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Ed.

Interactions among processes controlling successional change

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Connell and Slatyer (1977) proposed three alternative models to explain successional change (facilitation, inhibition, and tolerance). These models have become a constructive focus for recent research on plant succession. However, not all studies fit neatly into these three models (McIntosh 1981, Pickett et al. in press), so it may be premature to synthesize our understanding of succession into a unified theory (Finegan 1984). The purposes of this paper are (1) to review evidence that many successional processes occur simultaneously and therefore cannot always be grouped into alternative models; (2) to review experimental tests of the relative importance of these processes; and (3) to hypothesize the conditions under which each major successional process might be most important.

Process interactions

Each of the models proposed by Connell and Slatyer (1977) comprises several processes and interactions among species (Tab. 1). For example, the facilitation model incorporates life history traits (arrival time and longevity), facilitative interactions, and competitive displacement; the tolerance model involves life history traits (arrival time and growth rate), and competitive displacement; the inhibition model involves life history traits (arrival time and longevity) and competitive inhibition. This correctly emphasizes that no single process (e.g. facilitation) can individually explain successional change (Quinn and Dunham 1983).

However, there is no a priori reason to expect these

models to be the only way in which these and other processes might be combined. For example, components of all three models were important causes of successional change from alder (*Alnus incana*) to spruce (*Picea glauca*) on an Alaskan floodplain (Walker and Chapin 1986, Walker et al. 1986). Life history traits of alder (more rapid growth and shorter lifespan than spruce) could by themselves explain the *pattern* of successional change from alder to spruce following simultaneous colonization by both species. However, the addition of soil nitrogen by alder (Van Cleve et al. 1971, Walker 1985) reduced the degree of nutrient limitation of spruce seedling growth, suggesting that alder may facilitate spruce growth (Walker and Chapin 1986). On the other hand, root trenching and clearcut experiments with natural and transplanted seedlings demonstrated that the net effect of the thick alder canopy was to inhibit seedling growth (see also Binkley et al. 1984). Moreover, alder litter inhibited germination and initial establishment of spruce seedlings. Snowshoe hares browsed preferentially upon early successional species that might otherwise have competed with spruce seedlings for water and nutrients (Bryant and Chapin 1986). Large (10 to 100-fold) yearly variations in spruce seed abundance (Zasada et al. 1978), flood level, and abundance of snowshoe hares (Fox 1978) insert a strong stochastic element into the interaction between alder and spruce. In summary, stochastic, life history, facilitative, competitive, and herbivory processes all affect the interaction between alder and spruce during succession, and no single successional process or model (sensu Connell and Slatyer 1977, Tab. 1) adequately describes successional change on the Alaskan floodplain. Particularly

Tab. 1. Successional processes determining species replacement in three models proposed by Connell and Slatyer (1977).

Model	Developmental phase		
	Colonization	Maturation	Senescence
Tolerance	1a*	1b	2b
Inhibition	1a, 2a	2a	1c
Facilitation	1a, 3a	3b	1c, 2b

* Symbols are: 1, life history processes (a = arrival time, b = growth rate, c = longevity); 2, competition (a = competitive inhibition, b = competitive displacement); 3, facilitation (a = facilitation of establishment, b = facilitation of growth).

important was the observation that alder increased soil nitrogen content and reduced the degree of nutrient limitation of spruce growth (suggesting facilitation), although its net effect upon spruce growth was inhibitory (Walker and Chapin 1986).

Interactions of successional processes may be density-dependent (Quinn and Dunham 1983). For example, the rapid growth of nitrogen fixers in primary (Walker and Chapin 1986) or secondary (Binkley et al. 1984) succession can lead to dense stands that inhibit growth of associated species whereas less dense stands might have a net facilitative effect on associated species (Gadgil 1971, Dancer et al. 1977). The interaction of herbivores and competition can also be considered density-dependent. In cases where seedlings of late successional species are relatively uncommon, herbivores may eliminate these individuals and delay successional change. In cases where there is a more even mixture of early and late successional species, herbivores feed preferentially upon early successional species (Godfray 1985, Bryant and Chapin 1986), particularly if early species are more resource-limited (Schowalter 1981). This may change the competitive balance between early and late successional species and speed the rate of succession.

