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Long-Term Dynamics of Forest Ecosystems

Computer simulation models, which allow for numerous seedlings and the long lives of large trees, predict how forests will respond to different management techniques

Forests often represent a tranquillity associated with the apparent changelessness of large trees. Ironically, this tranquillity is largely a product of the human perception of time. Forests are, in fact, dynamic ecosystems with continual mortality in tree populations balanced by the tremendous reproductive capacities of trees. For each tree that grows to the forest canopy, hundreds of millions of seeds and seedlings perish (Hett and Loucks 1971). Heavy-seeded trees such as oaks or hickories may produce 200,000,000 seeds in a lifetime, and light-seeded trees like willows or cottonwoods may produce billions (Bessey 1904).

High rates of birth and death of trees in combination with their great potential longevity make actual observations of the mechanisms of forest dynamics beyond the realm of most investigations. However, there is an increasing need to understand how forest ecosystems are affected by natural and anthropogenic environmental disturbances. How do certain forests respond to altered atmo-

spheric pollutant levels and to major or minor climate change? How might responses of forests affect the global supply of atmospheric gases, particularly carbon dioxide? What may be the consequences of new forest management schemes? Can we ensure the survival of rare and endangered species in forests? Valuable tools that are being used to answer these and other more basic ecological questions are the computer models of the changing patterns of life in a forest—called succession—that have been developed over the past decade (Fries 1974; Shugart and West 1980).

Forest ecosystems are dynamic entities that may not be static in either time or space. Many of our concepts of ecosystem management are based on the hope that if a forest is left alone it will gradually return to its natural state. "Succession," "wilderness," "virgin forests," and "climax forests" are all concepts that appeal to the basic notion that forest systems should approach some equilibrium state with time. However, research using detailed computer models indicates that forests in a highly disturbed landscape may remain in a perpetual state of effective nonequilibrium. If the scale of disturbance is large, then the amount of land needed to absorb the effects of the disturbance is also large. A woodlot or even a small park may never become a pristine wilderness, simply because it is too small.

The fundamental data for understanding the dynamics of forests are the diameters and species of the trees that make up the forests. Tree diameter (typically measured at breast height and denoted DBH) changes for an individual tree as the tree grows.

Over a given area, the statistical distribution of tree diameters changes as a complex consequence of tree birth, growth, and death. Because a forest is composed of many trees and because the number of factors affecting the life of each tree is large, realistic models of forest dynamics based on individual trees have developed only as computing power has become available.

Before 1970 there were only a handful of these models, but today, owing to the increased availability and the decreased cost of computing, there are over 100 models in the United States alone. These models vary in their mathematical form, level of detail, success rate, and in the type of forest they mimic. The most elaborate models include the shape and location of each tree to determine tree competition and growth. The need for detailed mathematical descriptions of the shapes of trees limits the application of such models to commercial forests of one well-studied tree species (Shugart and West 1980). Simpler models, considering only the probability of one large tree being replaced by another of another species, are often used for more diverse forests. In this paper we will treat models that simulate forest dynamics by calculating the competitive interrelationships among trees in a restricted spatial unit—typically the gap in a forest canopy created by the death or removal of a large canopy tree. For this reason they are called gap models.

Gap models

Since gap models deal with birth, growth, and death of individual trees, one can incorporate into the model unique biological features of different

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Table 1. Tests of gap models^a showing structural and functional responses^b

