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Models, Mechanisms and Pathways of Succession

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I. Abstract

The study of succession has been hampered by the lack of a general theory. This is illustrated by confusion over basic concepts and inadequacy of certain models. This review clarifies the basic ideas of pathway, mechanism, and model in succession. Second, in order to prevent inappropriate narrowness in successional studies, we analyze the mechanistic adequacy of the most widely cited models of succession, those of Connell and Slatyer. This analysis shows that models involving a single pathway or a dominant mechanism cannot be treated as alternative, testable hypotheses. Our review shows much more mechanistic richness than allowed by these widely cited models of succession. Classification of the mechanisms of specific replacement, called for by existing models, is problematic and less valuable than the search for the actual mechanisms of particular seres. For example, the "tolerance" mechanism of succession has at least two contrasting meanings and is unlikely to be disentangled from the "inhibition" mechanism in field experiments. However, the understanding of particular species replacements through experiment and knowledge of the conditions of a particular sere and species life histories is a reasonable and desirable goal. Finally, we suggest the need for a broad mechanistic concept of succession. Thus, based on classical causes of succession that have survived recent scrutiny, we erect a framework of successional mechanisms. This framework aims at comprehensiveness, and specific mechanisms are nested within more general causes. As a result of its breadth and hierarchical structure, the framework performs two important functions: First, it provides a context for studies at specific sites and, second, is a scheme for formulating general and testable hypotheses. The review of specific successional mechanisms and the general mechanistic framework can together guide future work on succession, and may foment the development of a broad theory.

Resumen

La ausencia de una teoría general sobre la sucesión ecológica obstaculiza el logro de un mayor conocimiento en la materia, crea confusión en torno a los conceptos más fundamentales de la disciplina, y fomenta el diseño de modelos inadecuados. Esta crítica tiene como meta el aclarar conceptos fundamentales acerca de la trayectoria, el mecanismo, y el modelo de la

sucesión ecológica. En segundo lugar, intenta analizar la utilidad mecánica de los modelos de la sucesión ecológica más citados tales como el de Connell y Slatyer. Se señala por qué aquellos modelos con una trayectoria única o con un mecanismo dominante no deben considerarse como hipótesis válidas por probar. Por otra parte, se señala también la existencia de una riqueza mecánica que va más allá de lo admitido por los modelos más citados. La clasificación de los mecanismos de reemplazo esbozados en los modelos actuales causa problemas y tienen poca utilidad. El mecanismo de tolerancia durante la sucesión ecológica, por ejemplo, tiene por lo menos dos significados contrastantes, y muchas veces resulta difícil distinguir en pruebas de campo entre un mecanismo de inhibición y un mecanismo de tolerancia. Un mejor conocimiento del reemplazo de una especie—mediante la experimentación, conocimiento de las condiciones conducentes a la sucesión ecológica y del largo de vida de la especie—no obstante, sigue siendo una meta razonable y legítima. Se subraya la necesidad de un concepto mecánico de la sucesión ecológica más abarcador y se propone un marco de referencia para los mecanismos de la sucesión ecológica que toma en cuenta las causas clásicas de la sucesión ecológica más escudriñadas. Este marco de referencia desempeña dos funciones importantes: provee una estructura para el estudio de lugares específicos, y provee un esquema para la formulación de hipótesis generales por probar. Esta crítica tiene también como meta el servir como guía para futuros trabajos en la disciplina que fomenten el diseño de teorías generales de la sucesión ecológica.

II. Introduction

The study of succession, though central to plant ecology, has proven difficult (McIntosh, 1974, 1980). A number of factors may have contributed to this. First, although there is much information available on patterns of succession, there is currently no general theory to organize this information and to relate pattern and mechanisms. Second, the basic concepts required to focus successional study are poorly articulated. Third, the models that have been recently proposed, in an attempt to stimulate study of mechanisms and organize that information, are of limited scope or are poorly used in the literature.

No paper of moderate length could fully correct these lapses. Additional observations and experiments on succession are also required. However, raising the issues and reviewing the literature that addresses these problems can indicate the state of the discipline, and encourage further work toward remedying the lapses. While the time may not yet be ripe for the elaboration of a complete theory of succession and vegetation dynamics,

this review and analysis can advance that goal. In order to focus this undertaking, we orient our review around the influential paper by Connell and Slatyer (1977). The problems suggested by that paper or by its use by other investigators, illustrate the three lacunae in the study of succession.

The purposes of this paper are 1) to clarify conceptual and terminological problems concerning models and mechanisms of succession, 2) to demonstrate with examples from various successional studies the limits of the Connell and Slatyer (1977, hereafter C + S) models as alternative, testable hypotheses, and 3) to introduce a general, inclusive mechanistic framework for future studies of succession, a need emphasized by Finegan (1984).

III. Limitations of the Connell and Slatyer Models

In attempting to fill the need for a theoretical context in succession studies, Connell and Slatyer (1977) proposed that mechanisms of succession could be incorporated into three alternative, testable models: facilitation, inhibition, and tolerance (Table I). Facilitation is the Clementsian model of relay floristics (Egler, 1954) whereby early successional species modify their environment and facilitate the establishment of later successional species. According to the inhibition model, the initial invaders (Egler, 1954) regulate succession so that later successional species cannot invade and grow in the presence of healthy, undamaged early successional species. In the tolerance model, floristic changes may be a function of differential life history traits and the differential ability of late successional species to tolerate initial environmental conditions. To review the literature that addresses these models, evaluate the adequacy of the models and ultimately generate a broad framework of mechanisms of succession, we will first define three fundamental concepts: pathway, mechanism, and model. Then we will discuss the application of the Connell and Slatyer models to complex seres. Finally, we will discuss the testability of the models.

A. FUNDAMENTAL CONCEPTS

- (1) A successional pathway is the temporal pattern of vegetation change. It can show the change in community types with time, the series of system states, or describe the increase and decrease of particular species populations. A complex successional pathway from the Lake Michigan dune succession (Olson, 1958) serves as an example (Fig. 1).
- (2) A mechanism of succession is an interaction that contributes to successional change. A mechanism is an "efficient cause" in the Aristotelian sense.

Table I
Abstract of the Connell and Slatyer (1977) models of successional mechanisms^a

Step	Facilitation	Tolerance	Inhibition
A. Disturbance	Open site	Open site	Open site
B. Establishment	Only early species	Any species	Any species
C. Recruitment of later species	Early species disfavored	Early species disfavored	All recruitment disfavored
	Later species favored	No impact on later species	
D. Growth of later species	Later species favored	Later species grow in spite of earlier species	All subsequent invaders inhibited
E. Continuation	As above until no environmental change	As above until no more tolerant species available	No change in intact community
F. Change only with disturbance ^b	To A	To A	To A

^a The steps of each model are sequential. Disturbance can interrupt the process at any point, but is indicated here only at step F.

^b Specific site and species pool determines disturbance effects in all models.

