PLANT SUCCESSION: LIFE HISTORY AND COMPETITION

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The continuing generation of hypotheses concerning plant succession suggests that this phenomenon is still not fully understood. Recent work has clarified the great variety of patterns and mechanisms involved in succession (Drury and Nisbet 1973; Connell and Slatyer 1977; MacMahon 1981; McIntosh 1981) but has not produced a general theory based on underlying processes common to all successions (see Peet and Christensen 1980; Van Hulst 1980; Finegan 1984). We propose to demonstrate why a variety of models can reproduce the superficial patterns of succession but fail to explain the complex dynamics of plant interactions. Our approach is to review a series of succession models, beginning with an oversimplified example and ending with a process-oriented model based on interactions among individual plants. We argue that an individual-based model can explain the complex variety of successional dynamics that population-based models fail to explain. Individual-based models using a combination of life history and physiological traits offer the possibility of an integrated population, community, and ecosystem approach to understanding natural systems. One of the major implications of this approach is that the structure of correlations among life history and physiological traits constrains the successional patterns commonly found in nature to a small subset of the possible patterns.

By *succession*, we mean a sequential change in the relative abundances of the dominant species in a community (dominance based on biomass). *Sequential* implies that a once-dominant species or group of species will not become dominant again unless a disturbance or other environmental change intervenes. Thus, we focus on the intervals between disturbances rather than on the effects of the disturbances themselves (see Connell 1978; Huston 1979; P. White 1979). The changes that interest us occur within a time period of the same order of magnitude as the life span of the longest-lived organisms in the successional sequence.

This time scale allows us to avoid non-successional changes resulting from long-term climatic shifts as well as the long-term accumulated influence of physical processes on soil development. Shorter-term microclimatic and soil changes induced by vegetation are inherent features of both primary and secondary succession and may play a critical role in causing succession. These and other changes associated with succession form the focus of the ecosystem-level study of succes-

sion. Our primary concern in this paper is with the pattern of species replacement, which we believe is the basis of most successional patterns at the community and ecosystem levels.

This paper is based on three main premises.

1. Competition between individuals for resources occurs in all plant communities, although both the relevant resources and the intensity of competitive interactions may change through time and between communities.

2. Plants alter their environment in such a way that the relative availabilities of resources change, altering the criteria for competitive success.

3. Physiological and energetic constraints prevent any species from maximizing competitive ability for all circumstances. This produces an inverse correlation between certain groups of traits such that relative competitive abilities change over a range of environmental conditions.

These premises are not new (see Clements 1916; Salisbury 1929), but we believe that their importance has been overlooked in much of the recent literature on succession. We intend to demonstrate that, taken together, these three premises can form the basis for a unifying approach to the study of ecological succession. Because understanding succession requires understanding the mechanisms that cause succession, we focus on hypotheses and models based on mechanisms. Although the transition probabilities used in probabilistic Markov models (Horn 1971, 1975; Van Hulst 1979, 1980) derive from the mechanisms we discuss, we consider these models and differential-equation models (e.g., Shugart et al. 1973) to be descriptive rather than mechanistic, and we do not discuss them here.

LIFE HISTORY TRAITS AND COMPETITIVE ABILITY

One of the oldest and most widely accepted generalizations in plant ecology is the set of characteristics used to distinguish early- from late-successional species (table 1). We maintain that this generalization is the basis of understanding the similarities and complex differences in the great variety of successional patterns found in nature. This interpretation of succession is not new, but we believe that it has not been clearly stated or fully developed before. It was perhaps best expressed by Drury and Nisbet: "The basic cause of the phenomenon of succession is the known correlation between stress tolerance, rapid growth, small size, short life and wide dispersal of seed" (1973, p. 360). (Stress as used here refers to the unbuffered environmental variations often found in early succession, and it is not the same as the more extreme stresses discussed in Grime 1974 or Levitt 1972.)

The critical feature of this suite of life history characteristics is the tendency toward inverse correlation between traits that confer competitive success in early succession and traits that confer success in late succession. Some recent definitions of competitive ability ignore the alternative strategies possible through various combinations of life history traits and instead consider only the characteristics that confer success in late succession (at or near competitive equilibrium) as indicators of superior competitive ability. This equilibrium-based definition of competitive ability contradicts a more intuitive operational definition: the opportunistic species that grows rapidly, shading and suppressing "superior" competi-

TABLE 1

Physiological and Life History Characteristics of Early- and
Late-Successional Plants

Characteristic	Early Succession	Late Succession
Photosynthesis		
Light-saturation intensity	high	low
Light-compensation point	high	low
Efficiency at low light	low	high
Photosynthetic rate	high	low
Respiration rate	high	low
Water-use efficiency		
Transpiration rate	high	low
Mesophyll resistance	low	high
Seeds		
Number	many	few
Size	small	large
Dispersal distance	large	small
Dispersal mechanism	wind, birds, bats	gravity, mammals
Viability	long	short
Induced dormancy	common	uncommon?
Resource-acquisition rate	high	low?
Recovery from nutrient stress	fast	slow
Root-to-shoot ratio	low	high
Mature size	small	large
Structural strength	low	high
Growth rate	rapid	slow
Maximum life span	short	long

Sources.—Budowski 1965, 1970; Pianka 1970; Ricklefs 1973; Bazzaz 1979.

tors (Monsi and Oshima 1955) and producing abundant seeds, is the superior competitor in that bout of competition (see Grime 1973a,b; Al-Mufti et al. 1977).

Clearly, there is no such thing as absolute competitive ability, nor any measure (e.g., growth rate, shade tolerance, seed output, or maximum size) that confers competitive ability under all conditions. Competitive ability in two different situations may be based on completely different factors (Salisbury 1929; Grime 1974, 1979; Pickett 1976; Grubb 1986). Traits such as small seed size, high seed output and dispersibility, tolerance to certain stresses, and rapid growth are often important in determining success early in an episode of plant competition (beginning at low population densities in early succession), as well as in situations with a high frequency of density-independent mortality (disturbance). Traits such as large size and shade tolerance usually become more important later in an episode of competition as the system approaches competitive equilibrium (late succession) in the absence of disturbance. Our viewpoint differs somewhat from the three-way classification of plant strategies as competitors, ruderals, and stress tolerators (Grime 1974, 1979); we envision a continuum of plant strategies resulting in a different hierarchy of relative adaptation to each different set of conditions.

Many alternative strategies, with variations within each strategy, allow plants

to succeed under different conditions. For example, resistance to stress (e.g., low levels of light, water, and/or nutrients) may be achieved through either avoidance or tolerance (Levitt 1972; Chabot and Bunce 1979; Turner 1986). Each strategy has its costs in terms of physiological and morphological trade-offs that prevent any species from being optimally adapted to all conditions. The inverse correlations among adaptive characteristics cause a species' competitive ability to change as conditions change.

Inverse correlations among important physiological characteristics are well documented (see Bazzaz 1979; Bazzaz and Pickett 1980; Larcher 1980). The inverse relationship between the maximum photosynthetic rate and the light-compensation point is particularly important when light becomes limiting during succession. When both water and light are limiting, the relationship between the photosynthetic rate and the transpiration rate can produce a shift in competitive ability, as can the inverse relationship between the maximum growth rate and tolerance to low levels of nutrients when a particular nutrient is limiting (Mitchell and Chandler 1939; Chapin 1980; other references cited in Chapin et al. 1986).

Inversely correlated traits can result in a successional sequence of species replacement as the relative competitive values of these traits change. Any competition model that incorporates inversely related traits with changes in competitive values through time will produce a pattern resembling succession. Obviously, this entire discussion could be phrased in terms of r- and K-selection characteristics (in the sense of MacArthur and Wilson 1967; Pianka 1970; see Caswell 1982 for a nonequilibrium interpretation). Many of the early-successional traits listed in table 1 can be considered components of the parameter r, and many of the late-successional traits are associated with the parameters K and α_{ij} (the effect of species j on species i in terms of the effect of species i on itself). (See Boyce 1984 and Grubb 1987 for a discussion of the variety of life history strategies, including apparent exceptions to the above generalizations, that can result from r- and K-selection.)

Although the r/K dichotomy oversimplifies by aggregating many separate characteristics into a few parameters, it does capture the basic pattern of the inversely correlated traits. Not surprisingly, then, any model incorporating these two parameters in such a way that they affect competitive ability can produce a pattern of species replacement through time.

POPULATION-LEVEL MODELS

The basic features of inversely correlated life history and physiological traits can easily be incorporated into population models; indeed, they are explicitly or implicitly included in most such models. Two examples, the first without and the second with explicit modeling of resource availability, illustrate how population models can produce a successional replacement of species through time. Unfortunately, the simplicity that makes these models such useful heuristic tools limits their ability to provide more than simplistic insights into successional mechanisms. The shortcomings of population models provide the motivation for the individual-based approach that we describe below.