Type of test	Structural response	Functional response
Verification Model can be made to predict known feature of a forest	Is consistent with structure and composition of forests in New Hampshire (JABOWA), Tennessee (FORET), and Puerto Rico (FORICO), and floodplain of the Mississippi River (FORMIS) Compares to subtropical rain forest of known age (KIAMBRAM) Predicts Arkansas upland forests based on 1859 reconnaissance (FORAR)	Predicts forestry yield tables for loblolly pine in Arkansas (FORAR) Predicts relations of forest types in succession in middle altitudinal zone in Australian Alps (BRIND) Predicts response to clear-cutting in Arkansas wetlands (SWAMP) Predicts change in forest types as a function of flood frequency in Arkansas wetlands (SWAMP) and the Mississippi floodplain (FORMIS)
Validation Model independently predicts some known feature of a forest	Predicts frequency of trees of various diameters in rain forests in Puerto Rico (FORICO) and uplands in Arkansas (FORAR) Predicts vegetation change in response to elevation in New Hampshire (JABOWA) and Australian Alps (BRIND) Determines effects of hurricanes on diversity of the Puerto Rican rain forest (FORICO)	Predicts response of <i>Eucalyptus</i> forests to fire (BRIND) Assesses effects of the chestnut blight on forest dynamics in southern Appalachian forests (FORET) Predicts forestry yield tables for alpine ash in New South Wales (BRIND)
Application Model predicts the response of a forest to changed conditions	Predicts changes in a 16,000-year pollen chronology from East Tennessee in response to climate change (FORET) Assesses habitat management schemes for endangered species (FORAR), nongame bird species (FORET), and ducks (SWAMP)	Predicts response of northern hardwood forest to increased levels of CO ₂ in atmosphere (JABOWA) Predicts response of southern Appalachian hardwood forest to decreased growth due to air pollutants (FORET) Predicts response of northern hardwood forest (JABOWA), southern Appalachian forest (FORET), Arkansas upland forests (FORAR), Arkansas wetlands (SWAMP), and Australian subtropical rain forest (KIAMBRAM) to various timber management schemes

^a BRIND is a model of Australian *Eucalyptus* forests (Shugart and Noble 1981); FORAR of Arkansas mixed pine-oak forests (Mielke et al. 1978); FORET of Tennessee Appalachian hardwood forests (Shugart and West 1977); FORICO of Puerto Rican Tabonuco montane rain forest (Doyle 1981); FORMIS of Mississippi River floodplain deciduous forest (Tharp 1979); JABOWA of northern hardwood forest (Botkin et al. 1972); KIAMBRAM of Australian subtropical rain forest (Shugart et al. 1981); SWAMP of Arkansas wetlands forest (Phipps 1979).

^b Structural responses describe a forest at one time, or on the broad level of species composition only. Functional responses allow for more quantitative detail, examining a forest over a period of time.

determined by whether or not sites have been burned or flooded. Whether the ground surface is exposed mineral soil or organic matter can eliminate, reduce, or amplify the reproduction of a given tree species.

Gap models all use a basic growth equation that balances the increased photosynthate production of a large tree with the growing respiratory costs of maintaining living tissue as trees increase in size. The models all consider shading from taller trees as an influence on the growth of subordinate trees, based on use of the light extinction equation referred to as Beer's law. As conditions differ from the climatic optimum for a given species, or when there is crowding, growth is also reduced. The growth of each tree is computed each year.

Trees in a gap model are killed as a stochastic function of each species' expected longevity. Further, trees that are growing slowly or that have been damaged by fire are subject to an increased probability of mortality. Trees may also be killed by wildfire, blown down by a hurricane, or knocked over when a larger tree falls.

A model can be used in three ways (Shugart and West 1980), and these uses can be considered tests. The first test—verification—is whether a model can be made consistent with some set of observations. The second—validation—is whether the model agrees with observations that are independent of those used to structure the model and estimate its parameters. The third test—application—is whether it provides correct insights into either basic or applied problems. Applying a model often produces interesting predictions to be tested by future observations or experiments.

Gap models have been tested extensively, often at a very detailed level (Table 1). They have been used to simulate species composition and behavior through time in response to changed environmental conditions, and to provide qualitative descriptions of forests. For example, one test of a forest simulator is to predict the locations of changes in forest composition or structure along real or abstract environmental gradients (Shugart et al. 1980). An advantage of such a test is the ease with which the

tree species from different parts of the world. Each model begins with the random establishment of small trees in a gap. The models may compute survival based on the number of seeds or vegetative reproductive structures such as below-ground lignotubers, as found in some *Eucalyptus* trees, or on the production of stump and root sprouts by individual

trees that are of appropriate size and species.