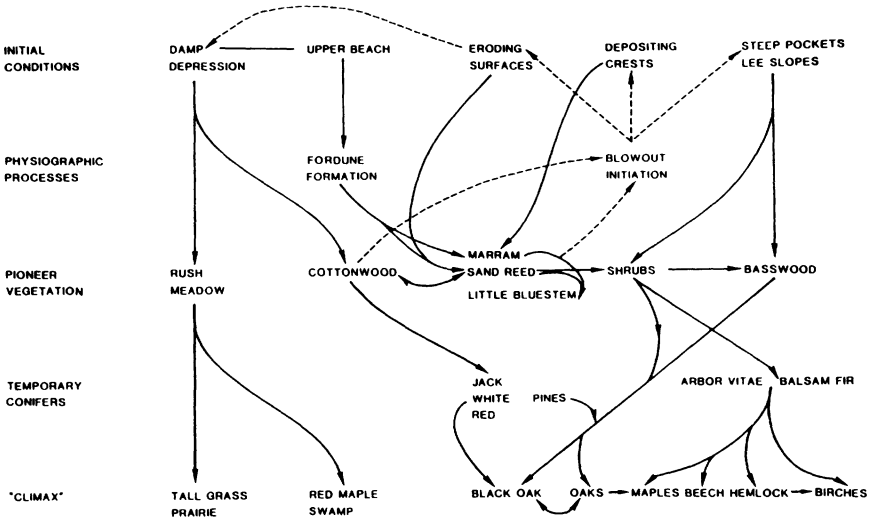


Fig. 1. Alternative successional pathways on the Lake Michigan Dunes. Except for the physiographic processes, no mechanisms are included. From Olson, 1958.

Which specific interaction will be called a mechanism depends on the level of organization addressed. At the community level, a mechanism of turnover in succession can be a general ecological process or interaction (e.g., competition, predation, establishment). As mechanisms of change in a community, facilitation, tolerance and inhibition fit this description. However, these mechanisms can also be addressed at lower levels of organization. For example, the interaction of inhibition may be subdivided into more detailed mechanisms that encompass the specific environmental resource and stress levels, the physiology of nutrient uptake and resource allocation by the interacting plants, and their resultant architectural and reproductive status. In studies where both levels of organization must be addressed, we suggest that the two corresponding levels of mechanism be differentiated. The most easily understood and least ambiguous way to do this is to specify the level of organization under discussion. In this paper we will need to speak of mechanisms in both general and specific senses.

- (3) A model of succession is a conceptual construct to explain successional pathways by combining various mechanisms and specifying the relationship among the mechanisms and the various "stages" of the pathway. To illustrate, we reproduce a schematic general model of succession (Fig. 2), devised by MacMahon (1980), which is applicable to many natural systems. These constructs can have verbal, diagrammatic, or quantitative forms.

S models to specific field situations. The first question is whether the individual C + S models account for the variety of successional pathways encountered in the literature. Although Connell and Slatyer did not address explicitly the multiplicity of successional pathways, their presentation of each model as the repeated operation of a mechanism implies a particular pathway. The facilitation model implies a linear, obligatory succession of stages (Fig. 3a). The tolerance model also implies a linear pathway, but the earlier stages may not be obligatory. Finally, the inhibition model implies a pathway that depends on the frequency of disturbance. If disturbance of high frequency (between steps D and E in Table I) occurs, the resultant pathway will resemble Horn's (1981) synchronous, large scale, chronic disturbance type (Fig. 3c). Alternatively, if disturbance occurs at a lower frequency (after step F in Table I), then an asynchronous, small scale, chronic disturbance pathway (Fig. 3b) is suggested.

The implied linkage of each C + S model with a specific pathway results in two problems. One is that the variety of pathways found in nature is larger than the range suggested by a literal reading of the C + S models (Fig. 3, e.g., Horn, 1981; McCormick, 1968; Shafi & Yarranton, 1973). Second, actual successions may exhibit complex combinations of pathways, as shown by Horn's (1981) competitive hierarchy (Fig. 3d). This complexity makes it unlikely that the C + S models will represent the entirety of many successions. To be sure, there is nothing in Connell and Slatyer's concepts that prevents combining various of their mechanisms in the study of an actual sere. Indeed some statements indicate that Connell and Slatyer intended combining mechanisms:

[T]he mechanisms of model 1 apply in the early stages of colonization of very rigorous extreme environments. Whether this model applies to replacements at later stages of terrestrial succession remains to be seen. . . . (1977, p. 1124)

[T]he first alternative (models 1 and 2 rejected) seems to apply to many forests in the intermediate stages of succession. (1977, p. 1127)

On the other hand, other of their statements suggest that a single model might, in some circumstances, apply to an entire succession:

The mechanisms of the facilitation model probably apply to most heterotrophic successions. . . . (1977, p. 1124)

It [facilitation] should apply to many primary successions. . . . (1977, p. 1127)

The three models of succession described earlier are based on three quite different views of the way ecological communities are organized. (1977, p. 1136)

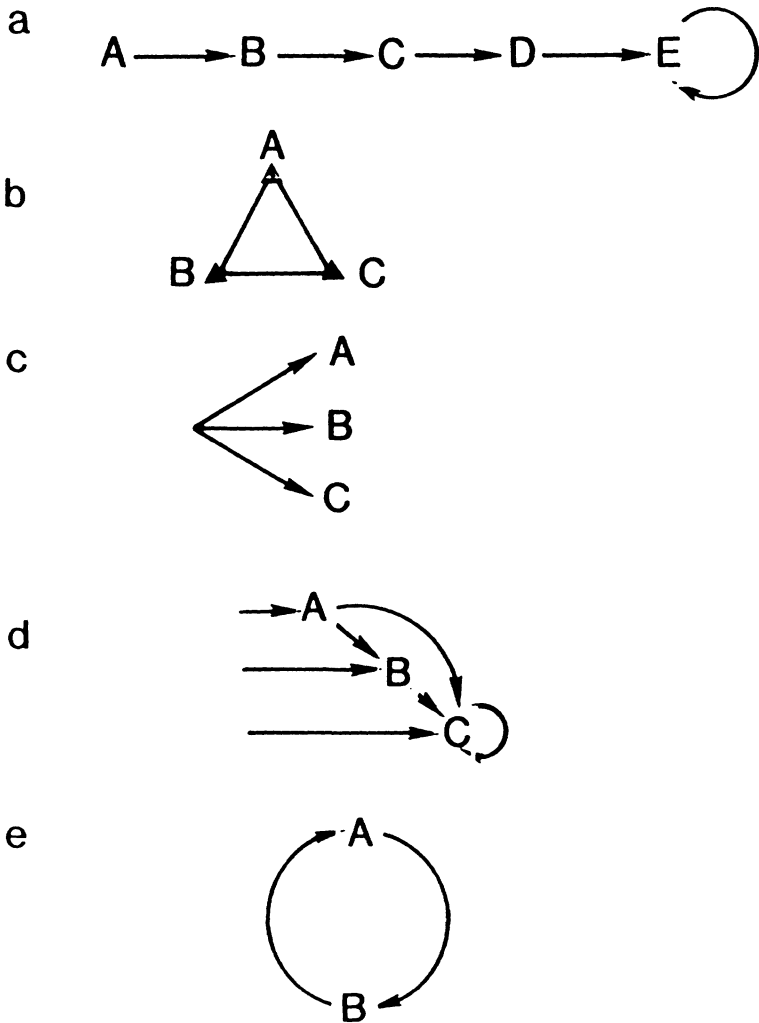


Fig. 3. Generalized successional pathways abstracted from referenced sources. a. Directional change with termination (McCormick, 1968). b. Chronic disturbance, asynchronous and small scale (Horn, 1981). c. Chronic disturbance, synchronous and large scale (Horn, 1981). d. Competitive hierarchy (Horn, 1981). e. Cyclic (Miles, 1979). A, B, C, D, and E represent different plant species. Real successions may be composed of combinations of these simplified pathways. In some original sources for these pathways, mechanisms were implied or stated; thus some are the graphic basis of models in the originals. Here, however, we represent them as pathways only.