A Lotka-Volterra Model of Plant Succession

The Lotka-Volterra model of competition has been analyzed and discussed primarily with reference to animals, for which the parameters r, K, and α can easily be visualized and simply defined. Although the basic concepts apply to plants also (see Caughley and Lawton 1976), they require some modification because reproductive individuals of a plant species may vary greatly in size and the reproductive output may vary with size (which is also true of animals with indeterminate growth). In addition, the rate of biomass increase is moderated not only by increase in numbers, but also by increase in size of individuals (Harper 1967; J. White 1979). The intrinsic rate of increase for plants is most reasonably defined as the rate of increase in biomass per unit of biomass, which must include both sexual reproduction and vegetative growth and reproduction. Likewise, K and N should be expressed in terms of biomass rather than of numbers of individuals (Wilhm 1968; Tramer 1975).

With the above interpretation, the Lotka-Volterra competition model produces a pattern of species replacement resembling succession. The dynamic properties of this equation, as opposed to its equilibrium solution, may be determined by computer simulations (King and Anderson 1971; Huston 1979). For the following examples (fig. 1), the system of equations was expanded to nine competing species and solved using a predictor-corrector method of integration. As modified for succession, this model begins with all species present in the initial stage and assumes that succession occurs in a uniform patch with no disturbances.

During the course of a simulation, the species with high rates of increase (regardless of K) predominate during the early stages, and the species with high K's (regardless of r) predominate in the later stages as the community of competitors approaches equilibrium (fig. 1a). If r and K are inversely related, as is the case with plants, one species inevitably replaces another (fig. 1b). This pattern of high growth rates in the early stages and low growth rates in the later stages, which is expected solely on the basis of the dynamics of competition, is similar to the general pattern found in the course of many plant successions (Richards 1952; Odum 1971; Whitmore 1975; Whittaker 1975).

Although the model in its simplest form, with all parameters constant, generates a sequential replacement of species through time, its behavior can be made more realistic by modifying it to reflect some of the dynamics of competition for light, a resource thought to be important during succession. Specifically, the competitive coefficients (α_{ij}'s) may be varied depending on the relative sizes of the plants. The relationship used in these simulations is $\alpha_{ij} = CN_j/(N_j + N_i)$, where α_{ij} is an expression for the negative effect of species j on species i; C is a constant (the maximum α_{ij} possible); and N_i and N_j are the biomasses of population i and j, respectively. This equation provides an approximation to the assumption that relative size is of primary importance in competition for light. With this modification, the behavior of the model changes significantly, generating a pattern of suppression and release (fig. 1c) similar to that found in many studies of secondary succession (see, e.g., Cremer and Mount 1965; Dyrness 1973; Tramer 1975).
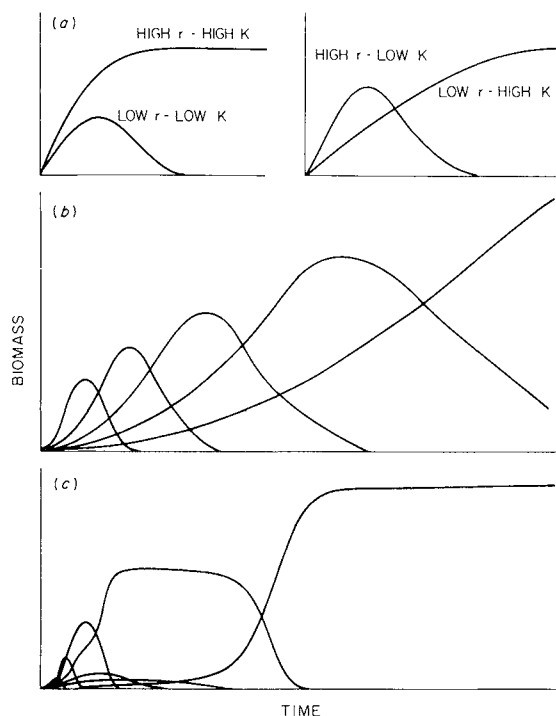
FIG. 1.—Simulation results using a Lotka-Volterra succession model. *a*, Two dynamically different approaches to an equilibrium in which only the species with a high K value survives. The only parameters that vary between simulations are the r values. *b*, Sequential species replacements generated by a Lotka-Volterra competition model with an inverse relationship between r and K (all $\alpha_{ij} = 1.0$). *c*, Pattern of suppression and release generated by a Lotka-Volterra competition model when α_{ij} varies depending on the relative sizes of the competitors (see the text) and when r and K are inversely related.

Although including inversely related competitive abilities in a model is sufficient to produce succession-like behavior, it is not sufficient to understand succession. A Lotka-Volterra model is capable of reproducing some general features of plant succession, but it does so without explicit mechanisms. Even though the properties of r, K, and α_{ij} can be considered relevant to light competition, no specific resources or competitive mechanisms are included in the model because it aggregates many complex life history traits and competitive mechanisms into a few oversimplified parameters. In addition, the model inappropriately attributes individual properties such as a height advantage in light competition to the population, thus creating the unreasonable condition that all individuals of each population be identical.

A Resource-Competition Model of Succession

A recently proposed population model of succession that deals explicitly with competition for resources is the resource-ratio hypothesis (Tilman 1985). Limiting

resources are reduced by the competing populations and resupplied at some rate characteristic of a particular environment up to some maximum level. This model has been applied to both primary and secondary successions and includes the critical assumption that the competing species "have a trade-off in their resource requirements, such that the superior competitor for one resource is an inferior competitor for the other" (Tilman 1985, p. 829).

Inversely related competitive abilities for light and a soil nutrient, generally nitrogen, are used to model changes in species composition in cases where light availability (at soil level) decreases and soil-nutrient availability increases through time. As a consequence of changes in relative competitive abilities as resource ratios change, the model produces a temporal replacement of species, that is, succession. The increase in nutrient availability that is a critical driving variable of this model occurs in some successional sequences, particularly during early succession on nutrient-poor soils, but it is certainly not a feature of all successions (Robertson 1982; Pastor et al. 1984).

A critical assumption of the resource-ratio hypothesis is that the competing species reach a competitive equilibrium at each point along the changing light-nitrogen gradient. Thus, the model's predictions about changing species composition along a temporal resource gradient are valid only as long as "the rate of change in resource availabilities is slow relative to the rate of competitive displacement" (Tilman 1985, p. 833).

The patterns of nitrogen and light availability during primary succession and the role of nitrogen-fixers in succession have been known for some time (Cowles 1899; W. Cooper 1913; Lawrence 1958; Olson 1958). Although the correlations are clear, the mechanisms are not necessarily simple. Competitive ability for light has several components, as does competitive ability for nitrogen or other resources. The resource-ratio hypothesis is subject to the same criticisms as the Lotka-Volterra model: it aggregates many components of competitive ability into a single parameter that cannot respond to environmental conditions with the same dynamics as several independent traits.

Light competition provides the clearest and most important examples of the complexity of competitive ability for a single resource. The major component of competitive ability for light is position relative to the source of light. A taller plant has a great advantage over a shorter competitor, regardless of the shade tolerance or other physiological properties of the smaller plant. This advantage increases with the relative difference in size (except in the case of low sun angles; see Terborgh 1985) and with increasing crown density of the larger individual. Of course, the effect on the smaller plant is greater if it is shade-intolerant.

The size advantage in light competition is a characteristic of individuals, not of populations or species. A small individual of a shade-tolerant species that can potentially achieve large size can be competitively eliminated by a larger individual of a shade-intolerant species with a relatively small maximum size. Thus, in a nonequilibrium environment, an individual's competitive ability resulting from large relative size because of early arrival or rapid growth can be more important than genetically determined species characteristics such as large maximum size and shade tolerance that would confer competitive dominance at equilibrium.

Another component of competitive ability for light is canopy density (a function

of total leaf area, leaf size and arrangement, leaf transparency, and so forth), which determines the amount of light captured per unit of height difference. Canopy density can be either an individual characteristic (crown density) or a population characteristic. For example, a dense population of small individuals produces a greater suppressing effect on competitors than does a less dense population (Winsor 1983).

The height profile of light availability changes autogenically through successional time because of the growth of plants. As a consequence, the traits that confer competitive ability for this single resource also change through time, producing a successional replacement of species through time along a single resource gradient.

Under equilibrium conditions with slow changes in resource availability, a situation that might occur in some cases of primary succession, inversely correlated competitive abilities for two or more inversely varying resources could produce a successional pattern of species replacements. Under nonequilibrium conditions, however, a single resource axis alone is sufficient to allow species replacement through time. Because changes in resources during succession usually occur much more rapidly than competitive equilibrium can be established, the resource-ratio model is a special case of a dynamic model based on inversely correlated competitive abilities.