A model for a particular forest should include any other factors affecting tree reproduction in that ecosystem. For instance, certain conditions are needed for transporting seeds to a germination site. Seed germination and seedling establishment may be

test can be validated. By changing the climatic conditions in a model to agree with those at different elevations on a mountain, and examining the mountain to determine if the predicted ecosystems occur in nature, one can assess the accuracy of the model.

Shugart and Noble (1981) used the BRIND model to predict the changes in *Eucalyptus* forests at different altitudes in the Brindabella Range in the Australian Capital Territory (Fig. 1). The transitions from one forest type to another appear to be a consequence of some kind of environmental alteration, such as climatic change, that affects the competitive relations of the tree species and could not be inferred from a knowledge of the physiology of each species alone; yet the structure and dynamics simulated by the model for different climatic conditions match the various real forests. Further, the simulated response of the forests to wildfires of different intensities agrees well with patterns observed on the mountainsides in the region and, more generally, for wet sclerophyll forests throughout New South Wales, Victoria, and Tasmania (Ashton 1980).

Other gap models have been tested by simulating different environmental gradients. The JABOWA model correctly predicted the elevation of the transition from hardwood to spruce/fir forest in the White Mountains in New Hampshire (Botkin et al. 1972), and the FORMIS model accurately reflected changes of forests in response to different degrees of inundation in the floodplain of the Mississippi River (Tharp 1979).

Forest ecosystems

Many tests of the gap models have produced results that could not easily be inferred from a simple tabulation of the attributes of the dominant species in an ecosystem. These results indicate that the whole ecosystem must be considered in attempts to extrapolate from the response of individual species of trees to the dynamics of forests. It is particularly important that such extrapolations should employ models based on species-level attributes of tree populations.

By comparing simulated behavior of several different forest systems, we

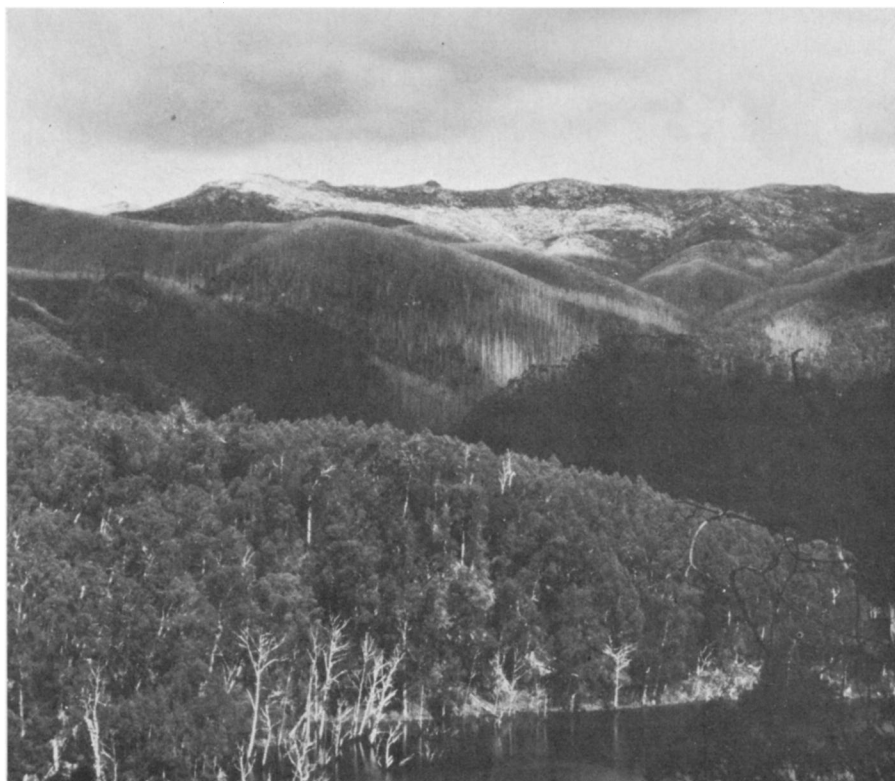


Figure 1. Computer models of a forest can allow for the different climatic conditions at various elevations on a mountain. The BRIND model successfully predicted the three vegetation zonations and their locations shown in this

photograph of the Australian Brindabella Range. Next to the lake in the foreground is a mixed peppermint forest; in the middle ground is alpine ash; in the background is snow gum.

