THE RESOURCE-RATIO HYPOTHESIS OF PLANT SUCCESSION

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In this paper, I present an alternative, simple theory of succession, the resource-ratio hypothesis. Ecologists have long been intrigued by succession because its repeatability in an area and the similarities among areas worldwide suggest that much of the pattern of vegetation dynamics following a disturbance may result from a few underlying processes (e.g., Cowles 1899; Cooper 1913; Clements 1916; Gleason 1917, 1927; Lawrence 1958; MacMahon 1981). As shown by Connell and Slatyer (1977), Peet and Christensen (1980), McIntosh (1980, 1981), Horn (1981), Botkin (1981), Tilman (1982), and others, however, there is, as yet, no consensus in ecology as to which mechanisms are most important in controlling succession. Different processes have been considered important in primary succession, in secondary succession, and in maintaining the composition of vegetation once change ceases (e.g., Drury and Nisbet 1973; Connell and Slatyer 1977; McIntosh 1981). Clearly, the uniqueness of the species involved in successions in different areas, the uniqueness of each particular habitat, and various historical factors all limit the potential predictive ability of any model of vegetation dynamics and structure. In the interest of parsimony, however, it may be useful to explore the possibility that the same theory can explain the general patterns observed in primary successions, in secondary successions, and in mature vegetation.

The resource-ratio hypothesis of succession is an attempt to explain what MacMahon (1981, p. 277) called "the surprising degree of pattern to successional processes in various parts of the world." It is an extension of a graphical theory of plant competition for resources in spatially heterogeneous habitats and along spatial gradients (Tilman 1982). The resource-ratio hypothesis of succession, which is meant to apply to species that are dominant sometime during succession, has two main elements: interspecific competition for resources and the long-term pattern of supply of limiting resources, which I call the resource-supply trajectory. According to this hypothesis, succession results from a gradient through time in the relative availabilities of limiting resources. In addition, succession should be a directional or repeatable process only to the extent that the resource-supply trajectory is repeatable or directional. In this paper, I suggest that a major

axis for the evolution and differentiation of terrestrial plants has been the gradient from habitats with resource-poor soils but high availability of light at the soil surface to habitats with resource-rich soils but low availability of light. This gradient and the evolution of plant life histories in response to it may be the cause of the otherwise difficult-to-explain similarity of primary and secondary succession.

The graphical theory of consumer-resource interactions used in this paper was developed in Tilman (1980, 1982) and is an extension of work by MacArthur (1972), Maguire (1973), Leon and Tumpson (1975), and Taylor and Williams (1975). So that its critical assumptions may be readily apparent, the resource-ratio hypothesis has been kept as simple as possible. Other potentially important processes, such as species-specific herbivory, differential colonization abilities, and temperature-dependent growth, have not been included in the model. If this simple formulation of the model proves useful, it would be possible to add other elements to the model to determine whether they could explain a significantly larger portion of the observed variance.

THEORY

Although the dynamics of resource supply are determined by numerous processes, resource supply at a given time can be approximated by a simple model (Tilman 1980, 1982). In the absence of consumption, let

$$dR_1/dt = a_1(S_1 - R_1) \qquad \text{and} \qquad dR_2/dt = a_2(S_2 - R_2)$$

where a_1 and a_2 are rate constants, R_1 and R_2 are environmental availabilities of the resources, and S_1 and S_2 are the maximal amounts of all forms of each resource in a habitat. S_1 and S_2 are somewhat comparable to carrying capacities for each resource. They are not equilibrium concentrations of the resources. The point (S_1, S_2) is called the resource-supply point. For the graphical model, I assume that $a_1 = a_2$. This simple definition of resource supply allows an easy mapping of resource-supply points into the associated equilibrium levels of R_1 and R_2 (fig. 1; Tilman 1980, 1982). Each resource-supply point is thus associated with a given outcome of interspecific competition. Note that both S and R have units of resource per unit area or volume, and thus validly can be graphed on the same axis. Changes in resource-supply rates can be represented as the trajectory of (S_1, S_2) through time.

Growth Isoclines

The process of resource competition is graphically illustrated in figure 1 (see Tilman 1980, 1982, for additional details). Two plant species, which differ in their requirements for two limiting essential resources, R_1 and R_2, are shown. Curve A is the resource-dependent growth isocline for species A. It shows the availabilities of R_1 and R_2 for which the reproductive rate of species A equals its mortality rate. If resource availabilities fall in the region outside this isocline, the population density of species A will increase. If they fall inside this isocline (toward the origin), the population density of species A will decrease. If species A is to exist
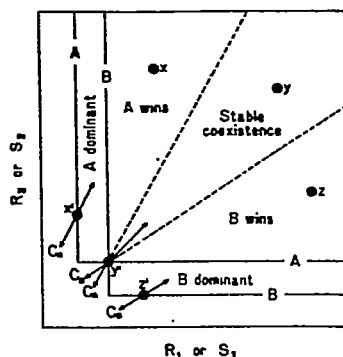
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Fig. 1.—Solid curves A and B (with right-angle corners) are the resource-dependent zero-net-growth isoclines for species A and B. The point at which they cross, y', is a two-species equilibrium point. The process of resource consumption will map habitats with various supply points, (S_1, S_2), into equilibrium points for which species A wins (such as supply point x), both species stably coexist (such as supply point y), or species B wins (such as supply point z), as shown. Note that there is an interspecific trade-off in resource requirements.

in a habitat at equilibrium, the equilibrium levels of R_1 and R_2 must fall on its isocline. The right-angle bend in the isocline means that R_1 and R_2 are essential resources for this plant, with its growth rate determined solely by the one resource in lower supply relative to need (Tilman 1980, 1982). Curve B is the resource-dependent growth isocline for species B. As shown, species A has a lower equilibrial requirement for R_1, but a higher requirement for R_2 than species B. These species thus have a trade-off in their resource requirements, such that the superior competitor for one resource is an inferior competitor for the other. Throughout this paper, I assume that all of the competing species have trade-offs such that the species are inversely ranked in their requirements for the two limiting resources. Vectors C_A and C_B are the consumption vectors of species A and B. Each vector shows the amounts of R_1 and R_2 consumed by a species per unit time. The slopes of these vectors reflect optimal foraging for these two resources (Tilman 1982). The unlabeled vectors are the resource-supply vectors associated with each resource-supply point (habitat). These vectors show the amounts of R_1 and R_2 supplied per unit time in a habitat. Each resource-supply point can be thought of as representing the resource supply characteristics of a particular habitat.