Our major criticism of this and the Lotka-Volterra model is that a population-based approach to succession obscures the central dynamics of plant succession, which are the interactions between individual organisms. Individuals in a population may vary greatly, in terms of size, age, and physiological state, as well as in the biotic and abiotic environment they experience. The successional role of a given species on a specific plot of ground varies depending on whether the species is initially represented by many small seedlings or by an equivalent biomass in a few taller saplings that may have survived the disturbance that initiated secondary succession. The major problem with population models for addressing questions such as succession is that they aggregate individuals with different growth rates, reproductive capacities, and mortality probabilities into a single population (see Gardner et al. 1982).

There are several critical differences between the resource-ratio hypothesis and the interpretation of succession we present below. First, our approach is based on interactions among individuals rather than among populations. Second, competitive ability is an individual characteristic based on the interaction of a set of life history traits with the individual's environment rather than a set of abstract parameters for an entire population and average environmental conditions. Third, our model is based on the nonequilibrium dynamics of competition rather than on competitive equilibrium for both primary and secondary succession. Finally, in our interpretation, the changes in resource levels (light or soil nutrients) that lead to changes in species dominance during primary and secondary succession are a direct result of the plants themselves; that is, succession is autogenic. In the resource-ratio hypothesis, "changes in resource-supply rates [light and nitrogen] are not assumed to be under the direct control of photosynthetic plants . . . , it is not a model of autogenic succession" (Tilman 1985, p. 845).

The great variety of successional patterns found in nature (see Drury and Nisbet

1973) has frustrated efforts to develop generalizations at the population and ecosystem levels (Reiners 1986). We believe that a focus on individual organisms provides the appropriate level of resolution both for understanding specific successional sequences and for developing a generalized theory of succession.

AN INDIVIDUAL-BASED MODEL OF SUCCESSION

If succession is a plant-by-plant replacement process (see Horn 1974), its dynamics should be understandable in these terms. Therefore, to examine the role of life history attributes and functional responses to resource abundance, we use an individual-based plant model, a modified version of the JABOWA/FORET forest-simulation model (Botkin et al. 1972; Shugart and West 1977; Shugart 1984). The model simulates the annual tree-population dynamics of a defined area (scaled to the maximum size of the largest species present) by considering the birth, growth, and death of all individuals in that area.

The model is analogous to the Lotka-Volterra model described earlier, with a logistic-type equation representing each individual plant rather than each population. Each individual plant has life history parameters identical to those of all other plants of that species, but its actual growth is determined by the environmental conditions that it experiences as a consequence of competition with other individuals. Light availability is explicitly modeled, and the light available to an individual of a given height is determined by the total leaf area of all taller individuals. After the light available to a given individual has been computed, an equation representing a photosynthetic-light response curve is used to decrease the growth of that tree, with the form of the curve dependent on the shade tolerance of the species.

Mortality is modeled as a stochastic process, and the probability of mortality for an individual in any given year is in part a function of the longevity (maximum age) of the species. In addition, the probability of mortality is increased when the growth of an individual falls below a defined minimum, as in the case of shading. Introduction of new individuals to the plot is a function of the maximum rate of sapling establishment for the given species, modified by site conditions such as available light at ground level (Aber et al. 1982b; Pastor and Post 1985). Sapling establishment, rather than seedling establishment, is used to model reproduction in order to reduce the number of individuals that must be followed in computations.

In summary, the model has three essential features.

1. The birth, growth, and death of each individual is followed through time.

2. Each individual is assigned species-specific life history traits of maximum size (height and diameter), maximum age, maximum growth rate, maximum rate of sapling establishment, and shade tolerance.

3. Light availability and competition for light are modeled explicitly by calculating the total leaf area above each individual plant and then altering each individual's growth and mortality probability by its degree of shade tolerance and light availability.

Other features such as tolerance to drought or nutrient shortage and the explicit

calculation of soil water and nutrient availability can be added to the model (Mann and Post 1980; Pastor and Post 1985, 1986), but they do not alter the conclusions drawn from its simplest conformation. This model is able to produce a wide range of complex behavior using one simple mechanism of competition because of the complex interaction of life history traits among individual plants.

The essential features of this model have been applied for 15 years in forest-simulation models (Botkin et al. 1972; Shugart and West 1977, 1980). We believe, however, that the implications of the model for understanding plant succession have not been fully developed.

<center>MODEL RESULTS</center>

The Interaction of Life History Characteristics

The general features of inversely related life history traits are discussed above. Here, we focus on forest succession and five traits that are important in competition among trees: maximum growth rate, maximum size, maximum longevity, maximum rate of sapling establishment, and shade tolerance. Each of these traits may be important either in creating or in escaping the effects of light competition. (For a similar approach considering the consequences of various combinations of life history traits as "vital attributes" that predict successional changes, see Noble and Slatyer 1980.)

The different patterns of succession (or lack thereof) that result from various combinations of life history traits can be illustrated by a series of computer simulations of two-species competition, the simplest situation in which succession can occur. For each simulation, we created species based on combinations of two levels of the five different life history traits. The parameters are representative of values for forest trees of eastern North America. Each simulation was run for 500 years for 10 separate 0.08-ha plots. All figures are based on means for 10 plots.

To explore the influence of the various life history attributes on vegetation dynamics, we altered the relative values of a single attribute while holding the other life history traits of the two species constant. In this way, we built a matrix of vegetation dynamics with only one life history attribute varying along each dimension, an approach analogous to partial correlation analysis. This technique allows us to decouple the correlations between traits or groups of traits that are normally related in a specific pattern (e.g., premise 3, above) and to determine the effect of different patterns of correlations among these traits on the temporal pattern of species interactions.

Among the 32 possible combinations of two values for each of the five traits, some combinations are not physically possible (e.g., a slowly growing large plant with a short life span). Other combinations are possible but represent maladaptation to conditions where light is limiting (a short, shade-intolerant species with a low maximum growth rate). In an environment where water or nutrients were limiting, other traits could be important, resulting in other trade-offs and patterns of correlations. For example, where water stress is important, a small, shade-intolerant species with a low maximum growth rate could pursue a viable strategy

of gaining drought tolerance at the expense of growth rate or size (see, e.g., Orians and Solbrig 1977). The values of the traits of any particular species can be evaluated only in relation to those of co-occurring species in an environment where those traits are ecologically significant.

Figure 2 shows the results of a series of simulations using different combinations of parameter values. Maximum ages were set at 175 and 350 yr (species 1 and 2, respectively), and the maximum size of species 2 was held constant in all runs, except where the growth rates, sizes, and ages of both species were made equal. The ratio between the growth rates was varied from 1 to 2 by altering the maximum size of species 1. The ratio of the sapling-establishment rates between species 1 and species 2 was set at either 1 or 5, reflecting the observation that small, fast-growing species have higher seed output (and dispersibility) than large slow-growing species.

The simulations can be classified into five groups based on the temporal pattern of species abundances: successional replacement, divergence, convergence, total suppression, and pseudo-cyclic replacement (fig. 3). The patterns are a consequence of the relative competitive abilities of individuals of each species through time; therefore, they allow us to examine the influence of each attribute in determining competitive ability throughout the successional sequence.

Classic *successional replacement* (fig. 3a) results from an inverse relationship between the two species in the attributes that confer early and late competitive advantage. Species 1 is able to dominate during early succession because of either a higher growth rate (fig. 3a, cases 1–6) or a higher rate of sapling establishment (based on fecundity, not shade tolerance; fig. 3a, cases 1, 2, 7, 8) or both (fig. 3a, cases 1, 2). Both attributes allow rapid dominance of the limiting resource (light, in these simulations) following a disturbance. As faster-growing individuals overtop individuals of the slower-growing species, the growth rates of the slow-growing individuals are reduced, and their probability of mortality increases. High relative rates of establishment also allow species to achieve early dominance, reducing the availability of sites for establishment of other species and quickly forming a dense canopy below which light is inadequate for further seedling establishment.

However, as biomass accumulates and light levels at the forest floor decrease, species 2 is able to dominate because of its greater height (fig. 3a, cases 1, 3, 5–7) or its higher actual regeneration (based on shade tolerance; fig. 3a, cases 1–4, 7, 8) or both (fig. 3a, cases 1, 3, 7). Situations found in nature in which early-successional species have both higher growth rates and larger sizes than late-successional species (e.g., loblolly pine [*Pinus taeda*] to oak [*Quercus* spp.]; white pine [*Pinus strobus*] to northern hardwoods) can be understood in this same context.