are beginning to formulate general predictions of the responses of forest ecosystems to disturbance. This amounts to using a model as if it were a single data point in a study on the long-term dynamics of a forest. The results that follow are derived from the gap models developed at Oak Ridge National Laboratory, but these results are consistent with those obtained from the JABOWA model (as discussed by Bormann and Likens 1979a, b) and Phipps's SWAMP model (1979).

A single, small patch within a forest is characterized by the growth of a number of small trees until one or two trees grow large enough to gain dominance over the others. After a hundred years or more these dominant canopy trees die, and a new cohort of more or less even-aged individual trees begins to grow. These young trees compete, grow, and die until one gains dominance and closes the cycle.

If the mass of plant material on a $\frac{1}{12}$

ha plot in a forest were weighed, a graph of this biomass over several centuries would be a cyclical sawtoothed curve (Fig. 2). We can think of a landscape as a mosaic of patches of this size, and a gap model can be used to predict the fate of each tree on each patch. By tabulating the responses of, say, a hundred of these

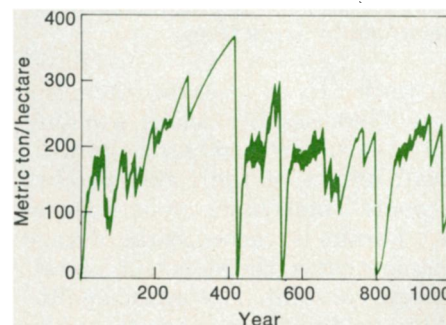


Figure 2. The biomass in a typical small patch of forest, a $\frac{1}{12}$ ha plot simulated here by the FORET model, fluctuates in response to the death of canopy trees and growth of their successors.

patches, the effect of random events (particularly events causing the death of canopy trees at a given location) begins to average out, and a larger-scale pattern of response becomes observable.

Bormann and Likens (1979a, b) noted this larger-scale response in what they call the “shifting-mosaic steady-state” concept of ecosystem dynamics. According to this concept, if all the patches that comprise a landscape are simultaneously altered, as by a fire or clear-cutting, the landscape will respond by an increase in the mass of total living material, reaching a maximum as, after a period of reorganization, each patch comes to be occupied by a large, mature canopy tree. Bormann and Likens felt that such a response was typical of the hardwood forests of the northeastern United States.

We found this general response in forests that are dominated by a single species or, as in the forests described by Bormann and Likens, when the important species in a forest have similar growth rates and longevities. In these cases, the biomass response of the forest through time depends largely on the establishment of a mature forest structure.

Following a large-scale disturbance all the plots representing a forest are simultaneously covered by trees of the same age. As these trees grow, the biomass across all the plots increases. One or two large trees on each plot become dominant through competition for light and nutrients. If the species that comprise the forest have similar longevities and growth rates, there is synchrony across the plots. If the species also are of similar size at maturity, then maximum biomass of the forest is attained at this stage because all plots are simultaneously occupied by large trees.

As these canopy trees die, there is a loss of biomass. Eventually, a mature forest structure emerges as growth/death cycles of the forest patches become nonsynchronous. Quasi equilibrium is reached as the average biomass across the plots remains relatively constant. This quasi equilibrium is directly analogous to the “shifting-mosaic steady-state” concept of landscapes, and is consistent with several other interpretations of equilibrium in landscape systems

(Heinselman 1973; Forman 1979) and in ecosystems in general (see, for example, Levin and Paine 1974). A mature forest of this stage in southern Appalachia features large trees

in stands with up to 600 metric tons/ha of biomass. Interspersed throughout the forest are patches where a canopy tree has recently died, containing several thousand stems per hectare and biomass values of 20 to 40 metric tons/ha; and older patches with larger trees of nearly equal age (Shugart and West 1977).