Herbivory can also interact with life history and stochastic processes in a density-dependent fashion. Decreased sapling densities in some shrub species between 1955–1965 on dunes in the Netherlands were ascribed to a coincidence of dry summers, low regeneration, high mortality rates, and high rabbit population densities (van der Maarel et al. 1985). Rabbit grazing combined with low seed input and low nutrient levels limited colonization of a limestone quarry in England (Davis et al. 1985).

The relative importance of successional processes may change through successional time (Connell and Slatyer 1977). For example, in pine woods of North Carolina, life history processes appeared most important in determining species composition of young stands, but competition became progressively more important in later stages (Peet and Christensen 1980). Similarly, plant composition on granite outcrops in Georgia was determined by stochastic fluctuations in temperature and moisture in early stages of succession; interspecific com-

petition influenced species composition later in succession (Shure and Ragsdale 1977).

Interaction of multiple processes has been clearly shown in marine succession. Facilitation and inhibition may occur simultaneously or at different successional stages (Turner 1983). These two processes may counteract one another or work in the same direction, e.g. when species A facilitates the establishment of species B by inhibiting species C (Breitburg 1985). Inhibition may more directly affect final species composition, whereas facilitation affects the rate of development (Dean and Hurd 1980). Stochastic events that clear patches for colonization interact with competition, herbivory, and life history processes in the colonization of epibenthic (Breitburg 1985) or rocky intertidal (Sousa 1979, 1984) communities.

In aquatic systems grazing can also either facilitate or inhibit successional change. Snails may graze preferentially on early successional algae of intertidal communities, creating space and thereby facilitating establishment of late successional algae (Lubchenco 1983). Alternatively, grazing by fish on storm-denuded reefs may prevent establishment of late successional kelp; kelp establish only when protected by fast-growing early successional algae (Harris et al. 1984).

Testing the importance of successional processes

Given that many successional processes may operate simultaneously or sequentially in any given situation (Hils and Vankat 1982, Lawton in press), how does one establish their relative importance? An experimental approach can be helpful in distinguishing the relative contribution of each process (Keever 1950, McCormick 1968, Hils and Vankat 1983, Walker and Chapin 1986).

Life history traits (propagule arrival and establishment, growth, and longevity) are often sufficient to account for the pattern and endpoint of successional change without invoking an important role for any biological interactions (Egler 1954, Noble and Slatyer 1980, Walker et al. 1986). Simulation models can predict the outcome of succession based on these life history traits (Botkin et al. 1972). Biological interactions are perhaps more important in determining the rate of succession than its final outcome.

The importance of stochastic events in determining the outcome of succession can be estimated from surveys of "replicate" communities on a given substrate that have established at different places or different times. At one extreme, if stochastic factors are unimportant, succession will be completely deterministic: substrate of a given age and composition will always have the same species composition, biomass, and productivity. To the extent that observations deviate from this prediction (e.g., Horn 1976), stochastic factors can be assumed to be important.

The relative importance of facilitation, competition, and life history traits can best be determined experi-