Since the ability to regenerate is a function of both sapling numbers and the probability of survival (i.e., shade tolerance), the dynamics differ when these two attributes are uncoupled. High reproductive potential (sapling establishment) per se does not confer a competitive advantage with respect to regeneration if the probability of survival is low relative to the other species because of shade intolerance (fig. 3a, cases 1, 2, 7, 8). If both species are of equal shade tolerance,
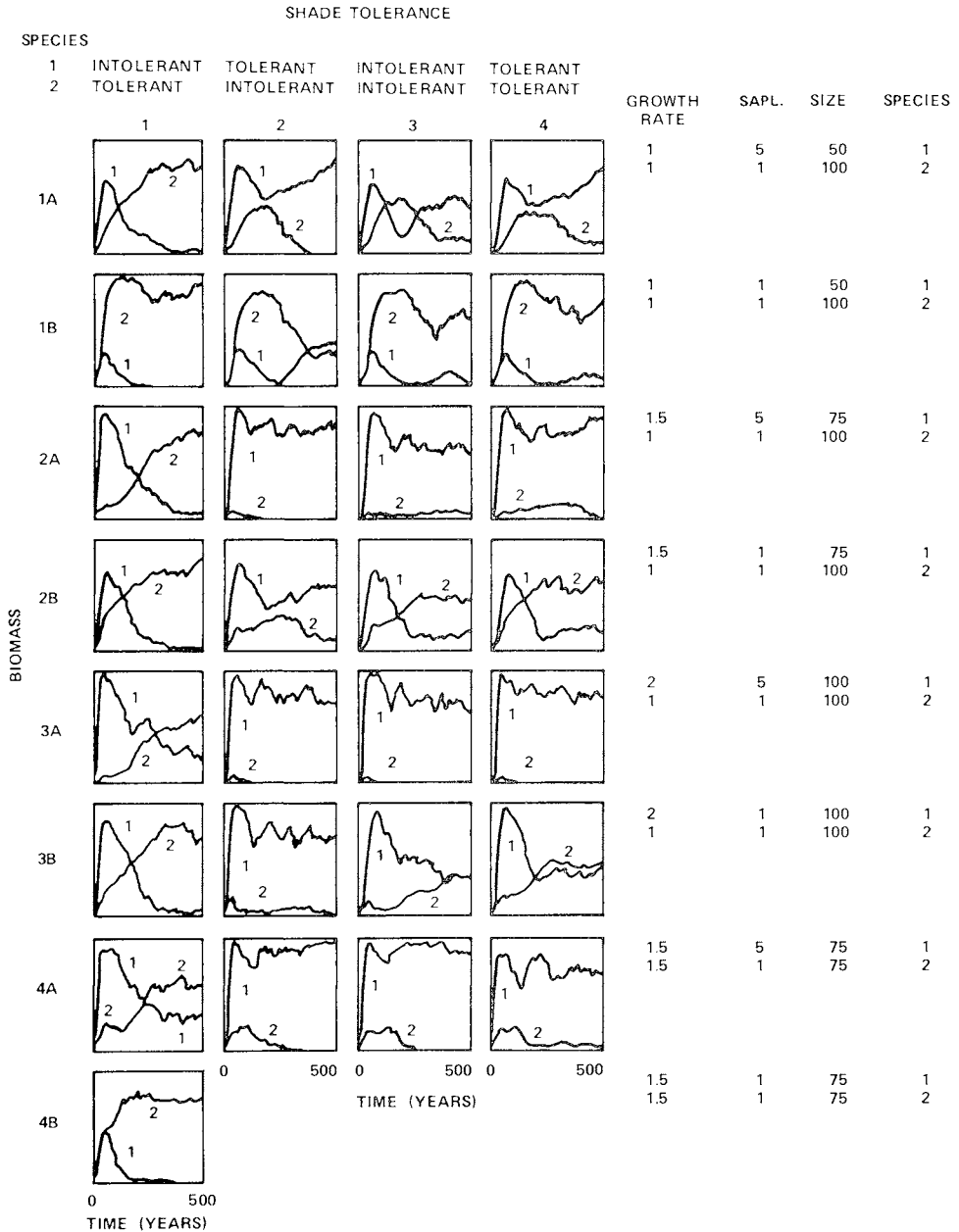
SHADE TOLERANCE

FIG. 2.—Dynamics of two-species competition with different combinations of life history and physiological characteristics. The rows labeled 1, 2, 3, and 4 differ in growth rate and size relationships (relative values indicated in columns to right of figure). Within each pair of rows, in row *A* species 1 has a fivefold advantage in sapling establishment, and in row *B* both species have the same sapling-establishment rate (relative values in the column SAPL). The columns in each row differ in shade-tolerance relationships (see the text for further discussion).

SUCCESSIONAL REPLACEMENT — DIVERGENCE — CONVERGENCE — TOTAL SUPPRESSION — PSEUDO-CYCLIC REPLACEMENT

BIOMASS (vertical axis) / TIME (horizontal axis)

Graphs: (a) Successional Replacement, (b) Divergence, (c) Convergence, (d) Total Suppression, (e) Pseudo-cyclic Replacement

SUCCESSIONAL REPLACEMENT (a)

CASE	SPECIES	Gr	SE	SI	TOL	
1	1	+	+	−	−	
	2	−	−	+	+	(2a1)
2	1	+	+	−	−	
	2	−	−	−	+	(3a1)
3	1	+	−	−	−	
	2	−	−	+	+	(2b1)
4	1	+	−	−	−	
	2	−	−	−	+	(3b1)
5	1	+	−	−	−	
	2	−	−	+	−	(2b3)
6	1	+	−	−	+	
	2	−	−	+	+	(2b4)
7	1	−	+	−	−	
	2	−	−	+	+	(1a1)
8	1	−	+	−	−	
	2	−	−	−	+	(4a1)

DIVERGENCE (b)

CASE	SPECIES	Gr	SE	SI	TOL	
1	1	−	−	−	−	
	2	−	−	+	+	(1b1)
2	1	−	−	−	−	
	2	−	−	+	−	(1b3)
3	1	.	.	−	−	
	2	.	.	+	+	(1b4)
4	1	−	−	−	−	
	2	−	−	−	+	(4b1)

CONVERGENCE (c)

CASE	SPECIES	Gr	SE	SI	TOL	
1	1	+	−	−	−	
	2	−	−	−	−	(3b3)
2	1	+	−	−	+	
	2	−	−	−	+	(3b4)

TOTAL SUPPRESSION (d)

CASE	SPECIES	Gr	SE	SI	TOL	
1	1	+	+	−	+	
	2	−	−	+	−	(2a2)
2	1	+	+	−	+	
	2	−	−	−	−	(3a2)
3	1	+	+	−	−	
	2	−	−	−	−	(3a3)
4	1	+	+	−	+	
	2	−	−	−	+	(3a4)
5	1	+	−	−	+	
	2	−	−	−	−	(3b2)
6	1	−	+	−	+	
	2	−	−	−	−	(4a2)
7	1	−	+	−	−	
	2	−	−	−	−	(4a3)
8	1	−	+	−	+	
	2	−	−	−	+	(4a4)

PSEUDO-CYCLIC REPLACEMENT (e)

CASE	SPECIES	Gr	SE	SI	TOL	
1	1	+	+	−	−	
	2	−	−	+	−	(2a3)
2	1	+	+	−	+	
	2	−	−	+	+	(2a4)
3	1	+	−	−	+	
	2	−	−	−	+	(2b2)
4	1	−	+	−	+	
	2	−	−	+	+	(1a2)
5	1	−	+	−	−	
	2	−	−	+	−	(1a3)
6	1	−	+	−	+	
	2	−	−	+	+	(1a4)
7	1	−	−	−	+	
	2	−	−	+	+	(1b2)