The resource-dependent isoclines and consumption vectors of these species define the types of habitats (i.e., sets of resource-supply points) in which neither species can survive, in which one species competitively displaces the other, and in which both species stably coexist at equilibrium (Tilman 1980, 1982). In all cases, an equilibrium will occur only if resource consumption equals resource supply and if the reproductive rate of each species equals its mortality rate. Habitats with low supply rates of R_1, but high supply rates of R_2, i.e., low $S_1:S_2$ ratios, would be dominated by species A, with species B extinct at equilibrium. In such habitats, both species would be limited by R_1. Species A has the lower equilibrial requirement for R_1. At equilibrium, species A would reduce R_1 to a level insufficient for the survival of species B. For instance, for resource-supply point x in figure 1,
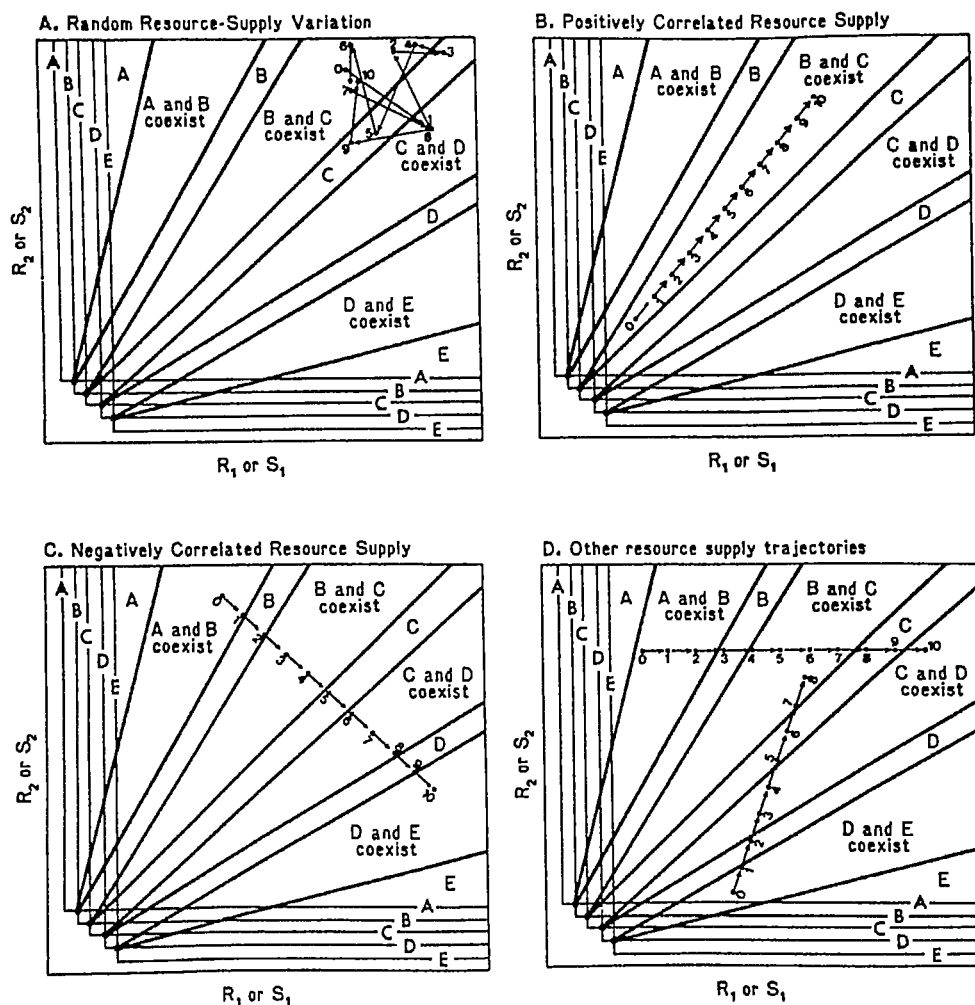
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FIG. 2.—Alternative resource-supply trajectories. Changes in resource supply rates can lead to changes in the composition or dominance of a plant community. Here I show 5 species that differ in their requirements for two essential resources. Their isoclines and consumption rates specify the types of habitats (i.e., resource-supply points) for which one species is dominant or a pair of species coexist. *A*, A case with random variation in resource supply rates and without a directional trajectory. *B*, Positively correlated resources. with both resources increasing from time 0 to time 10. *C*, Negatively correlated resources. with R_2 decreasing and R_1 increasing from time 0 to time 10. *D*, Two alternative trajectories. As shown in fig. 3. in all cases in which there is a directional change in $S_1:S_2$ ratios. there is a directional replacement of one species by another.

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resource availabilities would be reduced, at equilibrium, to point x' on the isocline of species A. At x', species A would equilibrate at the population density for which its consumption of R_1 and R_2 just balanced supply. The two species would stably coexist for habitats with intermediate $S_1:S_2$ ratios. They can coexist because each species is limited by a different resource, species A by R_2 and species B by R_1. The coexistence is stable because each species consumes relatively more of the resource that limits it at this two-species equilibrium point (Tilman 1980). The steeper slope for the consumption vector of species A means that it consumes more of its limiting resource, R_2, per unit of R_1 than does species B. Because of resource-dependent adjustments in the population densities of the species, resource availabilities would be reduced, at equilibrium, to point y' for any habitats with resource-supply points in the region of coexistence. Because species B has a lower requirement for R_2, it would competitively displace species A in habitats with high $S_1:S_2$ ratios (fig. 1), such as in the habitat with supply point z. In these habitats, both species are limited by R_2.

Resource-Supply Trajectories

For a plant community in which there are two limiting resources, there are three qualitatively different ways that resource supply rates may change through time. The first case could be considered a neutral case, in which the supply rates of each resource vary randomly and independently with a fixed mean and variance for each resource. Second, the resources could be positively correlated through time. Third, the resources could be negatively correlated. How might these different trajectories of resource supply affect the species composition of a plant community?

Consider a plant community with five species having the resource requirements shown in figure 2. The resource-dependent growth isoclines used in figure 2 assume that the five species are inversely ranked in their requirements for R_1 and R_2. The regions of coexistence of various pairs of species are based on the assumption that each species consumes the resources as if the species were foraging optimally (Tilman 1982). This causes all four of the two-species equilibrium points to be locally stable. The isoclines and consumption characteristics of the species define the habitats (resource-supply points) in which various species can exist at equilibrium (fig. 2).

In order to determine the effect of a given resource-supply trajectory on the dynamics of this five-species community, it is necessary to solve the differential equation model associated with the isoclines of figure 2 (see Appendix). For such solutions, the dynamics obtained will depend critically on how quickly resource supply rates change along the trajectory relative to the rate of competitive displacement. If the rate at which resource supply rates change through time is slow compared to the rate of displacement, the plant community will approach the equilibrium composition associated with each point along the trajectory. If the rate of change in resource supply is rapid relative to competitive displacement, an equilibrium will be reached only when (or if) resource supply rates finally stop changing. Figure 3 shows the actual dynamics predicted for a relatively slow rate
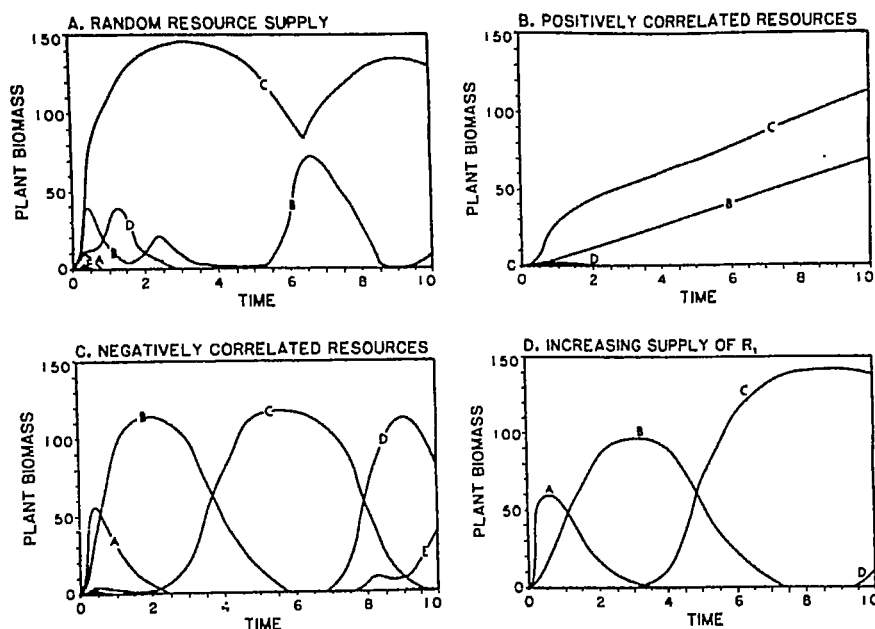
FIG. 3.—The plant population dynamics predicted by a differential equation model of resource competition (see Appendix) are shown in A, B, and C, respectively, for the resource trajectories of figs. 2A, 2B, and 2C. D, Plant dynamics for the trajectory numbered from 0 to 10 in fig. 2D.

of change of resource supply rates along the trajectories of figure 2, and is based on numerical solutions of the equations given in the Appendix. (Population dynamics based on numerical solutions of cases with rapid changes in resource supply are shown in fig. 5, and will be discussed later.)