We call this dynamic forest response the intrinsic biomass response. A particularly clear case of such a response is found in the alpine ash (*Eucalyptus delegatensis*) forests as simulated by the BRIND model (Fig. 3) (Shugart and Noble 1981). This intrinsic response is essentially that reported by Bormann and Likens (1979a, b) as well.

When forest growth is modified by external disturbances or when the dynamics of the forest involve changes in composition as well as in biomass, the intrinsic biomass response can be altered considerably (Doyle 1981). For instance, in diverse forests such as tropical and subtropical rain forests and southern Appalachian hardwood forests, trees on disturbed patches have less synchrony of growth, the biomass peak is lost, and the maximum biomass occurs during the mature phase. However, in other diverse forests the first species to colonize disturbed sites attain a larger size than the species that are found in mature forests, and the biomass peak is amplified and greatly overshoots the mature phase biomass values. Examples are when oak (largely *Quercus falcata*) replaces pine (*Pinus taeda*) as the dominant species in an Arkansas forest, or when alpine ash (*Eucalyptus delegatensis*) gives way to other *Eucalyptus* species in Australia after a fire.

In general, stresses that tend to reduce the rate of establishment of young trees also tend to modify the intrinsic biomass response. This occurs, for example, in FORMIS simulations of bald cypress (*Taxodium distichum*) swamps under conditions of regular prolonged flooding (Tharp 1979). Because bald cypress seedlings cannot be immersed in the floods except for short periods, in many sites the establishment of the species is episodic, requiring two years without prolonged flooding so that seedlings can survive. Frequent wildfires in a snow gum (*Eucalyptus pauciflora*) forest in Australia are another kind of

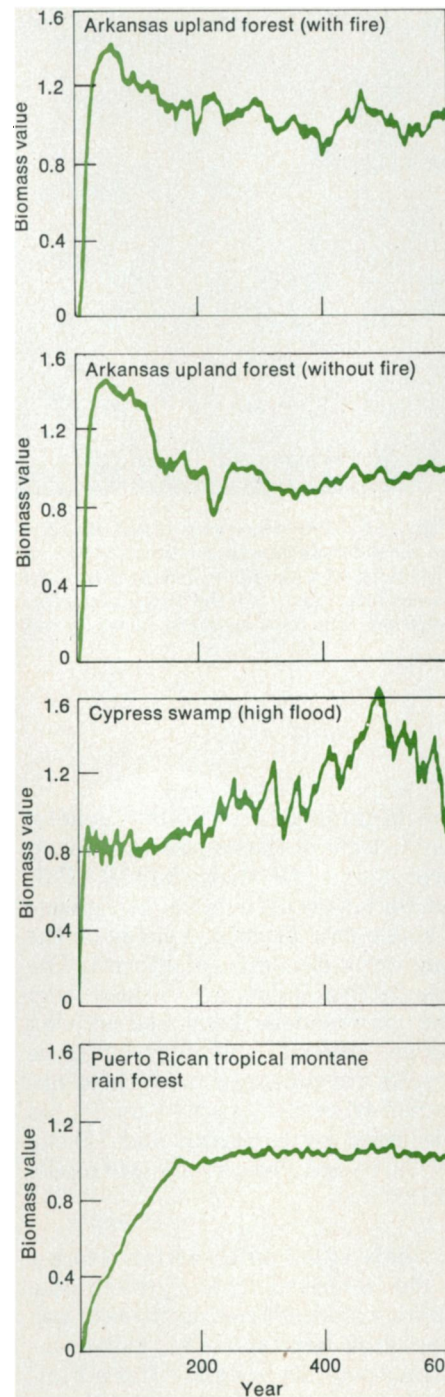


Figure 3. Natural disasters can cause the maximum biomass to occur at different stages of forest development. Fire in an Arkansas forest changes the dominant species from pine to the larger oak; prolonged flooding in a cypress swamp kills seedlings, thus delaying the biomass peak. A rain forest containing diverse species has no peak at all. For ease of comparison, each response is scaled to have a value of 1.0 at year 600.

stress that can drastically affect the regeneration of young trees.