Given the immense variety of actual successional pathways, it is advisable to recognize that particular mechanisms and pathways are not bound to one another. Rather, C + S mechanisms and models account for specific transitions within a sere.

The second question is whether the C + S models account for the full range of successional causes. Recognition of complexity in causality is required to answer this question. Causality can be construed in both broad (explanatory) and narrow (agent and effect) senses (Kuhn, 1977). Clements (1916) appears to have used both broad and narrow senses of causality in constructing his general classification of successional causes. Clements' (1916) mechanistic scheme is sufficiently broad to still be useful (MacMahon, 1980, 1981; Miles, 1979). There are no specific mechanisms, either demonstrated or possible, that cannot be incorporated within that scheme. Furthermore, the scheme is ordered, exposing the expected temporal sequence of interactions. We use that scheme to ask whether the C + S models address the entire range of causes that contemporary workers (Miles, 1979) have recognized.

The processes defined by Clements are

- (1) *nudation*, which is the removal of vegetation by disturbance on a site in which succession can occur,
- (2) *migration*, arrival of organisms at the open site,
- (3) *ecesis*, the establishment of organisms in the site,
- (4) *competition*, the interaction of organisms at the site, and
- (5) *reaction*, the alteration of the site by the organisms.

Here we omit "stabilization," Clements' "final cause," because it is a *result* of the other five causes, and because it reflects Clements' belief that succession was the development of a superorganismic climax vegetation. In this omission, we accept the arguments of Gleason (1917), Cooper (1926), Tansley (1935) and Whittaker (1951). Furthermore, we recognize that "competition" is not the only sort of interaction of interest.

Not all of Clements' categories of cause are variables that allow discrimination among the C + S models, though all receive some mention (Table II). The *nature* of the disturbance (size, severity, seasonality, relation to climatic cycles, isolation in space from other disturbances), is not discussed as a factor differentiating the models. It is evaluated relative to community stability. A brief mention of migration (propagule source, agents, residual propagules) is made in Connell and Slatyer's table 1. These omissions might cause the models to be inapplicable, either to a particular succession, or for comparing seres (see also Botkin, 1981). Of the Clementsian causes, the emphasis in the C + S models is on *ecesis*, *competition* and *reaction*. For example, whether early or late successional species have different competitive abilities, or whether site occupancy is a result of preemption is a critical switch in the C + S models. Likewise, whether or not establishment of later species depends on environmental modification by earlier species is critical. Whether later successional species establish immediately after disturbance is also a differentiating process

Table II

Correspondence of Clementsian "causes" of succession with aspects of Connell and Slatyer's (1977) models. F = facilitation, T = tolerance, I = inhibition

Clementsian causes	Level in Connell and Slatyer models ^a	Allows differentiation of model ^b			Considered as a variable in models?
		F	T	I	
Nudation	A, F	-	-	-	No
Migration	B, F	-	-	-	No
Ecesis	B	+	-	-	Yes
Competition	D	-	-	+	Yes
Reaction	C, D	+	-	+	Yes
Stabilization ^c					Irrelevant

^a Refer to Table I.

^b A "+" indicates that a particular Clementsian cause applies to one of the Connell and Slatyer models, a "-", that it does not apply.

^c Omitted from consideration for reasons given in text.

between facilitation and the other two C + S models, while the nature of reaction and competition appear to discriminate between tolerance and inhibition (Table II).

Each C + S model allows only one mechanism (*sensu stricto*) of succession (including both competition and reaction of Clements). For example, in stage D of the diagram of the C + S model (Table I), the facilitation model allows only environmental amelioration for later species, the tolerance model allows environmental alteration but with no effect on later species, and the inhibition model allows only competitive suppression, by whatever species are present, of subsequent colonists. It is quite likely, however, that actual seres show some combination of these mechanisms (Finegan, 1984). We review examples later in the paper.

C. TESTABILITY OF THE MODELS

Connell and Slatyer present the three models as testable alternatives. The models have been used in that way in both experimental and descriptive studies (e.g., Armesto & Pickett, 1986; Debussche et al., 1982; Glasser, 1982; Harris et al., 1984; Hils & Vankat, 1982; Houssard et al., 1980; del Moral, 1983; Sousa, 1984; Turner, 1983). Quinn and Dunham (1983) present a theoretical analysis of the testability of C + S models as they are most often construed in the literature. The existence of intransitive competitive relationships, indirect interactions among species within a sere, and species-specific mechanisms of interaction, may all mitigate against the models being clearly differentiable alternatives (Botkin, 1981; Quinn & Dunham, 1983). They can serve as testable hypotheses of the

mechanism of particular species replacements, but cannot explain the multispecies sequences that succession often entails. Because, as Quinn and Dunham (1983) among others (e.g., Clements, 1916; Miles, 1979) note, succession is a multifactored process, the use of univariate tests between alternative causes and effects is likely to be ineffective (see also Hilborn & Stearns, 1982). Quinn and Dunham (1983) propose a multivariate approach to understanding such ecological processes as succession. Our hierarchical scheme of successional causes, presented in Section V, can serve as a framework for such multivariate, mechanistic studies.

An additional problem in applying C + S models as testable alternatives is using the tolerance model as a null hypothesis (e.g., Quinn & Dunham, 1983). Because the tolerance model cannot be discriminated from the other two by the unique action of any Clementsian process (Table II) it may appear to be a neutral model. A problem with tolerance as a null model appears in the work of Hils and Vankat (1982). They could not differentiate between tolerance and inhibition models based on their community-wide experiments. Assuming adequate statistical design of the experiment, additional work on demography of the interacting species or on resource levels and use, would be required to discriminate between mechanisms of tolerance and inhibition. For instance, adding a late successional species to an early successional community (e.g., McDonnell & Stiles, 1982) may affect dispersers or herbivores and influence the appearance, density or growth of other species. A removal or addition experiment focused on the phenomenon at the level of the community could not discern such complicating effects. Thus, tolerance should not be used as a null model. In addition, C + S tolerance might be erroneously accepted because some interaction not exposed by the model is acting in a *sere*. An extreme and inappropriate statement of the view that tolerance is a null model, is that tolerance is a "neutral mechanism" of succession (Harris et al., 1984). It is more valuable to refer to a mechanism as acting or not in a particular situation, rather than being inherently neutral. Later we give other reasons for eschewing the view of tolerance as a null model.

D. SECTION SUMMARY

Along with their clear value (e.g., stimulation of experimental and mechanistic approaches and inclusion of animal effects), the models of Connell and Slatyer (1977) have some inherent limitations, which have not been recognized in various applications. The meaning of "model" can be confounded with specific mechanisms or pathways. Each of the C + S models implies a subset of all possible pathways of succession. More importantly, all of the major sorts of mechanisms that act in succession, or processes that modify the mechanisms in a particular succession,

are not included as variables. The Connell and Slatyer models will not often apply to entire successional pathways but usually will be appropriate only when applied to specific mechanisms within a pathway. Finally, taking these complex models as simple hypotheses, testable for whole seres, is likely to be unproductive or misleading.