Random resource fluctuations (fig. 2A) do not lead to a consistent, directional change in the species composition of the plant community (fig. 3A). Although such variation may allow more species to coexist than there are limiting resources (Levin 1970; Levins 1979; Armstrong and McGehee 1980), the major effect here seems to be fluctuations in the densities of species B and C. The dynamics in figure 3A are consistent with what would be qualitatively predicted using the isoclines and supply rates shown in figure 2A. The average of all the supply points for this case falls in the region in which species B and C should coexist, with species C about 15 times more abundant than species B. Positively correlated resources (fig. 2B) lead to increasing biomass of species B and C, but not to marked changes in community composition (fig. 3B). The dynamics are consistent with the qualitative predictions which would be made from the resource-supply trajectory shown in figure 2B. The supply points always fall in the region in which species B and C should coexist at equilibrium. As the supply points increase from time 0 to time 10, the biomass of species B and C is expected to increase. Negatively correlated resources (fig. 2C) cause a systematic replacement of one

dominant species by another (fig. 3C), a change like the idealized case of succession. Comparison of figures 2C and 3C shows that the actual dynamics predicted by numerical solution of the model lag, by about 0.5 time units, the qualitative dynamics which would be expected from figure 2C if the composition of the community immediately reached the equilibrium associated with each point along the trajectory. These simulations show that the simple isocline diagrams of figure 2 can be used graphically to approximate the effects of various resource-supply trajectories if the rate of change in resource availabilities is slow relative to the rate of competitive displacement. They also illustrate that a resource-supply trajectory with negatively correlated resources can lead to the directional replacement of one species by another.

These three cases represent distinctly different patterns of resource variation. There are intermediate cases. As illustrated in figure 2D, positively correlated resources can cause a directional replacement of one plant species by another, as can trajectories for which the supply rate of one resource is constant, and the other changes (figs. 2D, 3D). In both cases shown in figure 2D, there is a systematic change in the relative supply rates of the two resources. For all resource-supply trajectories along which there is a directional change in the $S_1:S_2$ ratio, there is a directional replacement of one plant species by another. Thus, I have called this the resource-ratio hypothesis of succession. This should imply not that only the ratio of limiting resources need be known to understand succession, or that succession need be a directional process, but that the relative supply rates of limiting resources can, in theory, control the sequence of species dominance. This hypothesis assumes that each plant species is a superior competitor for a particular proportion or ratio of limiting resources (see figs. 1, 2; Tilman 1977, 1982, pp. 139–145) and that vegetation composition changes as plant consumption, biogeochemical processes, and disturbance change the relative availability of limiting resources.

Let us consider cases in which limiting resources are inversely correlated through time. What would determine the eventual composition of such a community? According to this theory, a stable vegetation would be reached only if resource supply rates equilibrated at fixed levels. Because there are likely to be local differences in the composition, slope, aspect, and drainage of the parent material on which a soil forms, there will be local differences in the rate of soil change and in the equilibrium conditions that eventually may be obtained in the soil (Jenny 1980). For instance, soils formed on clays become more nitrogen-rich than those formed on sands. Such local differences in soil processes should be manifested in local differences in supply rates of limiting soil nutrients. Light may also be a limiting resource. Its availability at the soil surface will be greatly influenced by gap-producing disturbances. If local disturbance rates and biogeochemical processes caused resource supply rates to equilibrate at point 3 of figure 2C, species B and C would be dominant. If they equilibrated at point 6, species C and D would be dominant; and at point 10, species D and E would be dominant. Point-to-point differences in resource-supply rates within a region could allow numerous species to coexist on two limiting resources (Tilman 1982).

Long-term climatic change may modify both soil processes and the relative

competitive abilities of species, preventing the formation of an equilibrium community. Independent of climatic variation, soil processes may not go to equilibrium (Walker et al. 1981). As the rate of soil change slows, however, the species composition of the vegetation should tend to stabilize. It is predicted that the local species composition depends on the local rates of supply of the limiting resources. The resource-ratio hypothesis of succession predicts that succession should be a repeatable and directional process for a particular region only to the extent that the biogeochemical processes and disturbance rates controlling resource supply rates are repeatable and directional in that region. The resource-ratio hypothesis assumes that the same processes that cause change in vegetation also maintain its composition once change ceases. It is thus consistent with the call for parsimony made by Drury and Nisbet (1973), who argued that the same processes that explained changes in plant communities through time, i.e., succession, should explain changes through space, such as the separation of species along gradients.

IMPLICATIONS OF THE MODEL

To apply this model to a terrestrial plant community, it is necessary to know what the limiting resources are in that community. This can be determined only through controlled experimentation in that habitat. In a wide array of terrestrial habitats, experimental manipulations have shown that soil resources, especially nitrogen, water, phosphorus, potassium, magnesium, or various trace metals, may limit plant growth. Experiments performed in mesic habitats have shown that the largest and most frequent response often comes from nitrogen (e.g., Lawes et al. 1882; Milton 1934, 1947; Brenchley and Warington 1958; Willis and Yemm 1961; Specht 1963; Willis 1963; Thurston 1969; Mellinger and McNaughton 1975; Bakelaar and Odum 1978; Braakhekke 1980; Tilman 1984). Nitrogen fertilization leads to major changes in plant species composition (preceding references and Milton 1947; Huffine and Elder 1960; Gay and Dwyer 1965; Owensby et al. 1970; Kirchner 1977; Bakelaar and Odum 1978; Tilman 1982, 1983). Other studies of mesic plant communities have suggested that light, especially light available at the soil surface for seedlings and new shoots, is an important limiting resource (e.g., Anderson 1964; Grime and Jeffrey 1964; Sparling 1967; Horn 1971, 1975; Bjorkmann and Ludlow 1972). In forests, competitive ability for light, often referred to as the degree of shade tolerance, is frequently cited as a determinant of species replacement (Decker 1952; Horn 1971; Drury and Nisbet 1973).

Although my review of the experimental literature suggests that nitrogen is often the main limiting soil resource, the theory presented does not depend on nitrogen being the limiting soil resource, but, instead, on there being a negative correlation between the availability of a limiting soil resource and the availability of light at the soil surface. Water may also be an important limiting soil resource in mesic habitats. Because watering experiments have been done much less often than fertilization experiments, it is difficult to know if water is as frequently limiting as nitrogen in these habitats. Even in semiarid grasslands, nitrogen seems to be a major limiting resource except in unusually dry years (Power 1980). Because soil water-holding capacity, total soil nitrogen, and nitrogen mineraliza-

tion rates are highly correlated (e.g., Robertson and Vitousek 1981), further experimentation is required to determine the relative importance of nitrogen and water limitation in mesic habitats.