CASE 9 — species 1, 2 (no entries)
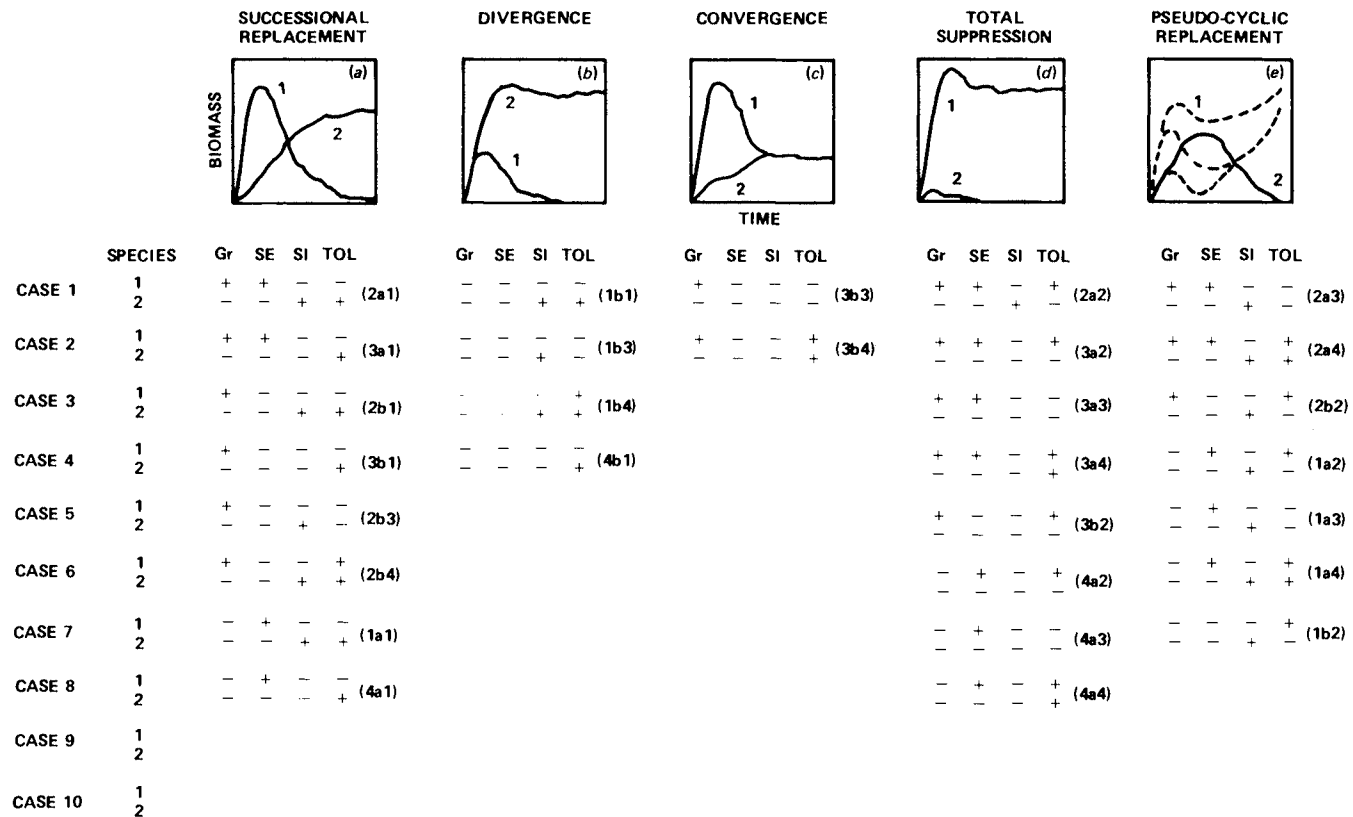CASE 10 — species 1, 2 (no entries)

FIG. 3.—Five general patterns of two-species interactions. Below each pattern are the combinations of relative trait values for the two interacting species that can produce that pattern and, in parentheses, the location of each example in figure 2. Gr, growth rate; SE, sapling establishment; SI, size; TOL, shade tolerance.

however, a high sapling-establishment rate can confer a competitive advantage in late succession that overrides any height advantage of the other species (fig. 3e, cases 1, 2, 5, 6). Obviously, shade tolerance and a high rate of sapling production provide a strong competitive advantage.

A large maximum height confers a competitive advantage only late in stand development and only when regenerative abilities are equal (compare fig. 3a, cases 5, 6, with fig. 3d, case 1, and with fig. 3e, cases 1–7). Growth rate and longevity appear to confer no competitive advantage to species late in stand development, aside from their correlation with other attributes such as size, reproductive potential, and shade tolerance.

The classic pattern of successional replacement results from a specific correlation pattern among life history parameters. When this correlation structure is altered, a variety of patterns results. Each of the following patterns can be found in nature, and each is usually interpreted as an exception to generalizations about succession (see Drury and Nisbet 1973).

Divergence (fig. 3b) occurs when competitive abilities are equal early in stand development (i.e., equal growth rate and reproductive potential), followed by a competitive advantage by one species as a function of regenerative ability and/or size.

Convergence (fig. 3c) is the inverse of divergence. One species has a competitive advantage resulting from a higher growth rate early in stand development, whereas competitive ability is equal as the stand develops. Seedling input must be equal in all cases, or it would confer an advantage in later succession because of higher actual reproduction.

Total suppression (fig. 3d) occurs when one species has a combination of attributes that confers a competitive advantage over the other species throughout stand development. In the examples in figure 3d, the rate of sapling establishment confers an advantage both in early succession (with or without an associated growth-rate advantage) and in late succession since species 1 always has equal or greater shade tolerance and thus higher actual regeneration.

Pseudo-cyclic replacement (fig. 3e) results from a temporary period of dominance or codominance by the initial cohort of species 2 during the period between the senescence of the initial cohort of species 1 and the maximum life span of species 2. Individuals of both species become established in the high-light environment of early succession, and because of greater longevity or height, the initial cohort of species 2 persists longer than the initial cohort of species 1. However, because of the competitive advantage of species 1 in later succession resulting from a higher actual regeneration, species 2 is replaced by species 1. In all cases, species 1 has higher actual regeneration because of greater shade tolerance or greater sapling establishment with equal shade tolerance. The relative abundances of species 1 and 2 during the intermediate period is a function of the initial competitive interactions and the shade tolerance of each species.

The patterns resulting from different combinations of life history attributes are a consequence of the equality or inequality of the attributes rather than the actual parameter values. Changes in the parameter values influence the quantitative behavior of the model (relative abundances and rates of change), but assignment

to one of the five general patterns (fig. 3) is influenced only by the qualitative relationship between species with respect to their relative competitive abilities through time.

In all of the above simulations, we made the assumption that both species are able to establish themselves on the site immediately following disturbance (e.g., "initial floristics"; Egler 1954). We have not explicitly considered differences in the ability of the two species to colonize the site. Such differences following disturbance would obviously influence the dynamics by conferring an initial competitive advantage on the earlier colonizer. If the earlier colonizer also has the combination of attributes that confers an early competitive advantage, early colonization merely magnifies the suppressive effect on later colonizers (figs. 3a,c,d,e, species 1). If the early competitive ability of the two species is equal, early colonization confers a decisive advantage in early succession because it is functionally equivalent to a greater reproductive advantage when both species invade simultaneously (fig. 3b, species 1). If the earlier colonizer also has a suite of attributes that confers later competitive advantage (i.e., higher actual reproduction and/or size), then the early colonizer may completely suppress the later colonizers (figs. 3a,b, species 2; figs. 3d,e, species 1).

Field studies confirm the importance of propagule input in altering the dynamics of succession. The time of creation of the successional site (see, e.g., Salisbury 1929; Keever 1950; Thurston 1951; Holt 1972; Grubb 1977; Harcombe 1977a) is important, as is the location of a site in relation to the sources of propagules (Grubb 1977; Harcombe 1977b; Opler et al. 1977). The size of the site determines the relative importance of input from plants on its perimeter versus long-distance dispersal (see, e.g., Watt 1934; Keever 1950; Platt 1975; Grubb 1977; Hartshorn 1978; Brokaw 1985), and it affects growth conditions within the site. The history of the site can determine what, if any, seeds are already present in the soil (Marks 1974) or whether vegetative propagules such as saplings and stump sprouts are destroyed, as by a fire, or survive to have a major advantage over plants that must start from seed. These factors can easily be incorporated into an individual-based model.

Although the stochastic element is large in the initiation of succession and even in its later stages, the patterns of dispersibility tend to reinforce the pattern derived from competition among species with inversely related traits. The seeds of the most rapidly growing plants tend to be the most dispersible because of their small size and large number (Salisbury 1942; Richards 1952; Harper et al. 1970; Whitmore 1975), and these seeds reach a successional site before the seeds of the plants that eventually predominate.

Just as energetic and physiological constraints tend to produce an inverse correlation between traits that confer a competitive advantage in early versus late succession, there may be trade-offs within any of the major strategies (groups of traits). Although small, fast-growing plants have a larger seed output per unit of biomass than do larger species with low maximum growth rates, some small plants may maximize seed output at the expense of growth rate, or vice versa. Likewise, there may be trade-offs, such as those between growth rate and longevity, among large plants. A fast-growing species may attain as large a size as a slow-growing

species but live for a much shorter time because it has not invested in the structural properties needed to resist storm damage and insect or fungal attack. The resistance to low-probability stresses necessary for long-term survival requires an investment of photosynthate that makes a short-term, high-growth strategy impossible.

The sequential species replacement that characterizes the classic successional sequence results from a specific pattern of correlations among the critical life history and physiological traits of the interacting species. The resemblance of most successional patterns found in nature to this type of sequential replacement suggests that this correlation structure is common in plant communities. There are, however, groups of plants where this pattern is not found. The general pattern is most likely to break down in groups consisting of only a few species, particularly if not all of the species are adapted to the same resource conditions. When some species have limitations resulting from adaptations to environmental conditions irrelevant in a particular situation and to which the other species in the assemblage are not subject, the correlations among critical life history traits probably differ from the usual pattern, and the successional pattern among these species will be atypical. Presumably, many of the exceptions to generalizations about succession can be explained in this manner.

Multispecies Succession

Natural successional sequences generally involve more than two species. The approach we have described can be expanded to any number of species. Figure 4 presents the results of simulations using three, four, and five species, showing the effects of adding species with traits that give a higher competitive ability in early succession. A "typical" successional replacement occurs even among late-successional species (fig. 4a) in the absence of species capable of dominating earlier in succession. Addition of an earlier-successional species (fig. 4d, species 1) greatly reduces the early dominance of the fastest growing of the late-successional species (species 3) and accelerates the rate at which the largest, most-shade-tolerant species (species 5) achieves dominance. This occurs because the short life span and small size of species 1 make it a poorer competitor with late-successional species than was species 3, which it eliminated. (For several examples of how a "third party" such as species 1 can alter the outcome of succession, see Grubb 1986.)