To prevent inappropriate application of the ideas, we suggest that a productive approach to understanding how succession proceeds is to focus on the specific mechanisms operating in succession, as did Connell and Slatyer, but put those mechanisms in the broader environmental and historical context that can affect their workings and outcomes. The next section reviews those mechanisms and gives examples of how they might operate.

IV. Mechanisms of Succession

Succession is fundamentally a process of (1) individual replacement and (2) a change in performance of individuals. Successional processes are essentially demographic, and have complex relations to biotic and physical environments. These processes have profound results at the level of community and ecosystem structure and function. This view of succession is an old one (Gleason, 1917), but it has been verified and effectively used to explain particular seres only rather more recently (Horn, 1974; van der Maarel, 1978; Peet & Christensen, 1980; Pickett, 1982). In order to illustrate the value and limitations of considering successional replacement in terms of facilitation, tolerance and inhibition, we present examples of these specific mechanisms in successions from several different systems. In presenting those examples we will subdivide the tolerance mechanism into passive overlap of contracting life histories and active tolerance of low resources resulting from competition.

Oldfields and mesic temperate deciduous forests provide a large number of studies of successional mechanisms. Even in these sites, however, no complete sere has been mechanistically examined. We exemplify the mechanisms of replacement using whatever cases are available. In fairness, we note that several examples postdate Connell and Slatyer's paper. There is a need to compare mechanisms in different sites and to examine the mechanisms throughout individual seres.

A. THE MECHANISM OF FACILITATION

Facilitation may operate through enhanced invasion, amelioration of environmental stress or increase in resource availability. This expands on Connell and Slatyer's (1977) conception since invasion is considered as a given in their model of facilitation. A clear example of facilitation appears in early oldfield succession at the Hutcheson Memorial Forest on

the New Jersey Piedmont. Small et al. (1971) report that survival of tree seedlings in the first year is quite low. Only with the deposition of litter on the bare soil or a persistent winter snow cover is survival of tree seedlings likely. With little or no snow cover, frost heaving kills most tree seedlings. This relationship is reflected in the high mortality of woody plants in the first few years after establishment (Pickett, 1982).

The establishment of trees in a Michigan oldfield has been found to be enhanced by a precedent species. *Rhus typhina*, a sumac, increases the survivorship of trees by thinning the dense herbaceous cover that had formerly excluded tree seedlings (Werner & Harbeck, 1982). This example illustrates a problem in applying the terms facilitation, inhibition or tolerance to whole successions. The successful establishment of trees in the herbaceous community was prevented or inhibited by the dense herb cover until *Rhus* invaded. Thus, part of the entire interaction, which involves three different life forms, is inhibitory (grass-tree seedlings), while part is facilitative (*Rhus*-tree seedlings). Labelling the entire interaction as one or the other seems fruitless. Indeed, Connell and Slatyer's step C in the facilitation model (C + S fig. 1) recognizes the compensatory trade-off between the mechanisms of facilitation and inhibition.

A similar pattern occurs in grasslands in the prairie-forest border region. In the absence of fire, woody vegetation may invade and dominate late in succession (Bragg & Hulbert, 1976; Collins & Adams, 1983). Petranka and McPherson (1979) demonstrated that the establishment and growth of tree seedlings during succession was enhanced by the presence of *Rhus copallina*. Few tree seedlings occurred in the prairie surrounding clones of *Rhus*. Within clones, tree seedlings were more abundant, light was reduced below the tolerance levels of many grass species, and nutrient levels were greater than in adjacent prairie.

Both examples of interaction among grasses, *Rhus*, and tree seedlings can be interpreted variously, depending not only on which member of the interacting pair of taxa is examined, but perhaps also on when experiments are performed (P. S. White, pers. comm.). If experimental removal of *Rhus* were to be performed after tree seedlings had overtopped the grass layer or established in the thinned sod, the *Rhus* would be labelled as an inhibitor rather than a facilitator. Altered timing of experiments might alter the interpretation of other mechanisms of turnover as well.

A species-specific example of facilitation is known to occur in North American deserts (Yeaton, 1978) where *Larrea tridentata* shrubs provide the sites for establishment of the cactus *Opuntia leptocaulis*. In arid zones, shrubs directly modify the environment beneath the canopy (MacMahon, 1981) which may provide adequate sites for establishment and growth of other species. This phenomenon of nurse plants is widely recognized in deserts (Niering et al., 1963; Turner et al., 1966) and has also been reported

to occur in Mediterranean shrublands in Chile (Fuentes et al., 1984). The early facilitation of an invader by a nurse plant often gives way to inhibition as the invader matures. This is the case in the example studied by Yeaton (1978) in which *Opuntia* eventually contributes to the demise of *Larrea*. This leads to a cyclic succession and, importantly, indicates that whether an interaction is inhibitory or facilitative depends on where in the cycle it is examined. In a similar case the tree *Cercidium microphyllum* facilitates the establishment of *Carnegiea gigantea* but the latter species eventually outcompetes and replaces its nurse plant (McAuliffe, 1984).

A final example of facilitation is the enhancement of invasion of woody species into fields by the presence of other woody occupants. The increasing importance of animal-dispersed species during post-agricultural successions is a widespread phenomenon (Bard, 1952). The role of facilitation in this trend has been documented in abandoned orchards in southern France by Debussche et al. (1982) and experimentally demonstrated by McDonnell and Stiles (1982) in Hutcheson Memorial Forest oldfields. Removal of woody stems or emplacement of artificial, branched structures altered the input of bird-disseminated seeds into fields (McDonnell & Stiles, 1982).

B. THE MECHANISM OF TOLERANCE

Discussion of tolerance is complicated because the term can be interpreted in two ways. On the one hand, it refers to the ability of an organism to endure low resource levels (Grime, 1979). On the other, it refers to successional turnover due to organisms having contrasting life histories, as when a longer-lived, slow-growing species dominates after a fast-growing, short-lived species senesces (Connell & Slatyer, 1977). We will call endurance of low resource levels the "active" mechanism of tolerance vs. the "passive" mechanism of tolerance through possession of contrasting life histories. The two interpretations are biologically related. High rates of resource use are often correlated with short life-cycle length, early maturity, and copious reproductive output (e.g., Pickett, 1976). High rates of resource use are inimical to tolerance of low levels of resource availability (Grime, 1979). Likewise, rates of resource use may be related to competitive ability, with more effective competitors outstripping the resource use of poor competitors.

This complication of the two meanings of tolerance is problematic because some users of the C + S models consider the tolerance model as a neutral meshing or complementarity through time (Fig. 4) of contrasting life histories (e.g., Harris et al., 1984). This interpretation derives from the statement (C + S, p. 1122) that "the sequence of species is determined solely by their life history characteristics." Also step D in C + S fig. 1

states that later species grow "despite the continued presence of healthy individuals of early successional species." In contrast, Connell (pers. comm.) states that Connell and Slatyer (1977) did not mean that interactions were totally absent in the tolerance model, and in fact they do generalize that late successional species can shade out early successional species.