For a mature forest to approach a state of biomass quasi equilibrium, it must contain 50 to 100 patches, each of which responds to independent small-scale disturbances such as the fall of a tree. This number tends to be larger in diverse forests, where the vegetative composition and thus the forest structure at a given point can be more variable. As the processes that disturb small pieces of a landscape are largely stochastic, the minimum number of patches needed to represent a landscape depends on how much variation around the landscape equilibrium is acceptable. We have found that forest landscape responses averaged over fewer than 50 plots, where each plot is the same size as the area of disturbance, are highly variable as they are overly influenced by the particular local history of disturbance.

Nonequilibrium landscapes

The need to average the behavior of 50 or more patches to obtain quasi equilibrium at the landscape level means that some landscapes may not be large enough to reach equilibrium (Fig. 4). Because the patch disturbed by the fall of a large canopy tree is on the order of 100 to 1,000 m², the minimal landscape large enough to absorb the effects of tree falls without leaving equilibrium is on the order of 10⁴ to 10⁵ m². As the size of the disturbance increases, proportionately more area is needed to average out its spatial effects.

For instance, most small watersheds that feed small streams in the southeastern United States are large enough to remain in quasi equilibrium when a tree falls, or some other small-scale disturbance occurs. However, a wildfire of the size commonly found in the southern Appalachian region would reduce these same watersheds to nonequilibrium. These systems are therefore effectively nonequilibrium landscapes, since large proportions of the small watersheds synchronously respond to each wildfire. The amount and type of vegetative cover may differ over time. It appears that only the larger national forests and recreational parks in the southern Appalachians may be of sufficient size to absorb the

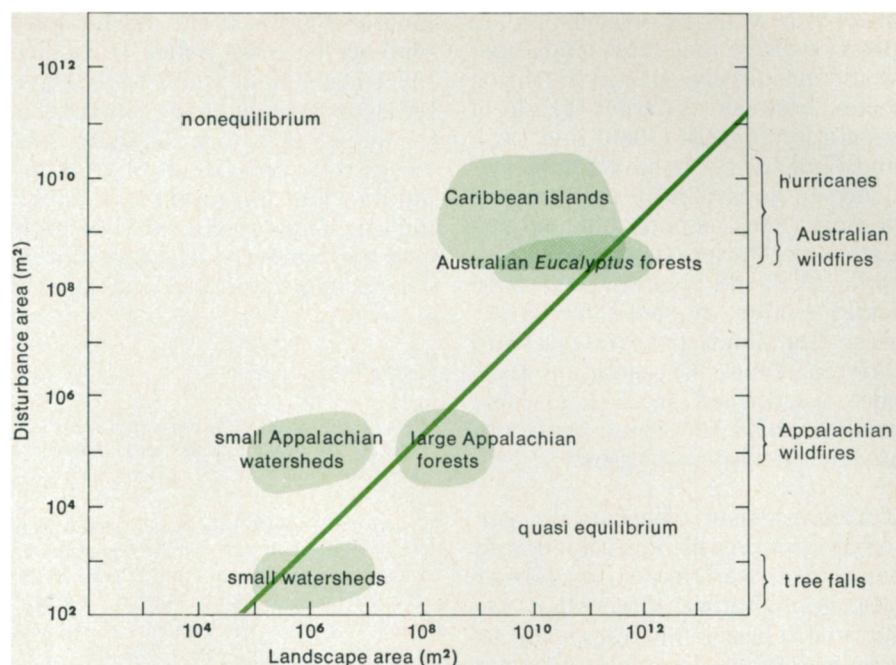


Figure 4. Some forested areas are too small to reach quasi equilibrium because they are subject to large-scale disturbances. A small

watershed can be relatively unaffected by the fall of a tree, but drastically altered by a massive fire.

random wildfires and remain in quasi equilibrium.