Addition of a "super-species" with rapid growth, large size, and long life (species 2, analogous to the tulip tree [*Liriodendron tulipifera*] in some habitats) reduces the relative abundance of both the early-successional species (species 1) and the mid-successional species (fig. 4g, species 3, 4).

These simulations show that the dynamics of multispecies succession can be interpreted using the same life history approach as was used for the two-species simulations. Any pair or group of species, whether it dominates in early or in late succession, can be subdivided on the basis of relative life history attributes. Within a group of early- or late-successional species, the dynamics can be described by the same five general patterns resulting from different correlations among life history characteristics.
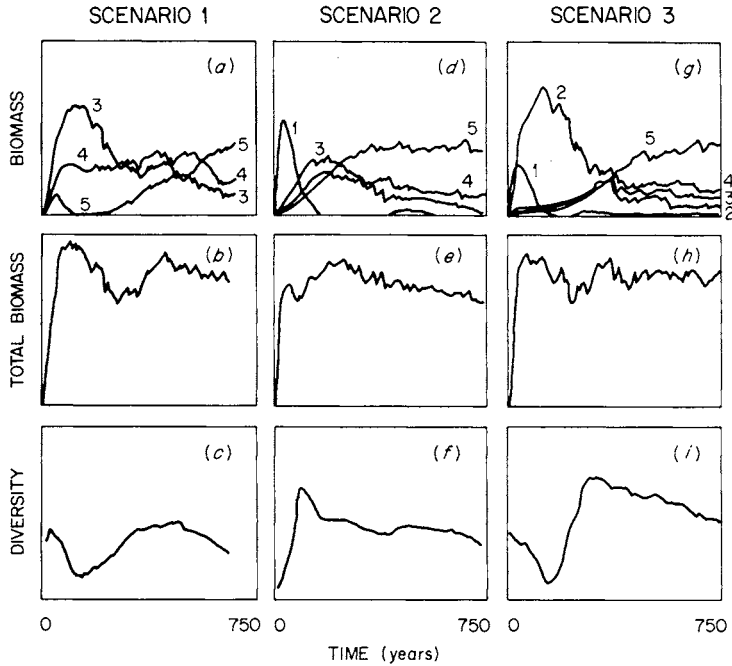
Species	Relative Growth Rate	Seed	Size dbh (cm)	Height (m)	Maximum Age	Shade Tolerance
1	2.17	5	50	15	50	Intolerant
2	1.87	5	150	35	350	Intolerant
3	1.43	1	100	30	300	Tolerant
4	1.09	1	100	35	400	Tolerant
5	1.00	1	150	35	650	Tolerant

FIG. 4.—Species biomass dynamics, community biomass, and diversity patterns for successional sequences with three, four, and five species. In scenario 1, all three species have late-successional characteristics but differ sufficiently in relative competitive abilities to produce a "typical" successional replacement. In scenario 2, an early-successional species is added to the three species in scenario 1. In scenario 3, a "super-species" with a high growth rate and large size is added to the four species in scenario 2.

Competition for Multiple Resources

In addition to light, soil nutrients and water often limit plant growth, and under some conditions plants compete primarily for these resources rather than for light. This can occur among the tallest plants in a community (Pastor and Post 1986) or when canopy cover is less than total. Temperature also affects plant growth. Each species has its own requirements and optima for these factors that determine how it performs under any set of environmental conditions. Competition for other factors can be incorporated into this model using the same approach we have described for light.

Tree species can be categorized by tolerance to low nitrogen availability just as

they can be by shade tolerance (Mitchell and Chandler 1939). Nitrogen responses and the interactions of the nitrogen and carbon biogeochemical cycles have been incorporated into a version of the model we have described (Aber et al. 1979, 1982; Aber and Melillo 1982*b*; Pastor and Post 1985, 1986). Complex feedbacks between species composition and soil-nitrogen availability are based on species-specific nitrogen requirements and the rate at which nitrogen from the leaves of each species is recycled (litter quality; see Meentemeyer 1978; Aber and Melillo 1982*a*; Melillo et al. 1982; Pastor et al. 1984; McClaugherty et al. 1985; Pastor and Post 1986).

Any factors such as temperature or water stress that affect tree growth can also affect soil-nitrogen availability, directly through their effect on microbial growth and indirectly through their effect on tree species composition and the resulting quality of litter. The species-specific effect of temperature on tree growth was included in the original version of the forest-simulation model JABOWA (Botkin et al. 1972); a frost-tolerance factor was added later (Solomon 1986). The effect of soil water-holding capacity, precipitation, and evapotranspiration on tree water stress have also been incorporated (Mann and Post 1980; Pastor and Post 1985, 1986).

Figure 5 demonstrates the influence of soil conditions on patterns of succession produced by a version of the model that includes soil-moisture effects and nitrogen cycling (Pastor and Post 1985, 1986). These simulations were run for climatic conditions similar to those in southern Kentucky, for three different soil conditions. Succession under favorable conditions (fig. 5*a*) is modeled with a silty loam 100 cm in depth (field capacity [FC], 0.4 cm/cm; wilting point [WP], 0.2 cm/cm) and initial total soil nitrogen of 1.6 Mg/ha. Succession under conditions of periodic water stress (fig. 5*c*) is modeled with a sandy loam 50 cm in depth (FC, 0.3 cm/cm; WP, 0.2 cm/cm) and the same nitrogen levels as in figure 5*a*. Succession under conditions of nitrogen shortage (fig. 5*e*) is modeled with the same depth of silty loam as in figure 5*a* but with only 0.01 Mg/ha initial nitrogen. All species were available for establishment in each of the three scenarios; the differences in species composition result from interactions, not from an initially different set of species.

The effect of water stress, modeled here by reducing the water-holding capacity of the soil, is to slow growth rates and the overall rate of successional replacement; it also shifts the species composition to those species with the highest annual growth rates for the specific water-stress conditions (compare fig. 5*c* with fig. 5*a*, which reflects adequate levels of all resources). Note the slower buildup of biomass, lower levels of nitrogen availability, higher levels of light availability at ground level, and higher species diversity with chronic water stress (fig. 5*d* vs. fig. 5*b*).

Although the classic primary successional sequence may rarely occur in nature (Drury and Nisbet 1973), successional sequences beginning with little or no soil nitrogen do occur, with a rapid buildup of nitrogen and development of forest under suitable conditions (Boring and Swank 1984; Van Auken and Bush 1985). In figure 5*e*, a nitrogen-fixing species (simulating the black locust, *Robinia pseudoacacia*) achieves rapid dominance because it is the species with the fastest growth
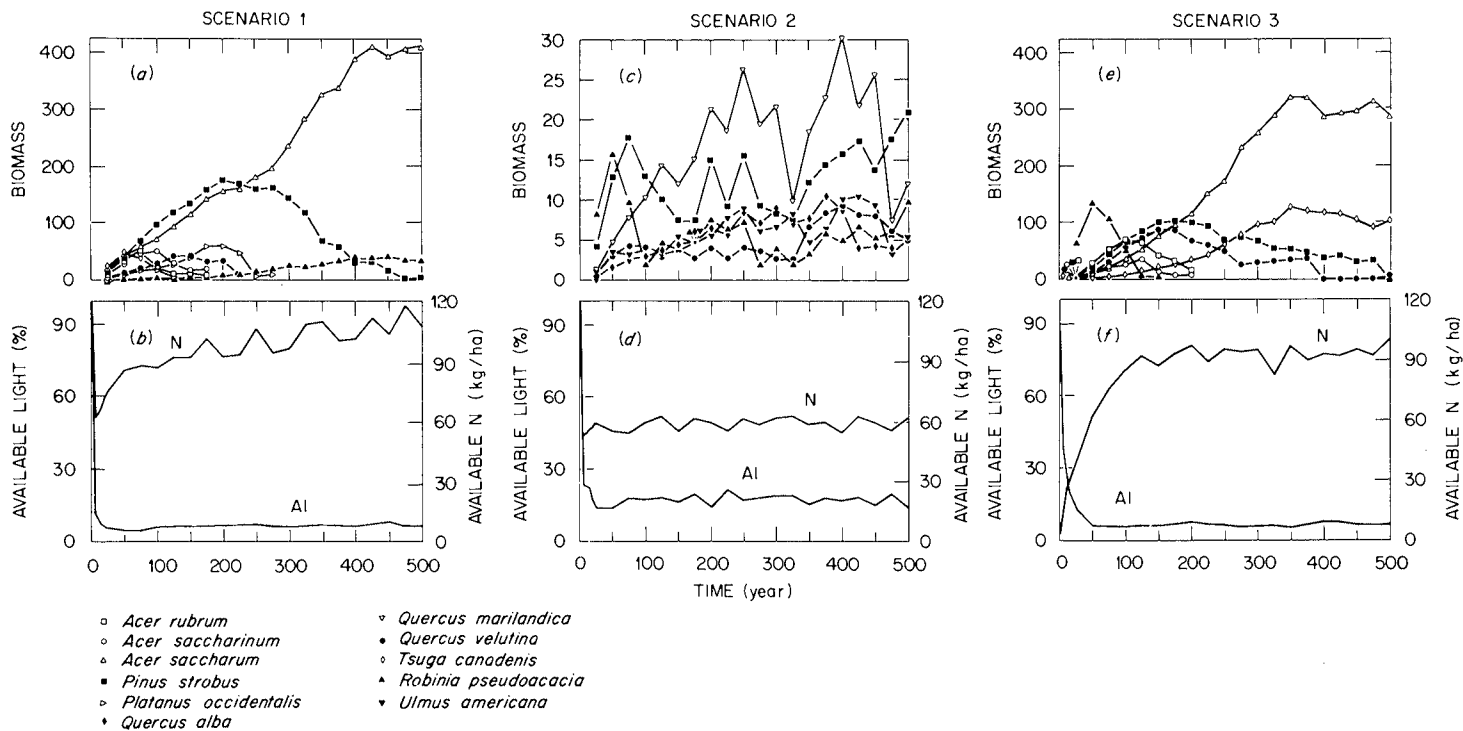
FIG. 5.—Patterns of species replacement and resource levels for succession under different environmental conditions modeled with multiple limiting resources. Scenario 1: secondary succession with no limitation by water or nutrients. Scenario 2: secondary succession under conditions of water stress. Scenario 3: primary succession with initial nitrogen limitation. All simulations began with the same set of species.