Thus, the tolerance model can be interpreted in two alternative ways. One requires active replacement of earlier by later species through, for example, exploitation competition. This case is supported by the statement (C + S, p. 1125) that "this model specifies that later species are superior to earlier ones in exploiting resources." The second way to interpret the tolerance model resides in using the term tolerance both for the model of turnover and one of the specific mechanisms by which it occurs. This interpretation is supported by the statement (C + S, p. 1126) that "the later species simply survive in a state of 'suspended animation' until more resources are made available by the damage or death of an adjacent dominating individual." This permits interpretation of the C + S tolerance model as one of passive turnover. The contrasting active and passive connotations of the term "tolerance" must be recognized and kept separate.

In noting the two major implications of the tolerance model, a significant difference between our approach and that of C + S becomes apparent. Connell and Slatyer (p. 1122) indicate that their interests are principally in "the mechanisms that determine how new species appear later in the sequence." Earlier, we noted our concern with both how species acquire *and* yield space in succession. We prefer the more comprehensive approach as it ultimately must be employed for a complete mechanistic understanding of succession.

Several studies in Mediterranean plant communities suggest both passive and active mechanisms of tolerance occur during succession in such communities. In France, Houssard et al. (1980) report that "woody species belonging to more mature stages of succession colonize very early. . . ." This may represent the passive case. Seventy-five percent of the species of the "terminal" (late successional) community are present one year after fire in garrigue ecosystems (Trabaud & Lepart, 1980). In mallee shrublands, seedlings of late successional shrubs are abundant one year after fire, together with herbs and grasses, but the percent cover of each species changes within six years from dominance by porcupine grass to mallee shrubs (Noble et al., 1980). Porcupine grass is still abundant in old stands, suggesting that its replacement as a dominant is the passive result of increase in cover of mallee shrubs (Noble et al., 1980). At the same time, other herbs are excluded from old stands, which may be due to either interference or passive life cycle complementarity.

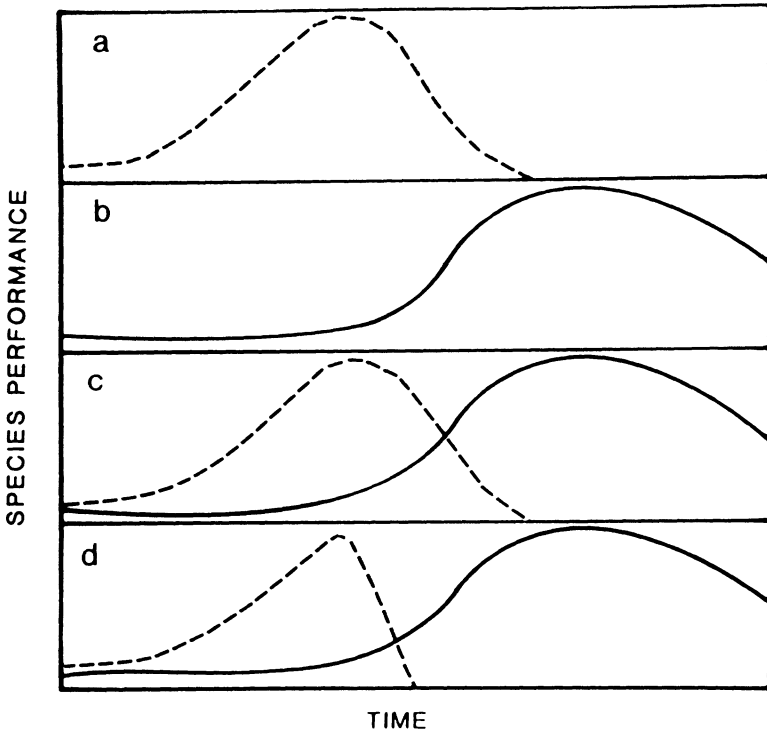


Fig. 4. Passive tolerance due to life history meshing. To clarify the definition of life history meshing, we present diagrammatic cases. a. and b. Performance of two species on the equivalent sites over time in the absence of one another. c. Performance of the two species on the same site when together. Passive meshing of life histories that differ, for whatever reason, is shown by the similarity of the performance curves of each species in panels a, b, and c. d. Successional pattern resulting in part from interaction of the two species, and in part from their inherently different life histories. The cases where both species are affected negatively or where the later species alone is negatively affected by the juxtaposition, are not shown. Conceptually, passive and active tolerance are two ends of a continuum of interaction.

Tolerance of low resource levels is an important mechanism during grassland succession. Levels of available nitrogen change during prairie succession. The $\text{NO}_3\text{-N}$ which predominates in early succession is easily leached from the soil (Rice & Pancholy, 1972) and requires more energy to exploit since it must be reduced to NH_3 . The late-successional prairie species produce significantly more biomass per unit N on $\text{NH}_4\text{-N}$ than on $\text{NO}_3\text{-N}$ (Smith & Rice, 1983). Detailed studies on permanent plots indicate that the late successional grasses *Schizachyrium scoparium* and *Andropogon gerardii* invade shortly after disturbance. Their poor performance during early succession is due, in part, to intolerance of low $\text{NH}_4\text{-N}$ availability in disturbed areas.

The replacement of pioneer trees by later successional trees in oldfields appears to be a particularly clear case of differential tolerance of resources driving successional turnover. In general, pioneer trees require higher levels of light than later successional trees (Bazzaz, 1979; Bazzaz & Carlson, 1982). Thus, seedlings of oaks (e.g., *Quercus rubra*) can survive beneath stands of pioneering *Juniperus* or *Pinus* (Bormann, 1953; Kramer & Decker, 1944; Oosting, 1942), but the seedlings of the pioneers are intolerant of any closed canopy. The same applies to beech (*Fagus grandifolia*) or maple (*Acer saccharum*) versus the pioneering oaks (Horn, 1971), and is reflected in the absence of oak regeneration beneath late-successional, mesic canopies where seedlings of the tolerant maples are present (e.g., Brewer, 1980; Miceli et al., 1977). Active tolerance may be a common mechanism of replacement because of the differential demand for nutrients (Parrish & Bazzaz, 1982a) and water (Bazzaz, 1979) of early versus late successional woody and herbaceous species. Again, however, we note that the correlation of life history length, rate of growth and resource demand complicate the interpretation of these cases.

Because the demography of pioneer stands has not often been monitored, or the causes of mortality documented, the mechanisms of turnover are not known. However, the presence of dead, or moribund pioneer trees in stands of tolerant species is common (Peet & Christensen, 1980). Coupling such observations with data on life history and ecophysiology discussed above suggests that the passive mode of tolerance does occur. Replacement results from the rapid growth and death of pioneers while the later successional species grow relatively unperturbed by the pioneer canopy [e.g., *Prunus pensylvanica* (Marks, 1974) in temperate forests and *Cecropia* (Bazzaz & Pickett, 1980) in neotropical forests].

Passive tolerance may also contribute to successional turnover because inherently contrasting life histories dovetail (Fig. 4) especially during early oldfield succession. Summer annuals dominate the first growing season after spring disturbance, while winter annuals dominate in the second. After fall abandonment, winter annuals dominate the first growing season (Bard, 1952; Keever, 1950; Raynal & Bazzaz, 1975). Similarly, life history characteristics of biennials restrict them to structural dominance of oldfield assemblages later than either winter or summer annuals. Keever (1950) reports that the replacement of early successional and shade intolerant *Aster pilosus* occurs because seedlings of larger shrubs and trees that "appear in small numbers along with the first herbaceous plants . . . continue to grow in number and size until they in turn dominate the community" (Keever, 1979, p. 307). Likewise, the replacement of the annual *Ambrosia artemisiifolia* by the biennial *Erigeron annuus* in early oldfield succession is the simple result of their different life histories (Raynal & Bazzaz, 1975), with neither facilitation nor tolerance involved, as shown experimentally by Armesto and Pickett (1986).