Primary Succession

It has been suggested that nitrogen and light are often the main limiting resources during terrestrial primary succession (e.g., Cowles 1899; Cooper 1913; Crocker and Major 1955; Lawrence 1958; Olson 1958). Primary succession begins when a bare, mineral parent material is exposed by some means, such as landslide, glacial recession, lake or ocean recession, or erosion. Except for nitrogen, all of the mineral elements required by plants occur in the parent material in which most soils form (Jenny 1980). Thus, plants colonizing the bare parent material of primary succession should be nitrogen-limited. The rapid recession of glaciers in Glacier Bay, Alaska, during the 225 yr since the Little Ice Age has provided a dramatic chronosequence of primary succession (Cooper 1923, 1939; Lawrence 1958). In Glacier Bay, many of the later dominants of succession, such as cottonwood, were among the first colonists of the newly exposed substrate, but did not survive, or survived in a stunted, chlorotic form indicative of extreme nitrogen deficiency (Lawrence 1958). Among the early dominants, the most common species were generally capable of nitrogen fixation (Lawrence 1979). These include the cyanobacteria that form "black crusts" on bare mineral soils (Worley 1973), lichens such as *Stereocaulon* and *Lempholemma*, various angiosperms, including the rose *Dryas drummondii*, the alder *Alnus crispa*, lupines, and other legumes (Lawrence et al. 1967; Reiners et al. 1971; Lawrence 1979). As the early dominants lost leaves and roots or died, nitrogen-containing organic matter became available to various soil-decomposer species. These retained much of this nitrogen as well as nitrogen from free-living nitrogen fixers and from atmospheric inputs. Through excretion of nitrogenous wastes by these decomposer species or upon their death, some of this nitrogen became available to vascular plants. Chronosequences of soil nitrogen for Glacier Bay (Crocker and Major 1955) and the Lake Michigan sand dunes (Olson 1958) suggest that such processes caused 5- to 10-fold increases in total soil nitrogen within 100 yr. As soil nitrogen increased, total plant biomass increased. At Muir Inlet of Glacier Bay, for example, the alders, which grew to heights of 3–10 m, were replaced by cottonwoods, which overtopped them and shaded them out. "By the time 50 years have passed since the melting of the ice, a dense alder thicket up to 10 m (33 ft) tall had developed at Muir Point from which have emerged the same cottonwood trees that became established soon after ice recession, but which could not grow erect, at some places for over 40 years, until the alder provided them with adequate amounts of nitrogen for rapid erect growth" (Lawrence 1979, p. 217). These cottonwood trees are then replaced by taller spruce and hemlock. During this 100-yr period, the habitat of newly establishing plants went from being a high-light but low-nitrogen habitat to being a high-nitrogen but low-light habitat. There was thus a strong gradient through time in the ratio of the availability of nitrogen and light. As will be discussed later, after a thousand or more years, an iron hardpan often develops

in this region, preventing the free drainage of water. These waterlogged soils have lower rates of mineralization of nitrogen and support a more open, muskeg vegetation.

It might be argued that total soil nitrogen is not related to the supply rate of available nitrogen, and thus that the trends in total soil nitrogen reported by Crocker and Major (1955) for Glacier Bay and by Olson (1958) for the sand dunes of southern Lake Michigan do not reflect trends in the supply rate of nitrogen. Recent work by Robertson and Vitousek (1981) and Robertson (1982), however, demonstrated that, in the southern Lake Michigan sand dunes, soils with higher levels of total soil nitrogen also had higher rates of mineralization of available nitrogen. Robertson and Vitousek (1981, p. 376) found that the "potential nitrogen mineralization in soils from the primary sere increased through the first five stages and then leveled off."

If any soil resource (nitrogen, water, phosphorus, etc.) is limiting, increases in its availability should lead to increased plant productivity and aboveground biomass. The increased biomass would lead to increased light interception. Thus, as nitrogen or any other limiting soil resource increases in availability, light should become relatively less available, especially for shorter plants such as seedlings and saplings. This would create a temporal gradient in the availability of the limiting soil resource relative to light, much like the gradient for negatively correlated resources shown in figures 2C and 3C. Point-to-point spatial variation in the availability of a limiting soil resource within a region should lead to a comparable negative correlation locally between the availability of the soil resource and light intensity at the soil surface. Nitrogen is a major limiting resource at Cedar Creek Natural History Area in Minnesota, as demonstrated by fertilization experiments (Tilman 1984). Consistent with the generalizations above, light penetration to the soil surface decreased significantly with nitrogen fertilization at Cedar Creek (Tilman 1984). Additionally, a survey of 4 old fields of different ages showed significant negative correlations between total soil nitrogen and light penetration to the soil surface both within each field and among all fields (D. Tilman, unpubl. data). The generality of this negative correlation between the availability of a limiting soil resource and the availability of light at the soil surface may be an important cause of the similarities that have been observed among many successional sequences and between successional and spatial gradients.

Figure 4A illustrates the major qualitative features of the resource-ratio hypothesis as applied to primary succession. The plant species are shown to differ in their competitive abilities for a limiting soil resource and light, with each species being a superior competitor for a particular ratio of the soil resource to light. Species A and B, the early successional species, are superior competitors under conditions with low availability of the soil resource but high availability of light at the soil surface. The late successional species, species D and E, are superior competitors for light but inferior competitors for the limiting soil resource. As various biogeochemical processes increase the availability of the limiting soil resource, the availability of light at the soil surface decreases, creating a gradient through time in the soil-resource:light ratio. This changing ratio leads to a replacement of one plant by another (fig. 4A). Because soil change is relatively slow
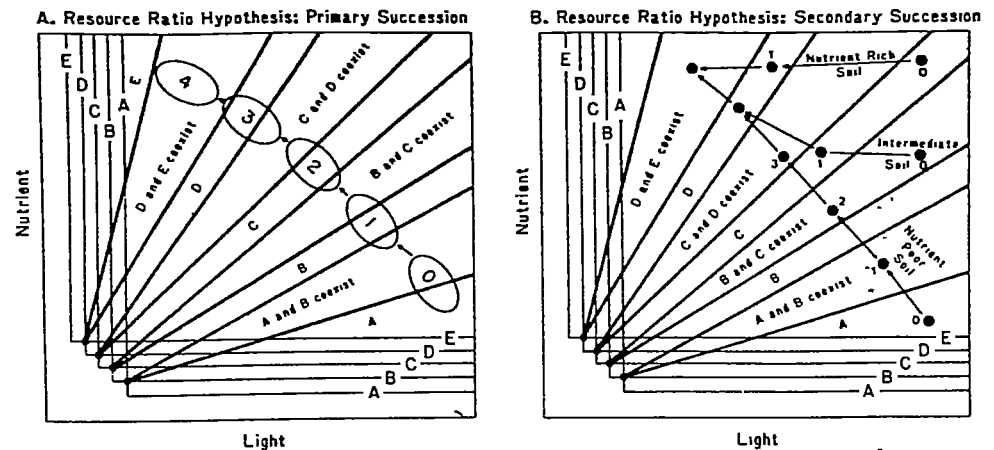
A. Resource Ratio Hypothesis: Primary Succession   B. Resource Ratio Hypothesis: Secondary Succession

FIG. 4.—*A*, It is hypothesized that primary succession depends on the relative availability of a limiting soil resource (nutrient) versus light available at the soil surface. At any time, these resources should be negatively correlated, as illustrated by the oval regions of resource supply. Through time, increasing availability of the limiting soil resource should lead to decreasing availability of the light at the soil surface. Thus, from time 0 to time 4, the community would be predicted to be dominated by species A, then B, then C, and then D and E. *B*, It is predicted that the rate of secondary succession depends on how nutrient-rich the soil is. On very nutrient-poor soils, secondary succession should be almost identical to primary succession. On nutrient-rich soils, succession should be much faster. It is predicted that early successional plants such as species A and B would be absent if plant dominance quickly approached equilibrium. Life history differences expected between early and late successional plants could explain the similarity between primary succession and secondary succession on rich soils (see fig. 5).

in primary succession (Crocker and Major 1955; Olson 1958), the effects of this soil-resource to light-supply trajectory can be approximated by assuming that community composition approaches equilibrium at each point. As will be discussed later, the underlying mathematical model can be solved to predict the actual dynamics (fig. 5, Appendix). The actual resource-supply trajectory followed depends on many aspects of the local habitat, and the change need not be directional. For at least the first 100 yr of primary succession, though, it seems that the trajectory often is directional, and qualitatively similar to that shown (fig. 4A), with nitrogen often being the main limiting soil resource.