under extreme low-nitrogen conditions. As a consequence of its nitrogen-fixing activity, however, soil-nitrogen levels rise (fig. 5f), and other species with faster growth rates, greater shade tolerance, and larger size are able to replace it. This example demonstrates that primary succession, as well as secondary succession, can be understood as a dynamic process in which species composition changes in response to autogenically changing environmental conditions without ever coming to equilibrium. Different environmental conditions produce predictably different patterns of succession.

<div align="center">DISCUSSION</div>

Modeling succession based on interactions among individuals provides insight into a broad range of population, community, and ecosystem processes. Microclimatic changes can be predicted on the basis of growth in height and the resulting shading. Nutrient-cycling processes such as nitrogen accumulation or loss can be estimated, as can such community properties as species-abundance relationships and diversity. Even the population dynamics of individual species can be modeled using this approach (Huston and DeAngelis 1987). In the following sections, we discuss some of the implications of this approach to understanding succession.

<div align="center">*Community Patterns during Succession*</div>

In contrast to equilibrium models, in which absolute or relative growth rates have no effect on patterns of species abundance, the role of growth rate is critical in a dynamic model. In general, high growth rates result in a higher rate of species replacement (i.e., successional change) than do low growth rates. This has important consequences for patterns within a successional sequence. Species replacements occur more rapidly in early succession than in late succession. This pattern is characteristic of natural successions (Shugart and Hett 1973) and is consistent with observations that the response to perturbation is most rapid in early succession (Hurd et al. 1971; Pinder 1975; Tomkins and Grant 1977; Sousa 1980).

Increased growth rates can also result in major differences between successional sequences that occur under different conditions (figs. 5a,c,e). An increase in growth rates (fig. 5a compared with fig. 5c) results in a more-rapid approach to domination by late-successional species and, as a consequence, a faster reduction in species diversity.

A further reduction in diversity in response to favorable conditions results from a generally greater response to a growth stimulus, such as fertilization, by fast-growing species than by slow-growing species (Mitchell and Chandler 1939; Grime and Hunt 1975; Mahmoud and Grime 1976; Chapin et al. 1986). Not only are the dynamics accelerated by compressing the time scale (a proportionate increase in all growth rates), but a disproportionate increase in the growth rates of the fastest-growing species results in relatively greater dominance by these species during early succession. If maximum size is also increased by higher resource levels, as is often the case, this dominance may be further increased. This mechanism seems to explain the reduced diversity in tropical successional plots that were fertilized,

compared with plots with no nutrient addition (Harcombe 1977*b*). In this case, a fast-growing herbaceous species, pokeweed (*Phytolacca* sp.), responded to fertilizer addition much more strongly than did woody species, and it suppressed them for the course of the experiment. Similar results were obtained using only woody species (Huston 1982).·

Because of inherent physiological differences, different species have a growth-rate advantage at sites where different nutrients are abundant (and others are limiting). Such an advantage may or may not result in long-term dominance by a particular species, depending on its other life history characteristics and the frequency and type of disturbances in its environment. This is the nonequilibrium interpretation of the patterns of species composition in areas with different resource ratios that have been attributed to an equilibrium balance of inversely related competitive abilities for two or more resources (Tilman 1980, 1982).

Within a successional sequence, growth rates usually decrease through time, as larger or more-tolerant species with slower growth rates come to predominate. As a consequence, coexistence among the species that predominate in mid- and late succession is greatly prolonged (figs. 1*b,c*, 4, 5). Further reduction in growth rates may result from changes in the environment, such as a reduction of resources available for growth as biomass accumulates or of nutrients by leaching (Bormann et al. 1968; Jordan and Kline 1972). Soil nutrients and water may be reduced in this manner (Toumey and Kienholz 1931; Korstian and Coile 1938; Bartholemew et al. 1953; Popenoe 1957; Zahner 1958; Marks and Bormann 1972; Brown and Bourn 1973; Harcombe 1977*a*), and this reduction is likely to have the greatest effect when the resources involved are in short supply (e.g., water in arid regions and nutrients in infertile soils). Such a reduction in growth rates allows increased diversity and prolonged coexistence (Huston 1979), and it augments the inevitable consequences of the lower maximum growth rates of later-successional species. This property of prolonged coexistence in mid-succession is a widely observed feature of natural successions (Shugart and Hett 1973; Sousa 1980).

The suppression and release behavior of the model leads to specific predictions about the patterns of change during succession. Biomass does not increase linearly but in pulses corresponding to the release of certain species from suppression (figs. 4*b,e,h*). In the examples of forest succession presented here, an initial pulse occurs during early succession, and a second pulse follows the decline of early-successional species. Relatively few studies have measured biomass changes over more than a few years, but pulsed or uneven rates of biomass accumulation have been observed (Odum 1960; Ewel 1971; Whittaker 1975; Bormann and Likens 1979; Peet 1981).

Patterns of species diversity show the same fluctuations as does biomass, although they are out of phase because evenness in species biomass decreases rapidly during a period of release when the biomass of one or of a few species is increasing (figs. 4*c,f,i*). Following this rapid decrease, evenness rises until another species begins to dominate the system. Fluctuating patterns of diversity have been found in a number of successional studies (Dyrness 1973; Bazzaz 1975; Whittaker 1975; Opler et al. 1977; Pearson and Rosenberg 1978).

In general, the overall evenness of a system is highest during the intermediate

stages of succession when the periods of coexistence become longer because of the predominance of slower-growing species. Under nonequilibrium conditions, coexistence is greatest among the most similar species (fig. 4; see Hutchinson 1967; Grenney et al. 1973; Caswell 1982). Evenness eventually decreases, however, as the system approaches competitive equilibrium (successional climax), and exclusion occurs. Without seed input, the richness component of diversity (the number of species) must inevitably decline. With seed input, richness may increase through the intermediate stages but generally decreases as equilibrium is approached.

Interspecific Interactions

A focus on interactions between individuals clarifies that in many cases there is no effective difference between inter- and intraspecific competition. Intraspecific competition is not necessarily more intense than interspecific competition, and in some cases such as light competition, it may be much more intense if the individuals of the other species are larger or faster-growing or have denser canopies. The potential intensity of competition must be evaluated specifically for each type of resource and the sizes, life histories, and physiological strategies of the species involved. Likewise, the evaluation of effective population size for questions of density-dependent effects on competition and selection should not be based only on the density of conspecific individuals, which may be low compared with the density of equivalent competitors of other species.

The concepts of facilitation, tolerance, and inhibition have played a prominent role in discussions of plant succession. A recent definition of these interactions (Connell and Slatyer 1977) has stimulated a number of new studies of succession, but it has generated some argument about which mechanisms are supported by the data. We believe that part of the controversy stems from an overly narrow definition of these mechanisms and from their application at the population and community level rather than at the individual level, where all three processes can occur simultaneously.

