont. Through a keypunch error, we had accidentally given the model a warmer climate than that appropriate for East Tennessee—a climate that was, in fact, appropriate for the Georgia Piedmont.

Observations of model behavior such as this do not constitute model experi-

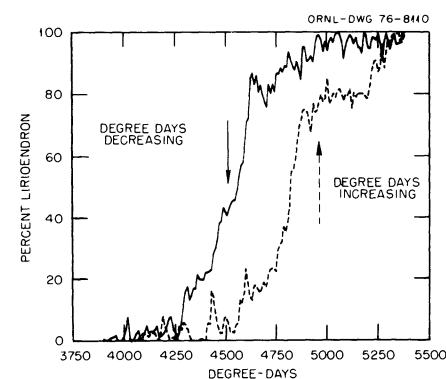


Figure 2. Percentage of total stand biomass attributable to yellow-poplar (*Liriodendron tulipifera*) under gradually changing, growing degree day values. One curve (dashed line) illustrates the mean value of 5 simulated $1/12$ ha forest stands as the annual value of growing degree days is increased from 3800 to 5300 at a rate of 1.0 degree day year⁻¹ following an initial equilibrium period of several hundred years. Solid line illustrates the same conditions with growing degree days reduced from 5300 to 3800 growing degree days. (From Shugart et al. 1980b)

ments and rarely surface in the professional literature, but they do provide the user with a sense of the reliability of the model's predictions. We have learned from various personal communications that others, who have either developed or used forest succession models, have experienced these difficult-to-derive-from-intuition anecdotal occurrences. Their importance as exploratory model tests is probably underestimated.

MODEL APPLICATIONS

Most models built strictly for forestry use are usually intended for applications in a restricted set of specified circumstances. However, several of the succession models presented in Table 1 have been used to evaluate environmental impacts on naturally occurring forests. Botkin (1973, 1977) considered the effects of CO₂ enrichment on plant growth and subsequent effects on forest dynamics. He found that an arbitrarily assumed percentage change in rate of photosynthate production at the individual plant level in CO₂-enriched atmospheres was not manifested directly as a change in forest increment. Other effects, such as plant competition and shading, tended to lower the magnitude of the system response.

McLaughlin et al. (1978) and West et al. (1980) performed model experiments (Figure 3) on chronic air pollution stress, expressed as a change in growth rates of pollution-sensitive trees. They noted that the response of growth over the long-term in natural forests might vary in direction as well as in magnitude from what one might predict from laboratory or greenhouse studies.

All of these studies identify a common problem—namely, that in natural forests in which trees vary in spacing, size, and competitive responses, one cannot extrapolate directly from laboratory studies to field conditions. Forest succession models can provide a necessary adjunct to laboratory-based assessments of environmental effects.

Johnson and Sharpe (1976) have used their model to inspect land-use changes in the Georgia Piedmont in response to different levels of forest harvesting and fire. We suspect that most of the forest models we have listed could (with proper changes in parameters) be used toward a similar goal. Such applications might motivate regional planners to take greater consideration of the dynamics of landscapes as opposed to the more static approach in use today.

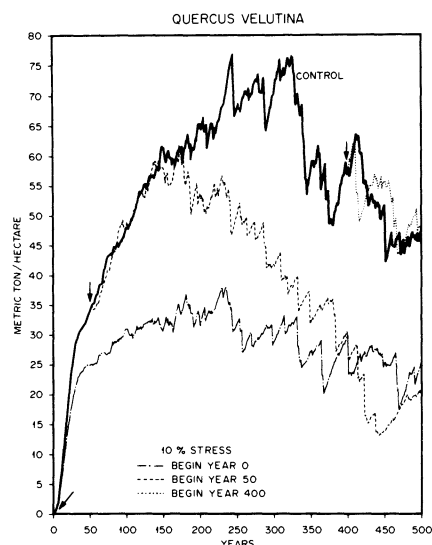


Figure 3. Changes in biomass in black oak (*Quercus velutina*) starting from bare ground at year 0 with a 10% reduction in growth rate compared to control (black line). When the species is stressed from year 0, there is an appreciable reduction in biomass through succession. Stress applied at year 50 was an appreciable effect only after 100 years, and stress applied at year 400 had no effect. These very different responses in the reaction of black oak to altered growth are a product of a complex interaction of forest structure and the vigor of the trees stressed. (From West et al. 1980)

Important future applications of succession models, particularly gap models, would involve evaluating large-scale and long-term changes in the ambient levels of pollutants and assessing the effects of climate change. If human activities alter environmental conditions on a global scale, models will become increasingly important as tools for prediction. This has been true of almost any application in which ecologists made observations on the behavior of forest ecosystems in an environment that had been altered in some way. At some level, this case is probably already appropriate to all forest ecosystems.

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