The resource-ratio hypothesis does not say that succession occurs as light becomes a more important limiting resource than some soil resource. Rather, it says that the gradient through time in the relative availability of a limiting soil resource and light will sequentially favor the species that are superior competitors at particular ratios. When species A and B coexist at time 0 in figure 4A, species A is limited by light and species B is limited by the soil resource. At time 1.5, when species B and C coexist, species B is limited by light and C by the soil resource. At time 4, when species D and E coexist, species D is limited by light and species E by the soil resource. Throughout the full successional sequence, both light and the

soil resource remain important limiting resources. Although light clearly becomes less available at the soil surface during forest development, the resource-ratio hypothesis predicts that some of the dominant plants will be limited by a soil resource, not light, on all but the richest soils. This is consistent with the observation that nitrogen fertilization increases tree growth even in forests on relatively rich soils (e.g., Miller and Miller 1976; Albrektson et al. 1977; Waring et al. 1978; Brix 1983) and with Vitousek's (1982) review suggesting that nitrogen is the most important limiting soil nutrient in temperate forests.

Edaphic Variation

Within a given geographic region, it is likely that there will be persistent habitats that differ in the relative availability of the limiting resources. Each such local habitat could be thought of as a different region along the soil-resource:light gradient of primary succession in figure 4A. Each could function as a long-term "refuge" for a particular group of successional species. Thus, if resource-supply rates for various points within a habitat equilibrated in the region labeled 1 in figure 4A, species A, B, and C would coexist. If they equilibrated in region 3, species C, D, and E would coexist. The occurrence of such edaphic (i.e., soil-caused) variations in vegetation led to the rejection of the monoclimax theory of vegetation (Whittaker 1953). Indeed, Whittaker (1953, p. 44) said that "references to edaphic factors occur throughout the literature, such effects apparently being observed in every vegetational area studied with sufficient intensity." Olson (1958) reported vegetation variations in the "mature" vegetation of the southern Lake Michigan sand dunes that corresponded with local differences in total soil nitrogen levels. Lower-nitrogen sites were dominated by a relatively open black oak and blueberry vegetation whereas richer sites were dominated by a more closed-canopy red oak and sugar maple vegetation. Many other studies show that the local composition of mature stands of vegetation is correlated with the availability of soil resources (e.g., Beard 1944, 1955, 1983; Cody and Mooney 1978; Jenny 1980; Rabinovitch-Vin 1983).

It could be asked what processes prevent species dominant early in succession from being displaced from a geographic region. One explanation is that they are "pioneer" species that exist by virtue of their ability to colonize recently disturbed sites. Marks (1983) offers contrary evidence for the native North American plants that are now common during old-field succession in northeastern United States. He found that these plants occurred "primarily in persistent open habitats rather than in temporary forest openings" (Marks 1983, p. 225). The persistent, open habitats in which these early successional plants were maintained "on the time scale of centuries or millennia" (Marks 1983, p. 225) tended to be areas with high-light availability but nutrient-poor soils, such as limestone outcrops, gravel bars, talus slopes, sandy soils, and steep, eroded stream banks. The ability of early successional species to maintain stable populations in such low-nutrient but high-light habitats is consistent with the predictions of the resource-ratio hypothesis of succession (fig. 4A).

Life History Differentiation along a Soil-Resource:Light Gradient

By discussing evolution along a soil-resource:light gradient, I do not wish to imply that all soil resources have the same effect. Species that are good competitors for water have markedly different morphologies and physiologies, for instance, than those that are good competitors for nitrogen. The root surface enzymes involved in the active transport (uptake) of nitrate are different from those for phosphate, which differ from those for magnesium, etc. Additionally, limitation by phosphorus leads to dominance by a very different set of plant species than limitation by nitrogen or light, as evidenced by the results of over 125 yr of fertilization in the Park Grass Experiments at Rothamsted, England (Thurston 1969; Tilman 1982). Rather, I wish to suggest that the inverse relation between a limiting soil resource and light available at the soil surface created a gradient which was an important axis for the evolution of plant life history differences. The process of plant life history evolution presented here differs from that of Grime (1979) in some important ways. Grime considered stress, disturbance, and competition to be the three major axes along which the life histories of plants have differentiated. The view presented here distinguishes between the stress caused by low levels of a soil resource and the stress caused by low availability of light at the soil surface, and considers intraspecific and interspecific competition to be the mechanism determining the effects of soil resources and light on life history evolution.

A soil resource, such as nitrogen, is a belowground resource, whereas light is an aboveground resource. To acquire more of a soil resource, a plant must allocate its potential growth to belowground structures for nutrient uptake, but to acquire more light, a plant must allocate its growth to aboveground photosynthetic structures. Thus, individual plants face a trade-off in their competitive abilities for a limiting soil resource versus light (Orians and Solbrig 1977). Because nitrogen (or any other soil resource) and light are essential resources, foraging theory (Rapport 1971; Covich 1972; Tilman 1982) predicts that the optimal pattern of allocation to these conflicting needs is the pattern that leads a plant to be equally limited by both. Thus, each point along a soil-resource:light gradient (fig. 4A) should be associated with a different pattern of allocation to tissue for nutrient acquisition versus photosynthetic tissue.

On a very poor soil, total plant biomass would be low, causing little attenuation of light. A plant that allocated more of its potential growth to belowground structures for resource acquisition would be favored over a plant that allocated more to aboveground photosynthetic structures, because the former would acquire more of the limiting resource and thus reproduce more rapidly (Orians and Solbrig 1977). In contrast, in a habitat with a nutrient-rich soil, high plant biomass would be produced, causing significant attenuation of light. This would favor an individual that allocated more of its potential growth to aboveground structures for acquiring or efficiently using light. Chapin (1980) reports that plant species from poor soils do tend to invest more heavily in roots and in mycorrhizal associations than those from rich soils. Additionally, within a species, individuals

have higher root:shoot ratios on lower-nutrient soils (e.g., Grime and Hunt 1975; Shamsi and Whitehead 1977; Grime 1979; Parrish and Bazzaz 1982). Because roots function as support structures for stems, as storage organs, and as nutrient uptake structures, however, root:shoot ratios may be a poor index. Clearly, taller plants require more support than shorter plants, and perennial herbaceous plants in low-light but seasonal habitats such as prairies require significant energy stores to produce tall stems and leaves early in the season.

A critical characteristic of a plant in a light-limited habitat is its height. Because light tends to be a directional resource, taller plants intercept more light (Horn 1971; Grime 1979; Givnish 1982). As soils become richer and light attenuation increases, plants that grow to a greater height at maturity should be favored. Givnish (1982) reported that forest understory herbs followed such a pattern, with taller species dominant on richer soils and with herbs of low stature dominant on dry or sterile soils. Similar patterns have been reported in the canopy species of many areas. For instance, the natural vegetation in the Coolgardie Botanical District of southwestern Australia ranges from 3-m-tall scrub species on nutrient-poor sandy soils to 25-m-tall salmon gum woodland on rich clay soils (Beard 1983). In the areas of California, Chile, and Italy with Mediterranean-like climates, the vegetation ranges from species 0.3 m tall at maturity in the driest areas to species more than 10 m tall at maturity in the wettest regions (Cody and Mooney 1978). On sandy soils in Michigan, Wisconsin, and Minnesota, lichens, grasses, and forbs dominate the poorest soils, with richer soils dominated by the relatively short burr and pin oaks, and even richer soils dominated by maples (Hole 1976; personal observations).

For structural reasons, taller plants must produce stronger tissues to support their leaves in the canopy (Greenhill 1881; Horn 1971; McMahon 1973), and thus must have a greater allocation to such tissues (Givnish 1982). Deciduous species must also have energy and nutrient stores for leaf production at the beginning of the growing season. Because seedlings of taller species often grow in the shade of other plants and because they allocate much of the limiting energy they obtain to the production of structural tissues and to energy stores, their rate of growth should be low compared with that of early successional species. This is consistent with Horn's (1971) generalization that early successional trees are fast growing but require high light levels, and late successional trees are slow growing (even in full sunlight) but can survive in deep shade. The prediction that the maximal rate of growth of early successional plants should be greater than that of late successional species also seems consistent with the data that Grime and Hunt (1975) obtained on 132 species of British plants. Growing these plants under controlled conditions of relatively high light, water, and nutrient availability, they found that perennial plants grew more slowly than annuals, and that woody plants were the slowest-growing perennials.