What is observed as life history complementarity, however, can indirectly be the product of species interaction. Early successional biennials can live for longer than two years when other species interfere with their performance (Werner, 1977). They may flower only after reaching certain thresholds of size (Gross, 1981). Peterson and Bazzaz (1978) reported that *Aster pilosus*, which normally behaves as a short-lived perennial requiring several years to flower, behaves as a biennial or even an annual when supplied with high resource levels. Research into the life histories of a number of species suggests that obligate bienniality is rare (Hart, 1977; Silvertown, 1984). Thus, what might be observed in the field to be non-interactive meshing of life histories, supportive of a tolerance mechanism, might in fact have an inhibition facet (Fig. 4). The fundamental caution here is that of complex, decomposable causality (Hilborn & Stearns, 1982). Rather than classifying mechanisms of turnover into supposedly exclusive categories, hypotheses about the use of resources, role of life cycle complementarity, and effect of endurance of low resource levels, for example, are likely to be more useful in understanding succession.

C. THE MECHANISM OF INHIBITION

Structural or competitive dominants in a community can prevent the establishment or ascendancy of later successional species, or, for that matter, species of any successional status (Connell & Slatyer, 1977). Incorporating this concept into the broad framework of succession is certainly one of the valuable contributions of Connell and Slatyer. The physiological senescence of a dominant or its death due to an acute biotic or physical disturbance may open space and free resources. The clearest and most widely documented evidence for this mechanism comes from forests. In dense mesic forests, replacement of canopy individuals most commonly occurs when some disturbance opens a gap or large patch (Brokaw, 1982; Denslow, 1980; Runkle, 1982; Veblen, 1985). Although large gaps usually favor pioneer species, most gaps in mesic forests are small, and late successional species tend to accumulate over a sequence of such disturbances (Connell & Slatyer, 1977).

In oldfields, disturbance may relieve competitive inhibition and advance succession as it does in forests. Many oldfield communities have several strata and a dense overstory that reduces light and moisture in the understory. Opening the overstory can permit the invasion of new species or enhance the growth of subordinate species in the community. The invasion of woody species is encouraged by certain thinning treatments (Armesto & Pickett, 1985). Gross and Werner (1982) have also shown successional turnover to be advanced by disturbance in oldfields. In other cases, however, depending on time and size of disturbance, earlier successional species persist in the patch (Armesto & Pickett, 1986). A

similar phenomenon occurs in grasslands where biotic and abiotic disturbances are common (Collins & Uno, 1983, 1985).

The mechanism of inhibition is a complex one. It may in fact grade into the mechanism of tolerance depending on whether the interaction is seen from the viewpoint of the incumbent or the challenger. For example, one reason that late successional species tend to accumulate over relatively long times is that their juveniles have the ability to tolerate low resource levels beneath an inhibitory overstory (Connell & Slatyer, 1977). Such tolerance should permit the accumulation of late successional canopy species to be more rapid than allowed simply by their great longevity. Even the long-lived and highly shade-tolerant species, e.g., *Fagus grandifolia*, *Tsuga canadensis*, and *Acer saccharum* require gaps to ascend into the canopy and do not simply grow slowly up through the closed canopy (Canham & Marks, 1985; Hibbs, 1982; Poulson, pers. comm.).

Inhibitory chemical substances have been found in many shrub species of chaparral communities in California (Halligan, 1975; Muller et al., 1964). These substances may play a role in maintaining the dominance of shrubs and restricting annual herbs to the early stages of succession after fire. Their real importance in arresting vegetational change is still controversial (Bartholomew, 1970). Overstory-understory relationships in sclerophyllous vegetation appear to constitute the best examples of inhibitory effects. Gradual exclusion of understory species seems to occur as a result of the sequestering of nutrients by shrubs (Kruger, 1983). Cycles of vegetational change are thus related to senescence of overstory species, and confound inhibition with passive tolerance.

An additional axis of gradation between inhibition and tolerance mechanisms lies in the variety of modes of disturbance not considered as variables in the C + S models (Table II). Disturbance is commonly defined as an event that destroys biomass (Grime, 1979), and alters community structure and resource availability (Bazzaz, 1983; White & Pickett, 1985). The result is the same whether the disturbance is caused by a physical event originating outside the assemblage, or is caused by a biotic interaction involving resident predators or herbivores, or is caused by the senescence of dominant individuals. The division between "autogenic" and "allogenic" processes is artificial (Miles, 1979). Successional turnover can be due to physiological senescence of the dominant or to some physical or biotic disturbance independent of the life history of the dominants. According to C + S models, the first case would be labelled as tolerance, while the second would be a clear case of inhibition. Furthermore, physical disturbance events may have different effects on the community depending on whether the dominant(s) is in a senescent or moribund state. In such cases, it would be difficult to assign the turnover to either active or passive tolerance or to inhibition. The common recognition of alternating

phases of stand deterioration and stand or canopy consolidation (Bormann & Likens, 1979; Odum, 1960; Oliver, 1981; Peet & Christensen, 1980) suggests that the interaction of individual life cycles and disturbance may be a common but periodic one in succession. This further suggests that a single species may participate in different types of turnover mechanisms depending on its own life history, the condition of its neighbors, the presence and tolerance of competitors, and the disturbance regime, among other factors. For example, the invasion of *Aster* species may be the result of their own life history patterns meshing with those of prior dominants (Keever, 1950), while their demise may be the result of their being overtopped by more tolerant, woody species, or taller herbs (Pickett, 1982).

D. GENERALIZATIONS ABOUT MECHANISMS OF REPLACEMENT

The examples of successional mechanisms drawn from oldfields, forests, grasslands and shrublands suggest some cautions in the use of the C + S models and support several generalizations. (1) One succession may exhibit several mechanisms. Thus, a single sere cannot be characterized by one mechanism and [to the extent that Connell and Slatyer's (1977) models imply a link of specific mechanisms with a specific pathway] neither can single C + S models apply to a sere. (2) Different mechanisms of replacement may act in one sere at a given time. (3) One species can participate in several mechanisms, depending on competitive rank and which portion of the sere is under examination. (4) The mechanisms can be discriminated only by determining demographic and ecophysiological causes of turnover. Both experimentation and observation will be required but simple species removal or addition experiments may not be readily interpretable in terms of the three conceptually distinct mechanisms. (5) Coordinated work is needed on environmental change and the demography and ecophysiology of successional turnover.

Because the terms facilitation, tolerance, and inhibition are useful in describing particular interactions in a sere, as intended by Connell and Slatyer, and in emphasizing that succession proceeds by a variety of modes of turnover, they should be restricted to describing particular replacements of species in succession. The limitations of the Connell and Slatyer models, and the difficulty of discriminating the three types of mechanism, exposed in this review, suggests a different approach. Understanding how succession as a whole occurs would be best served by addressing the specific array of mechanisms and circumstances acting at a time and place rather than by dividing that suite into classes (see also Finegan, 1984 and Breitburg, 1985). In the next section, we present a framework for examining the mechanisms of succession. The models of Connell and Slatyer can continue to play an important heuristic role of conceptually identifying

nodes in the vast web of successional interactions, but the distinction between models and mechanisms must be maintained.