The notion of tolerance to various types of stress (shade, drought, low nutrient availability) has a long history in the succession literature, but Connell and Slatyer (1977) concluded that there were few if any convincing examples of their "tolerance model." In the tolerance model as defined by Connell and Slatyer, "modifications wrought on the environment by the earlier colonists neither increase nor reduce the rates of recruitment and growth to maturity of later colonists" (1977, p. 1122). By this definition, if there is any evidence of competition, the tolerance model is falsified. This is an unreasonable definition of the role of tolerance in succession (see also Botkin 1981) because tolerance is irrelevant except in the context of competition (inhibition). Likewise, the definition of inhibition (Connell and Slatyer 1977, p. 1123) completely eliminates the role of tolerance and is just as unreasonable as a definition of tolerance that precludes the existence of competition.

Facilitation, defined as occurring "when later [species] can become established and grow *only* after earlier [species] have suitably modified the environment" (Connell and Slatyer 1977, p. 1123), occurs most prominently during primary

succession. This restrictive definition may be contrasted with "relative facilitation," which occurs in all successions in which individuals modify their environment in a manner that favors individuals with other combinations of life history traits.

Facilitation, tolerance, and inhibition describe processes and properties that are relative, not absolute. They can occur simultaneously, with varying degrees of importance, during every successional sequence.

Super-Species—Exceptions to the Rule

Although correlations among life history and physiological characteristics exist, sets of species can always be selected that demonstrate exceptions to the general pattern (see Grubb 1987). Exceptions such as the comparison of large, slow-growing, shade-tolerant canopy trees and small, slow-growing, understory perennial herbs can be dismissed as being an inappropriate comparison of two very different life forms, which are adapted to different environments. Likewise, because relative relationships among organisms growing in the same environment are the important factors, comparisons of organisms from different environments, such as forests and deserts, are clearly inappropriate, unless all of the relevant resource axes and selective pressures are considered. Even among comparable species, however, exceptions in the relative ranking of certain traits can be found. It should be obvious why some of these apparent exceptions are among the most successful species in their environment over both ecological and evolutionary time.

In the forests of southeastern North America, a few species seem to have escaped some of the constraints that limit most other species. The tulip tree (*Liriodendron tulipifera*) is a rapidly growing, shade-intolerant, early-successional species that often grows in pure stands on abandoned fields. Yet it can live several hundred years and achieve diameters in excess of two meters, often sharing dominance with hemlock (*Tsuga canadensis*), a slow-growing, shade-tolerant, "late-successional" species (cf. fig. 4g). Although the seedlings of *L. tulipifera* cannot survive in the shade, they successfully regenerate in the gaps formed by the death of large adults (Shugart 1984). This species has not escaped all constraints, however, because it is most successful on mesic sites with fertile soil. White pine (*Pinus strobus*) and redwoods (*Sequoia sempervirens*) also dominate in both early and late succession under certain conditions. Similar examples can be found in forests around the world.

Ecosystem Processes during Succession

Biogeochemical processes ultimately depend on the actions of individual organisms. The rates and proportions in which nutrients are absorbed from and returned to the soil are functions of species-specific physiological characteristics interacting with the biotic and abiotic environmental conditions that affect individuals of each species. As a consequence, in an individual-based model such as we have described, the levels of various resources can be predicted through time (incorporating inputs to and losses from the ecosystem), as can the abundances and population structures of species.

Ecosystem processes and properties that have been explicitly modeled using this approach include leaf area and leaf production; aboveground biomass; aboveground net primary production; forest floor weight; nitrogen availability, mineralization, and immobilization rates; nitrogen fixation and nitrogen loss; soil water; and effects of climatic change (temperature and CO_2) (Aber et al. 1979, 1982; Pastor and Post 1985, 1986; Solomon 1986). The predicted ecosystem patterns are discussed in detail in the papers cited above; here we summarize a few of the general results.

Leaf area increases rapidly to its maximum (except in cases where growth is limited by nutrients or water), but total biomass increases much more slowly. This pattern has been documented in numerous ecosystem studies (Marks 1974; Covington and Aber 1980; A. Cooper 1981). An important consequence of this pattern is that the light available to small plants decreases rapidly during succession (figs. 5b,d,f).

Nitrogen mineralization and immobilization are strongly dependent on the properties of the decomposing organic matter that, along with climate, determine the rate at which the organic matter decomposes (Meentemeyer 1978; Melillo et al. 1982). Because the nitrogen content and decomposability of leaf litter is a species-specific property that varies widely among species (Aber and Melillo 1980, 1982a), changes in species composition can affect nitrogen availability through the course of succession (Pastor et al. 1984; McClaugherty et al. 1985; Pastor and Post 1985, 1986).

The overall patterns of nitrogen availability produced by the model are qualitatively similar to those that have been documented in primary and secondary succession (Aber and Melillo 1982b; Robertson 1982; Pastor and Post 1986). In a primary succession starting with very low nitrogen levels, nitrogen availability increases gradually through time to a steady-state level because of nitrogen fixation and atmospheric input (fig. 5f). In a secondary succession following a disturbance, nitrogen availability drops from its pre-disturbance steady-state level and gradually increases to some steady-state level (figs. 5b,d).

Obtaining parameters for this type of ecosystem is feasible because the relevant parameters are based on individuals. Because individuals of different sizes and ages contribute disproportionately to different ecosystem processes (e.g., through leaf litter vs. woody litter), many ecosystem processes can best be understood by summing individuals rather than by modeling the processes at higher levels.

Landscape-Scale Community Patterns

The dynamics of succession are central to an understanding of the community structure of all plant communities. Drury and Nisbet (1973) observed that although succession is a temporal phenomenon, most of the evidence for successional changes comes from spatial sequences of vegetation on adjacent sites, and they argued that a general theory of succession should explain both temporal and spatial patterns. Models based on resource competition and life history strategies are applicable to both temporal and spatial gradients (see Pickett 1976; Tilman 1982).

We have demonstrated how different environmental conditions can produce

different successional patterns from the same set of species. If undisturbed, these successions would lead to very different equilibrium (climax) communities (see Watt 1947). Even though competitive equilibrium is rarely achieved, a steady-state dynamic equilibrium representing a balance between a characteristic disturbance regime and the local successional dynamics can occur (Loucks 1970; Grime 1973a,b, 1974; Levin and Paine 1974; Horn 1975; Levin 1976; Pickett 1976; P. White 1979; Doyle 1981; Shugart 1984). Since diversity is generally lower in later succession, disturbances before late succession can prevent a reduction in diversity. Very frequent disturbances that maintain early-successional conditions reduce diversity, leading to dominance by fast-growing species. The properties of steady-state communities in a landscape can be predicted using models based on the dynamic equilibrium between different frequencies and intensities of disturbance and different rates and patterns of succession (Huston 1979).

Resolution, Scale, and Applicability

The approach we advocate for understanding succession emphasizes the importance of using the appropriate functional units and time scale for the phenomenon of interest. The level of aggregation of functional units determines the resolution that can be achieved in understanding and predicting specific processes (Gardner et al. 1982). For certain processes and properties, such as leaf area or net primary production, the resolution of an individual-based or even a species-based model is unnecessary, and more highly aggregated functional groups are appropriate. For understanding species replacements during forest succession, we argue that the appropriate functional unit is the individual tree, and a yearly time-step is adequate. Fish population dynamics and interactions with lower trophic levels have also been modeled using individuals (Adams and DeAngelis 1986; Huston and DeAngelis 1987).

In contrast to forests, phytoplankton communities are composed of species of virtually identical individuals. As a consequence, individuals may be aggregated into populations in phytoplankton models without any loss in predictive power for most questions. Using a computer model of phytoplankton dynamics analogous to the forest population model we have described, it was demonstrated (Lehman et al. 1975) that a seasonal succession of phytoplankton species could be produced by the interaction of species-specific physiological parameters with autogenically decreasing resource levels (particularly phosphorus).

Although the examples of succession we use are based on forests and the physiological and life history properties of trees, it should be obvious that the basic principles hold true for any plant community, as well as for many animal communities. Changes in relative dominance among herbaceous species and combinations of herbaceous and woody species can be understood using the same general approach we describe for trees. Parallel examples with similar life history trade-offs and patterns of succession can be found in marine intertidal and benthic systems (Lubchenco and Menge 1978; Pearson and Rosenberg 1978; Sousa 1979, 1980), kelp forests (Reed and Foster 1984), and tropical coral reefs (Huston 1985).

SUMMARY

An approach based on competition among individual plants is presented as an explanation for species replacements during plant succession. Inverse correlations among life history and physiological traits that confer competitive ability under different environmental conditions are shown to be sufficient to produce successional replacements but not sufficient for understanding the complex variety of successional patterns unless they are applied at the individual level rather than at the population level or higher. With models based on competition among individual plants, various combinations of life history and physiological traits can produce the great variety of population dynamics found in natural successions. The classic successional pattern of species replacement results from a particular structure of correlations among life history and physiological characteristics. Atypical patterns of succession result when this correlation structure is altered. Both primary and secondary succession are modeled as nonequilibrium processes, capable of interacting with disturbances to produce steady-state communities whose properties depend on abiotic conditions, such as temperature and resource levels, and on the type and frequency of disturbances.

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