All else being equal, selection strongly favors traits that allow an earlier age of first reproduction (Cole 1954). For plants that are good competitors for soil resources, there are few factors that would favor delayed reproduction. Significant delays before initial reproduction, however, might be favored in plants that are superior light competitors. Such delays in reproduction would allow a more

rapid increase in height. Increases in height can lead to exponential increases in light captured (Horn 1971), because light is often attenuated through the canopy in a negative exponential manner. Because these plants are growing in a high-nutrient but low-light habitat, these increases in light captured could give exponential increases in seed production, thus compensating for the cost of delayed reproduction.

This suggests that plants that are superior competitors for soil resources may have a higher ratio of absorptive root biomass to shoot biomass, be shorter at maturity, grow more rapidly, and reproduce at an earlier age than plants that are superior light competitors. There should be a relatively smooth gradation in these traits from one species to the next along a soil-resource:light gradient. There are other physical and biotic constraints on plants, other ways for plants to exploit nutrients and light, and thus other axes of life history differentiation. This discussion is meant to apply to species that are dominant sometime during succession. It suggests that the negative correlation between the availability of a limiting soil resource and the availability of light at the soil surface may represent a major axis for life history differentiation in plants.

Secondary Succession

In a recent review, McIntosh (1981, p. 20) stated that "virtually all current discussion of succession considers only secondary succession," and that the current models of succession "advocate a population-based approach emphasizing life history attributes of organisms . . . as the essential basis of a modern theory of succession" (p. 11). The resource-ratio hypothesis was devised for both primary and secondary successions. Because secondary successions often occur on nutrient-rich soils, it is likely that there will be rapid changes in the availability of both light and soil resources during the early stages of secondary succession. If these rapid changes were ignored and it were assumed that plant communities tended toward equilibrium at all points along the resource trajectory, early successional species, such as species A and B of figure 4B, could never be dominant during secondary succession on rich sites. This can be seen by noting that the resource-supply trajectory for a rich soil (fig. 4B) does not include the types of habitats in which species A and B are superior competitors. Many cases of secondary succession on rich soils, however, have a species sequence which includes initial dominance by such early successional species, with a rapid replacement of these species by later successional species. Under what circumstance might a dynamic solution of the resource-ratio hypothesis predict this pattern for secondary succession on a rich soil?

The isoclines and regions of coexistence in figure 4 describe equilibrium conditions. Many different dynamic models can lead to these same equilibria, but approach the equilibria quite differently. Two such models, both giving identical isoclines and regions of coexistence (those shown in fig. 4), are given in the Appendix. The solutions to these two models, obtained numerically, are given in figure 5. Both are models of competition for nitrogen and light and both make identical equilibrium predictions, but they differ in the maximal growth rates used
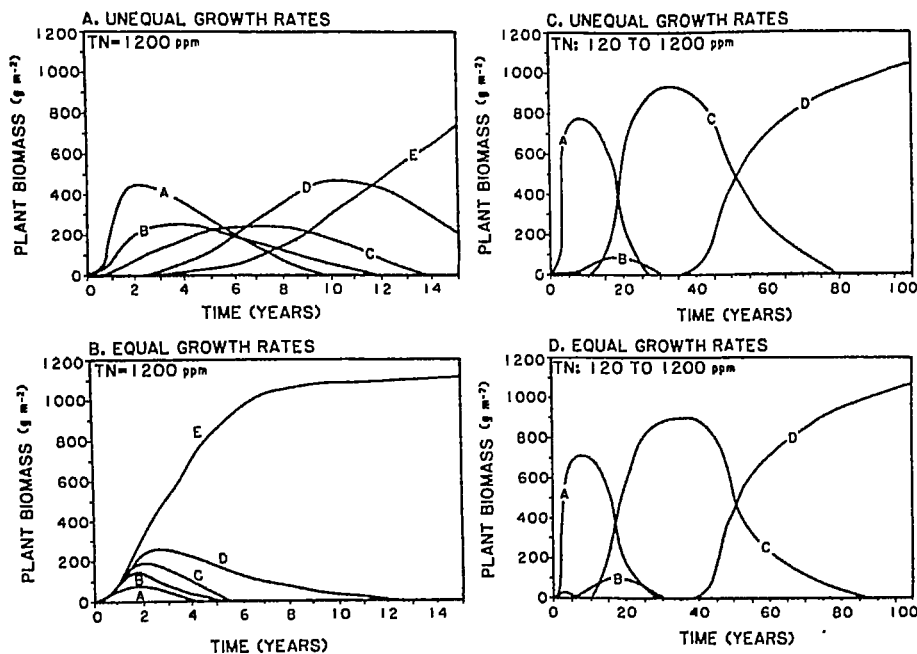
Fig. 5.—A, B, For secondary succession on nutrient-rich soils (total nitrogen = TN = 1200 ppm; see Appendix), successional sequence is highly dependent on the maximal growth rates of the plants. If, as in A, the species that are superior nutrient competitors (species A and B) have greater maximal growth rates, the secondary successional sequence is similar to the primary successional sequence (given in fig. 5C) of this figure. If, as in fig. 5B, the growth rates of all species are equal, the superior light competitor, species E, is dominant from the start, and early successional species are never dominant in the secondary succession. C, D, For secondary succession on poor soils, the successional sequence is similar whether or not the species have equal growth rates (D) or unequal growth rates (D). Note that the time scale for C and D is much longer than for A and B. Theory predicts rapid succession on rich soils.

for species A to E. For the "equal growth rates" model, all species had the same maximal (resource-saturated) rate of weight gain per unit weight. For the "unequal growth rates" model, species A, the superior competitor for nitrogen, had the highest maximal rate of weight gain, followed by species B, C, D, and then E, which had the lowest maximal rate of weight gain. For the unequal growth rates case, the growth rates of the plants changed along the nitrogen:light gradient as predicted by the preceding discussion of life history evolution. Two cases are shown for each model. In one case, total soil nitrogen increased from low to high levels (from 120 ppm to 1200 ppm) over a period of 100 yr, mimicking secondary succession on a poor soil. In the other case, soil nitrogen was high from the beginning, mimicking secondary succession on a rich soil. All species were assumed to be equally capable of colonizing the disturbed area, all being present in the same initial densities at the start of succession.

The numerical solutions show that during secondary succession on poor soils,

the dynamics of species replacement are essentially identical whether the species have equal or unequal growth rates (figs. 5C, 5D). For secondary succession on rich soils, however, very different population dynamics are predicted by the model with equal growth rates than by the model with unequal growth rates (figs. 5A, 5B). In both cases, the eventual equilibrium outcome is identical. Species E, the superior competitor for light, displaces all the other species. If the maximal growth rates of all species are equal, species E is always the dominant species. It rapidly displaces the other four species (fig. 5B). If the species have unequal maximal growth rates, there is a long period during which species A through D are dominant, even though they cannot coexist in the community at equilibrium (fig. 5A). Their dominance through the first 11 yr of these simulations is a transient response caused by their maximal growth rates being greater than that of species E, which is the superior competitor for the conditions.

The results in figure 5 suggest that the similarity of the species sequence observed in primary succession to that in secondary succession on rich soils could be caused by the life history traits, especially maximal growth rates, which plants have evolved for different points along the soil-resource:light gradient. For primary succession, the predicted population dynamics of the species can be closely approximated with the simple graphical model (figs. 2C, 4A) by assuming that competition goes to equilibrium at each point along the resource-supply trajectory. For secondary succession on a rich soil, the population dynamics are not an equilibrium prediction of the model, but represent transient dynamics that are critically dependent on the maximal growth rates and resource requirements of the species. The simulations in figure 5 suggest that the transient dynamics of secondary succession will be similar to, but much faster than, the dynamics of primary succession if early successional species have a higher maximal rate of weight gain than late successional species. In contrast, the assumption of higher growth rates for early successional species is of little importance during the much slower secondary succession on a nutrient-poor soil (cf. figs. 5C and 5D).