It is difficult to provide constant levels of habitat for some plant or animal species in nonequilibrium landscapes. Such habitat constancy could be obtained by altering the scale of disturbance or by increasing the area under management, but often neither of these strategies is an available option. In the case of the Appalachian forest landscape, sufficient area is involved so that a national park could be managed with the diversity of landscape patches remaining in relatively constant proportions, even given the scale of wildfires in the region.

However, the amount of forest burned annually by wildfire in Australia approaches the size of the entire range of many of the *Eucalyptus* species that make up these forests (Luke and McArthur 1978). For example, the effects of a holocaust in 1939 are manifested today in the unstable age and size structure of the total population of the alpine ash (Hillis and Brown 1978). Disproportionately large numbers of the population were established in 1939 in response to favorable conditions for germination caused by the fire. Trees older than 1939 are relatively rare.

Only the largest island of the Caribbean, Cuba, might possibly have a landscape in equilibrium despite hurricane disturbance. Given the scale and regularity of hurricanes in the Caribbean, the vegetation on any smaller island could be expected to be in an effectively nonequilibrium state (Doyle 1981). An instance is Dominica, where some of the most extensive stands of mature rain forest in the Caribbean were severely damaged by hurricane David in 1979.

All the landscapes discussed above have a common feature. Computer simulation of their dynamics, using a gap model, indicates that if enough landscape patches can be averaged together the vegetative composition of these landscapes tends, over time, to approach an equilibrium. However, results from similar models identify the theoretical possibility that landscapes in certain environmental regimes are intrinsically nonequilibrium (Shugart and Noble 1981; Shugart et al. 1980).

For forests dominated by species with quite different typical life histories, it is possible to have two stable vegetation types at a given location (Walker 1981). The results from the gap models and from other, somewhat less detailed, models (Cattalino et al.

1979; Noy-Meir, in press; Noble, in press) indicate that these landscapes would most likely occur in transition zones between different types of vegetation. Griggs (1946) and Leak and Graber (1974) have found evidence on mountains of the presence of more than one potential and persistent vegetation type; Marie-Victorin (1929) and Polunin (1937) have found similar evidence for larger areas. The simplest case involves two different types of vegetation that, once established in a landscape, would each be self-sustaining in relatively constant proportions.

If a management decision changed the proportion, the landscape would not return over time to its former proportion, but would remain at the new one. These landscapes could be most unforgiving to a land manager who made an incorrect decision regarding the stewardship of the land. An undesirable landscape configuration, once produced, would not revert to its former state when left alone; it would remain in the undesirable state until it was actively transformed to some other state.

Other aspects of these results should be considered in developing plans for forest management. The ability of gap models to simulate independent data from a variety of contexts with great detail gives increased credibility to their results. The models use attributes of individual species to determine the growth of each tree in a sample plot, but they consistently indicate that there must be an explicit consideration of interactions among species to predict ecosystem response. The implication is that, for example, pollutant effects measured on individual trees will not necessarily be the same in magnitude or even direction when applied across an entire forest (West et al. 1980). The development of experimental programs to assess environmental effects in forests must take into account ecosystem dynamics of forests as well as data collection on the performance of trees.

Our studies indicate that to understand and manage forests we must think of them as large ecosystems. The studies also indicate that a static concept of ecosystems as unchanging in time is not a necessary part of a theory of ecosystem dynamics. A pattern of great change in the forest composition over the past several

thousand years, borne out by much evidence on fossil pollen (Brubaker 1975; Davis and Webb 1975; Davis 1981), casts doubt on the concept that the forests of eastern North America are, in toto, ecosystems of great antiquity. The importance of understanding forest ecosystems lies not in their age, but in the relevance of what is happening in forested landscapes at present.

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