V. A Comprehensive Causal Framework

Connell and Slatyer (1977) chose to focus on specific aspects of the successional process. However, the applications of the C + S models in the literature have often extended beyond the limits noted earlier. This indicates a need for broad analysis of successional causes. Because a complete understanding of succession must ultimately consider all important influences on succession, and not just mechanisms of turnover, we believe it would be valuable to incorporate all causes of succession in a complete mechanistic scheme. We build on Clements' (1916) classification of successional causes because of its generality and comprehensiveness (Miles, 1979).

While the resulting framework is not itself a completely elaborated theory, it is more than a simple list of successional causes. It is a conceptual structure to help organize various aspects of successional theory. A complete successional theory would be a broad and inclusive conceptual construct used to understand the process. It would include explicitly stated assumptions, definition of units and phenomena, generalizations about trends and relationships, models of various component processes and phenomena, and it would suggest hypotheses and predictions. Space and the state of the discipline prevent us from elaborating more than the mechanistic superstructure of that theory here. That superstructure is the causal framework we derive from the Clementsian causes. The framework will be useful in guiding the development of successional theory. Specific models of various successional processes and phenomena can be related to the framework to determine their inclusiveness and generality, and the need to link them to other models, concepts, and phenomena. Without mechanistic inclusiveness, and linkages between different aspects of successional process, a complete understanding will not be possible. Because the framework is hierarchically organized, theoretical developments and empirical work in one aspect (branch of the hierarchical tree) or on one level of generality (order of branching) can be related to work on other branches or levels. Without such a framework, we suspect that theoretical work on different aspects of succession will remain isolated. Furthermore, in the absence of a framework the need and strategy for theoretical and empirical syntheses would not be apparent.

There are additional values of adopting a comprehensive mechanistic scheme. It need not be biased toward an endpoint in general, and certainly not one in particular. It is not inherently biased toward a single or dom-

inant mechanism or driving force. Finally, it is not married to any particular pathway of succession. A mechanistic, "process-oriented" approach (Vitousek & White, 1981) is applicable to a broad variety of biomes and situations. The mechanistic framework can incorporate specific models and subtheories that will generate predictions for field or other appropriate tests. However, we cannot include all detailed subtheories in this paper. Indeed, many such subtheories have yet to be developed.

Although we have based our comprehensive mechanistic framework on the causal scheme of Clements, we depart from it for several reasons. Clements' scheme confounds different levels of generality in causation. It also inappropriately includes Aristotelian final cause. In addition, some of Clements' "causes" (Table II) are actually effects (e.g., stabilization) and others are permissive conditions (e.g., nudation). These problems can be remedied by creating a hierarchy of causes ranging from the most general and universal to those that are site- and situation-specific. The higher level causes can be decomposed into the more specific, lower level causes. We also include formerly neglected influences on succession, such as herbivory, predation (Connell & Slatyer, 1977; MacMahon, 1980, 1981), and disturbance (Grubb, 1977; Pickett & Thompson, 1978; Pickett & White, 1985b; White, 1979).

We begin the mechanistic hierarchy at the most general level by asking, "What causes succession?" The universal answers are that (1) open sites become available, (2) species are differentially available at a site and (3) species have different, evolved or enforced capacities for dealing with a site and one another (Table III). These answers are explanatory and not predictive, but they apply to all cases, and guide our search for more specific causes about which testable predictions are possible in specific sites. These answers also apply to all spatial and temporal scales (e.g., Delcourt et al., 1983) of vegetation dynamics and thus emphasize the commonality of causation in various processes involving species replacement (e.g., seasonal turnover, post-glacial migrations), regardless of whether they are called succession or not (Pickett & White, 1985a).

The second level of the hierarchy (Table III) is constructed of the answers to the question, "What interactions, processes or conditions contribute to the general causes of succession?" The answers are broad categories of ecological phenomena, which suggest the range of processes that must be considered to understand each case of vegetation dynamics.

The third and most detailed mechanistic level encompasses site-specific factors or behaviors that determine the nature or outcome of interactions of the plants and other organisms that affect them. These interactions are the essence of succession. These organism- and site-specific features are responsible for the great variety in the successions we observe. The specific

Table III

A hierarchy of successional causes and references demonstrating the action of factors in particular successions

General causes of succession ^a	Contributing processes or conditions ^b	Modifying factors ^c
Site availability	Coarse-scale disturbance	Size
		de Foresta, 1983
		Davis & Cantlon, 1969
		Denslow, 1980
		Curtis, 1959
		Miles, 1974
		Grubb, 1982
		Severity
		Malanson, 1984
		Monte, 1973
		Time
		Small et al., 1971
		Keever, 1979
		Altieri, 1981
		Perozzi & Bazzaz, 1978
Numata, 1982		
Abugov, 1982		
Dispersion		
Differential species availability	Dispersal	Landscape configuration
		Forman & Godron, 1981
		Livingston, 1972
		Olsson, 1984
		Dispersal agents
	Propagule pool	Time since last disturbance
		Wendel, 1972
		Leak, 1963
	Land use treatment	
	Oosting & Humphreys, 1940	
	Resource availability	Soil conditions
		Bard, 1952
		Tilman, 1982, 1984
		Grime, 1979
		Bazzaz, 1979
Robertson & Vitousek, 1981		
Robertson, 1982		
Chapin, 1983		

Table III
Continued

General causes of succession ^a	Contributing processes or conditions ^b	Modifying factors ^c
		Topography
		Microclimate
		Site history
Differential species performance ^d	Ecophysiology	Germination requirements Pickett & Baskin, 1973 Willemsen, 1975 Peterson & Bazzaz, 1978 Grime et al., 1981
		Assimilation rates Wallace & Dunn, 1980 Bazzaz & Carlson, 1982 Parrish & Bazzaz, 1982a, 1982b Zangerl & Bazzaz, 1983 Bakuzis, 1969
		Growth rates Marks, 1975 Bicknell, 1982 Sobey & Barkhouse, 1977 Grime, 1979
		Population differentiation Hancock & Wilson, 1976 Hancock, 1977 Roos & Quinn, 1977
	Life history strategy	Allocation pattern Horn, 1981 Stewart & Thompson, 1982 Soule & Werner, 1981 Beefink et al., 1978 Campbell, 1983 van der Valk, 1981
		Reproductive timing Baalen & Prins, 1983
		Reproductive mode Noble & Slatyer, 1980 Smith & Palmer, 1976
	Environmental stress	Climate cycles Buell et al., 1971

Table III
Continued

General causes of succession ^a	Contributing processes or conditions ^b	Modifying factors ^c
		Site history
		Woodwell & Oosting, 1965
		Prior occupants
		Whitford & Whitford, 1978
		Carmean et al., 1976
	Competition	Hierarchy
		Kramer et al., 1952
		Raynal & Bazzaz, 1975
		Parrish & Bazzaz, 1982c
		Kozlowski, 1949
		Presence of competitors
		Werner, 1976
		Identity of competitors
		Carvell & Tryon, 1961
		Petranka & McPherson, 1979
		Collins & Quinn, 1982
		Werner & Harbeck, 1982
		Within-community disturbance
		Gross, 1980
		Werner, 1977
		Armesto & Pickett, 1985, 1986
		Predators and herbivores
		Berendse & Aerts, 1984
		Resource base
		Huston, 1979
		Maly & Barrett, 1984
		Fowler, 1982
		Tilman, 1985
	Allelopathy	Soil chemistry
		Jackson & Willemsen, 1976
		Rice, 1984
		Soil structure
		Microbes
		Neighboring species
		Quinn, 1974

Table III
Continued

General causes of succession ^a	Contributing processes or conditions ^b	Modifying factors ^c
	Herbivory, predation and disease	Climate cycles Predator cycles Schimpf & MacMahon, 1985 Maarel, 1978 Kirkpatrick & Bazzaz, 1979 Reader, 1985 McBrien et al., 1983 Ashby, 1958 Plant vigor Plant defenses Community composition Smith, 1975 Brown, 1985 Southwood et al., 1979 Patchiness Smith, 1975

^a The highest level of the hierarchy represents the broadest, minimal defining phenomena.