Retrogressive Succession

Although many successional sequences are often approximated as being a pattern of directional change, at least for the first 100 or 200 yr, it has long been recognized that some successions are not directional (e.g., Gleason 1927; Whittaker 1953). One of the better studied "retrogressive" successions occurs on the Cooloola sand dunes of eastern Australia (Walker et al. 1981). These Quaternary dunes, which have not been subject to recent glaciations, form a chronosequence of six dune-systems ranging in age from ca. 6,000 to ca. 400,000 yr since deposition. From the youngest to the oldest dunes in this chronosequence, the vegetation goes from being a grassland with dwarf trees (*Callistris columellaris*) to a grassland with tall trees (*Banksia serrata, Casuarina littoralis, Casuarina torulosa, Eucalyptus intermedia*), to a closed canopy forest with 30-m-tall trees, to a tree-shrub association, and then, on the oldest sites, to a shrub and dwarf tree (*B. aemula, E. signata*) association (Walker et al. 1981). Within this 400,000-yr chronosequence, there is a period of increase both in total aboveground plant

biomass and in the height at maturity of the dominant species. This is followed by a period of decline in both of these (the "retrogression"). These periods of increase and decrease are paralleled by the pattern of soil development and leaching. For the initial ca. 30,000 yr of this chronosequence, soil phosphorus and calcium levels increase in the A1 and A2 horizons and light intensity at the soil surface decreases. The continual downward movement of phosphorus and calcium via leaching, coupled with low rates of atmospheric input, however, leads to decreases in their availabilities in the upper 6 m of soil after ca. 100,000 yr post deposition. The "retrogression" of the vegetation toward dwarf trees and shrubs corresponds with marked decreases in the availability of phosphorus and calcium and increased light penetration. This suggests that retrogressive succession may result from a resource-supply trajectory that forms a U or a "loop." Further experimental work is needed in the Cooloola dunes to determine what the limiting resources are at different times during the chronosequence and how the supply rates of the limiting resources change through time.

COMPARISON WITH OTHER THEORIES

Peet and Christensen (1980) mention four main groups of alternative approaches to succession: (1) the facilitation hypothesis (Clements 1916); (2) succession as a gradient in time (Drury and Nisbet 1971, 1973; Pickett 1976); (3) the differential-longevity hypothesis (Egler 1954); and (4) stochastic (often Markovian) models of plant replacement (Horn 1971, 1975; Van Hulst 1979). These approaches share many elements, but differ in some important aspects. The basic outline for all of them is the general theory of succession proposed by Clements (1916). Clements visualized succession as depending on the type of disturbance, the dispersal abilities of the species, the abilities of the species to establish and grow given the constraints of the physical environment, how the species modify the physical environment, and the competitive interactions among the species. MacMahon (1981) asserted that Clements' processes, when expressed in this general way, are sufficient to describe succession. Different approaches to succession, however, emphasize different steps in this sequence as being of overriding importance or invoke different mechanisms for a given step.

Many have objected to Clements' assertion that early successional species modify the habitat in ways that harm themselves but favor other species. This has been called the facilitation hypothesis of succession (Connell and Slatyer 1977; Peet and Christensen 1980). Because experimental removals of early successional species have shown strong competition, not facilitation, among the annuals and the perennials that replace them during succession (McCormick 1968 cited in Hils and Vankat 1982; Abul-Fatih and Bazzaz 1979; Hils and Vankat 1982), the facilitation hypothesis has been rejected by many (Peet and Christensen 1980). The resource-ratio hypothesis assumes that all species compete for limiting resources, and is thus consistent with the results of the species-removal experiments. It is similar to Clements' theory, however, in that it stresses the importance of changes in the environment, specifically, in the relative supply rates of limiting resources. Unlike the facilitation hypothesis, these changes in resource-supply rates are not

assumed to be under the direct control of the photosynthetic plants. The soil properties leading to changes in the supply rates of limiting soil resources result from numerous biogeochemical processes. Models of soil dynamics (e.g., Cole et al. 1978; McGill et al. 1981; Coleman et al. 1983) include atmospheric nutrient inputs, inputs of organic compounds containing mineral nutrients from plants, and modification of these by members of the decomposer community. The decomposer species eventually, and indirectly, create the refractory organic compounds which, with the parent material, compose the soil. Thus, the trajectories of soil resources are an evolutionary *indirect* result of growth by early successional plants. The resource-ratio hypothesis does not include any direct facilitation, i.e., it is not a model of autogenic succession.

The resource-ratio hypothesis shares the view of Drury and Nisbet (1971, 1973), Pickett (1976), and others that much of the pattern of succession can be understood as a gradient through time. It is a reductionist, population-based approach to succession. The resource-ratio hypothesis is more explicit than these preceding papers in stating the factors changing through time and how such changes lead to species replacements. Pickett (1976) suggested that much of the pattern of secondary succession might result from life history attributes that plants had evolved along major environmental gradients. In this paper, I have suggested that different soil-resource:light levels represent a major gradient along which the life histories of plants have differentiated and that the initial dynamics of secondary succession on rich soils may reflect mainly these life history differences.

Egler (1954, 1976) and others have discussed the possibility that the dynamics of secondary successions may reflect merely differential longevity of species. Their approach assumes that each individual inhibits all others by holding onto its site, and that succession occurs as short-lived plants are replaced by long-lived plants. It has been called the "inhibition hypothesis" by Connell and Slatyer (1977). Although the resource-ratio hypothesis includes inhibition, the process of species replacement is assumed to depend on plants' competitive abilities for limiting resources, not on their life spans. The differential-longevity hypothesis seems to suggest that succession should always lead to dominance by the longest-lived plants. The discussion of the evolution of life history traits along a soil-resource:light gradient suggested that later successional plants should be taller, slower growing, and later to reproduce. Although these traits may lead them to have longer life spans, the resource-ratio hypothesis does not predict that all successions should end in dominance by the longest-lived or tallest plants, but that the composition of the local plant community should be determined by the relative supply rates of the limiting resources. Marks' (1983) review supports the resource-ratio hypothesis, but not the differential-longevity hypothesis, because it suggests that there are persistent regions of early successional species in open, marginal habitats.

Horn (1971, 1975, 1976), Van Hulst (1979), and others have developed probabilistic models of succession as a plant-by-plant replacement process. One of the appeals of Markovian models is that they emphasize the stochasticity often observed in plant communities. For these models, it is necessary to derive the transition probabilities from observations at each site. Markov models are thus

more descriptive than mechanistic. It would be possible, however, to use more mechanistic models, such as the resource-ratio hypothesis, to predict the transition probabilities of the Markov model and their dependence on characteristics of a site. Another group of models that Peet and Christensen (1980) included as "stochastic" are the light-gap replacement simulations of succession (e.g., Botkin et al. 1972; Shugart and West 1977; Botkin 1981; Shugart et al. 1981). These complex simulation models include numerous life history traits that influence how well plants compete in a patchy (light-gap) environment. The main difference between these simulation models and the model presented in this paper is simplicity. Perhaps complex models will be needed to predict the pattern of succession. It may be, however, that simple models, such as the resource-ratio hypothesis, can encompass the predictable elements of succession.

CONCLUSIONS

The resource-ratio hypothesis offers many opportunities for falsification because it makes many interdependent predictions. If it is correct, there should be the same qualitative separation and ordering of species along a spatial resource-ratio gradient as is observed along the comparable temporal resource-ratio gradient of succession. It is predicted that the order of the species depends on the requirements of the species for limiting resources and the availabilities of the resources, as illustrated in figures 4 and 5. These requirements can be determined by controlled, single-species, resource-limited growth experiments. Additionally, the outcome of competition under controlled conditions should be determined by the relative availability of limiting resources in a manner consistent with both the resource requirements of the species and their distributions along natural gradients. Also, the addition or removal of limiting resources in natural communities should lead to long-term changes in the composition of the community, consistent with both the observed pattern of natural variation in mature vegetation and with predictions based on the requirements of the species for these limiting resources. The short-term dynamics of change in response to such perturbations may be quite different, but should be consistent with the predictions of the dynamic model (as in fig. 5 and the Appendix). The theory, as formulated, can be rejected if any of these interrelated predictions is not supported by observational or experimental evidence.

In its most general form, the resource-ratio hypothesis states that plant species are specialized on different proportions of limiting resources and that the composition of a plant community should change whenever the relative availability of the limiting resources changes. Whatever the factors, be they herbivory, limiting resources, or limiting factors (*sensu* Levin 1970), if species are differentiated in their responses to them, and if the relative importance of these factors changes through time, succession will result. Now terrestrial plant ecologists need to identify experimentally the important environmental and biotic factors and determine if changes in these can explain the patterns observed in primary succession, secondary succession, and mature vegetation.

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SUMMARY

The resource-ratio hypothesis assumes that each plant species is a superior competitor for a particular proportion of the limiting resources and predicts that community composition should change whenever the relative availability of two or more limiting resources changes. It is suggested that (1) the major limiting resources for mesic terrestrial habitats are often a soil resource, especially nitrogen, and light; (2) these resources are naturally inversely related, the habitats with poor soils having high-light availability and the habitats with rich soils having low-light availability; (3) the life history of a plant should depend on the point along the soil-resource:light gradient at which the plant is a superior competitor; and (4) primary succession and secondary succession on poor soils result from a temporal gradient in the relative availabilities of a limiting soil resource and light. If, as hypothesized, plants specialized on low-nutrient habitats are relatively short in height, short-lived, and fast growing, and if they reproduce early in life compared to plants dominant when light at the soil surface is limiting, these life history differences could explain the similarity of secondary succession on rich soils to primary succession and secondary succession on poor soils.

APPENDIX

DYNAMIC MODELS OF RESOURCE COMPETITION

COMPETITION FOR ESSENTIAL RESOURCES

The model of competition for two essential resources used to predict the dynamics shown in fig. 3 assumed that the specific rate of weight gain, dW/Wdt, of each species was a Monod (hyperbolic) function (Tilman 1977, 1982) of resource availability and that resources were supplied as in eq. (1) in the text. Thus, in its general form, the model was as follows:

$$dW_i/W_i dt = \underset{j=1,m}{\text{MIN}} [r_i R_j/(R_j + K_{i,j})] - D_i W_i$$

$$dR_j/dt = a_j(S_j - R_j) - \sum_{i=1}^{n} Q_{i,j}(dW_i/dt)$$

where subscript i ranges from 1 to n, the total number of species; subscript j ranges from 1 to m, the total number of limiting essential resources; W_i is the biomass per unit area, r_i the maximal specific rate of weight gain, and D_i the specific rate of weight loss (i.e., herbivory) for species i; $K_{i,j}$ is the half-saturation constant, and $Q_{i,j}$ is the amount of resource

consumed per unit biomass of species i for resource j; S_j is the maximal or supply concentration, R_j is the environmental concentration or availability, and a_j is the supply rate constant for resource j.

For the numerical solutions shown in fig. 3, the parameters for the above model were chosen to give the resource-dependent isoclines and regions of coexistence shown in fig. 2. These parameters cause each of the two-species equilibrium points to be locally stable. The differences between parts A, B, C, and D of figure 2 come from the different trajectories of resource-supply points, (S_1, S_2), through time. Species 1 through 5 below are, respectively, species A to E of figs. 2 and 3. The parameters used in the simulations were $r_i = 1.1$ for all species; $K_{1,1}$ to $K_{5,1}$ were 10, 20, 30, 40, and 50; $K_{1,2}$ to $K_{5,2}$ were 50, 40, 30, 20, and 10; $Q_{1,1}$ to $Q_{5,1}$ were 0.1, 0.2, 0.3, 0.4, and 0.5; $Q_{1,2}$ to $Q_{5,2}$ were 0.5, 0.4, 0.3, 0.2, and 0.1. D_i was 0.1 time^{-1} for all species, and a_j was 0.2 for all resources. For the simulations, time ranged from 0 to 1000, with 10 iterative solutions performed per time period. This time was rescaled to correspond to the 0 to 10 scale shown in figs. 2 and 3 by division by 100.

For figs. 2A and 3A, S_1 and S_2 were chosen from a random-number table within the range from 22 to 36. The actual mean value for S_1 was 27 and for S_2 was 29. This average supply point falls in the region in which species B and C should coexist with C about 15 times more abundant than B. For figs. 2B and 3B, the supply point, (S_1, S_2), was (7, 8) at time 0 and increased linearly to (27, 35) at the end of the simulation. For figs. 2C and 3C, the supply point went from (12, 33) to (33, 12). For the case shown in both figs. 2D and 3D, the supply point went from (7, 25) to (33, 25) during the simulation.

COMPETITION FOR LIGHT AND NITROGEN

The model above was slightly modified for cases of competition for light and a limiting soil nutrient such as nitrogen. The modified version was used to give the dynamic solutions shown in fig. 5. Species 1 through 5 below are, respectively, species A through E of figs. 4 and 5. Under conditions in which a plant was limited by light, it was assumed that plant growth rates were related to L, light intensity at the soil surface, according to a Monod function, as given above. The amount of light available at the soil surface was assumed to be controlled by total aboveground plant biomass, B, such that $L = \exp(-0.0045B)$. Additionally, it was assumed that 10% of the total pool of the limiting soil nitrogen was potentially mineralizable at any given time, and that the full 10% would be available immediately following a disturbance. These parameters and the others chosen for the simulations give light attenuation, total nitrogen, and total biomass relations like those at Cedar Creek (Tilman 1983, 1984). The parameters chosen for the 5 species gave resource-dependent isoclines and regions of coexistence like those illustrated in fig. 4. This was done using two different sets of parameters, however. In one case ("equal growth rates" of figs. 5B and 5D), all species had the same maximal specific rates of weight gain, dW/Wdt. In the other case ("unequal growth rates" of figs. 5A, 5C), the species that were the best competitors for the limiting nutrient had the highest resource-saturated rates of weight gain, and these growth rates decreased progressively as species were better competitors for light. Both sets were chosen to give identical equilibrium isoclines and population densities. The parameters were as follows.

Equal growth rates.—For all species, $r_i = 0.6$. Where resource 1 is the limiting soil resource (nitrogen) and resource 2 is light, $K_{1,1}$ to $K_{5,1}$ were 5, 10, 15, 25, and 35; $K_{1,2}$ to $K_{5,2}$ were 0.15, 0.108, 0.075, 0.045, and 0.025; $Q_{1,1}$ to $Q_{5,1}$ were 0.05, 0.07, 0.1, 0.15, and 0.2; a_j was 0.2; D_i was 0.1 for all species, and $Q_{1,2}$ to $Q_{5,2}$ were not directly specified but were determined indirectly by the relation between total biomass and light penetration. For the numerical solutions, time ranged from 0 to 1000, with 10 iterations of the equations per time unit. Every 10 time units were considered to be a growing season (year).

Unequal growth rates.—The parameters for unequal growth rate cases were identical to those above except that r_1 to r_5 were 1.0, 0.7, 0.5, 0.3, and 0.2; $K_{1,1}$ to $K_{5,1}$ were 9, 12, 12, 10, 7; $K_{1,2}$ to $K_{5,2}$ were 0.27, 0.13, 0.06, 0.018, and 0.005. These parameters were chosen to

give isoclines (i.e., resource levels at which growth equals the imposed loss of 0.1) and consumption vectors identical to those for the equal growth rates case. Note that species 1, the superior competitor for nutrients, has the highest maximal rate of weight gain, whereas species 5, the superior competitor for light, has the lowest.

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