^b The intermediate level represents mechanisms of change or causation of the higher level.

^c The lowest level of the hierarchy contains the particular factors that act to cause or limit change in the second level, and which are discernable or quantifiable at specific sites. For simplicity, interactions among factors at each level are not shown.

^d Consists of both species properties and environmental determinants.

features can be quantified and incorporated into the flow model of MacMahon (1980) (Fig. 2) and used to predict species replacement patterns and associated community and ecosystem level phenomena.

The nature and use of the third, most detailed level of the hierarchy requires some explanation. We present a brief overview rather than a complete review (Table III). Because we are concerned with succession, the availability of open sites is the first component of the mechanistic hierarchy. The conditions within open sites depend on the characteristics of the disturbance (Connell & Slatyer, 1977; White, 1979). For example, the size of a disturbance affects environmental conditions and heterogeneity within open patches. The severity of a disturbance (Sousa, 1984; White & Pickett, 1985) affects the survival of propagules and advanced regeneration, as well as the openness of the site. The time of a disturbance, whether on the seasonal scale, or relative to the maturity of the dominants, can determine whether in fact a particular site is available to particular species.

The processes that affect species availability are dispersal and the nature of the propagule pool. Whether diaspores reach an area will depend on the features of the landscape (*sensu* Forman & Godron, 1981) in which the disturbed site is embedded. How large the opening is and whether it is isolated by barriers to biotic or abiotic dispersal vectors, will affect availability of different potential occupants. Alternatively, species may be made available through persistence in the soil seed bank or pool (or in many cases as advanced regeneration). The time since last disturbance interacts with the depletion rate, through death and germination, of the seed pool. Likewise, the nature and length of the prior disruption of the site (land use) will determine the size and composition of the seed pool.

The differential performance of species that arrive at the open site is the third general determinant of succession. Differential species performance can be determined by evolved species characteristics (Pickett, 1976) and by interaction with other species and the changing environment of the sere (Bazzaz, 1979). The physiological ecology of the species has several relevant aspects: germination requirements (dormancy, stratification, light, water, etc.); assimilation rates (photosynthesis, nutrient and water requirements); and integration of the assimilation behavior into whole-plant growth rates and architecture. Finally, whether the individuals of a species present early in the sere differ genetically or not from those present later will affect turnover and structure of the sere.

The life history differences among species in a sere are important causes for their differential behaviors (Pickett, 1976). That species differentially allocate biomass and nutrients to different components is an important reason for their different behaviors in succession. Whether they reproduce early in their lives or not; whether they rely entirely on sexual reproduction or have the capacity for vegetative spread (Pitelka & Ashmun, 1985); and the horizontal and vertical architecture resulting from these components of the species strategy, are critical determinants of their performance relative to other species.

Environmental stress can differentially affect performance of various species in succession. This item refers to the unpredictable imposition of stress during the succession. Climate cycles can trigger droughts and affect fire probabilities, for instance. The recent history of a site may determine whether the soil is capable of storing water or supplying nutrients to different degrees. The identity and performance of species occupying the site before initiation of the present sere may affect the availability of soil-mediated resources, or the existence of safe sites. To the extent that different species are differentially tolerant of the stresses, resources, and opportunities presented throughout a sere, these factors and processes outlined above will determine, in part, the course and rate of succession.

The direct ecological interactions among organisms, which determine

the progress of succession can include, at the least, competition, allelopathy, predation and herbivory. Various mutualistic interactions can be considered under the specific resource or life history feature they affect, or be grouped as a class along with the various interactive processes listed here.

Competition will affect succession if species differ in their competitive rankings (Connell & Keough, 1985). If competitive hierarchies are absent, transitive, or cyclic, then the course of succession may differ. Specifically, the presence of competitors and their identities at various stages must be known to understand the role of competition in a succession. Whether the small-scale component of the disturbance regime, that which acts within a community without obliterating it, has a different impact on the species in the sere must be known. Predators and herbivores can be considered a within-community component of the disturbance regime (Denslow, 1985; Karr & Freemark, 1985) and may alter the outcome of competition in a similar manner to physical disturbance.

An additional factor affects the outcome of competition. Generally, competitive exclusion will proceed faster where the available resource base is greater (Huston, 1979). Thus, the resource base at the outset of succession, or its change over time, can influence the outcome of competition and hence the rate of succession. The presence or abundance of mycorrhizae can influence succession through competitive effects or directly through access to resources (Allen & Allen, 1985). Little information is available on this aspect of succession, but certain levels of disturbance can alter mycorrhizal abundance (Doerr et al., 1984). Subsequent changes in mycorrhizae can contribute to successional change (Reeves et al., 1979).

Allelopathy is an important process in some successions (Rice, 1984). Whether and how strongly it acts will depend on soil characters, like texture, chemistry, moisture and microbial activity. It will also depend on the allelopathic potential, vigor, and dispersion of neighboring species.

Herbivory and predation, though potentially quite important processes that might affect succession, are under-investigated in that context (Brown, 1984). They are both influenced by such factors as climatic cycles, cycles of their own and interacting predator populations, and the vigor of the host species as determined both by biotic and abiotic limitations. Additionally, the defensive capacity of the plants, both constitutive and inducible, are influenced by resource levels and environmental stresses. The identity and palatability of plant neighbors and patchiness of the host species may also affect predation and herbivory.

This enumeration of the various processes that cause succession and the component modifying factors is meant to be illustrative rather than exhaustive. We have not tried to note all the interactions between factors and processes within a level of the hierarchy. Undoubtedly mechanistic

and experimental studies will identify additional factors and specific parameters required to make sound mechanistic predictions of successions and to understand completely the mechanisms of any particular succession. This is only a first attempt at a mechanistic framework called for in recent reviews (e.g., Finegan, 1984; Horn, 1981). A mechanistic framework for successional causation shows the context of specific models of various components of succession. Furthermore, it is needed to complement general models (Breitburg, 1985) such as those of Connell and Slatyer (1977), or MacMahon (1980), when the goal is to understand a particular sere. The framework indicates the specific factors that must be accommodated in translating from the general theoretical statements to useful testable predictions relevant to specific seres. Most importantly, the mechanistic framework represents the initial tentative outline of a complete successional theory. The development of a broad, inclusive, mechanistic theory is one of the principal goals of contemporary plant ecology. This review has indicated the mechanistic richness that such a theory must incorporate.

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