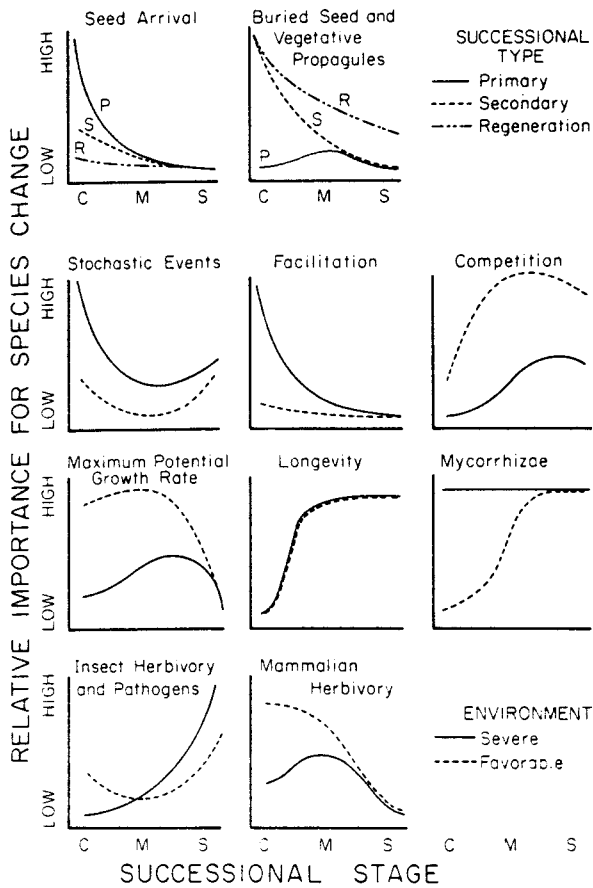


Fig. 1. Influence of type of succession (top) and environmental severity (bottom) upon major successional processes that determine change in species composition during colonization (C), maturation (M), or senescence (S) stages of succession.

mentally by (1) removing species that establish in early succession that may facilitate or compete with species that establish later (Keeve 1950, McCormick 1968, Hills and Vankat 1982, Armesto and Pickett 1986); (2) sowing seeds (Walker et al. 1986) or planting seedlings into natural successional communities (Collins and Quinn 1982, Walker and Chapin 1986); or (3) adding and removing shade and litter or removing the effects of root competition with trenching (Lutz 1945, Burton and Mueller-Dombois 1984, Monk and Gabrielson 1985, Walker and Chapin 1986). If removal of species A (or its roots, litter, or shade) causes an increase in growth of species B, competitive inhibition is suggested; if this causes a decrease in growth of species B, facilitation is occurring; if there is no change in growth of species B, one cannot reject the null hypothesis of no interaction between species A and B, although the same result could be obtained by an interaction between competition and facilitation. The impact of herbivory can be determined by exclosures (Sousa 1979, Davis et al. 1985) or by attracting larger numbers of herbivores (Waring and Pitman 1986).

Predicted importance of successional processes

One of the most constructive contributions of Connell and Slatyer's (1977) paper was to provide a theoretical framework for experimental studies. We argue that successional forces cannot be neatly subdivided into their three models and therefore suggest an alternative framework of hypotheses. We suggest that the major factors influencing importance of successional processes are (1) stage of succession, (2) type of succession (primary, secondary, or regeneration after disturbance), (3) availability of environmental resources (particularly water and nutrients), and (4) type, frequency, and intensity of disturbance. Succession is a continuum from early stages where factors governing colonization are most important, to late stages where factors governing senescence and mortality predominate; disturbance generally prevents the community reaching this senescent stage (i.e., stage of canopy breakup). The type of succession is important primarily in determining the mode by which initial colonizers arrive. Resource availability then governs the relative importance of other successional processes. Type of succession and resource availability are often linked; for example, postglacial primary succession begins on infertile soils, and old-field secondary succession often begins on fertile soils. However, primary succession on alluvium deposited in river deltas or secondary succession following a desert fire provide very different combinations of type of succession and resource availability. Infrequent, intense disturbances tend to reverse successional trends, whereas moderate disturbances either delay succession or modify it in ways that are specific to each community or disturbance type.

Fig. 1 (top) suggests ways in which type of succession affects the mode of colonizer arrival. Fig. 1 (bottom) suggests ways in which the influence of stochastic events, facilitation, competition, life history processes, and herbivory on species composition may vary with stage of succession and environmental severity. Additional processes (e.g. mutualism, allelopathy) may also be important in certain instances (Pickett et al. in press). Below we briefly outline the evidence upon which Fig. 1 is based. We are concerned here with major processes that determine change in plant species composition rather than change in community properties such as productivity or species diversity.

Mode of arrival differs strikingly among different types of succession (Fig. 1 top). In brief, dispersal mechanisms promoting seed arrival from distant sources are most important in primary succession (Viereck 1966, Finegan 1984, Davis et al. 1985, del Moral and Clappitt 1985), whereas buried seed and surviving vegetative propagules are more important in colonization of secondary successional sites and in regeneration following fire and other disturbances (Livingstone and Alessio 1968, Marks and Mohler 1985).

Stochastic variation can strongly influence coloniza-

tion in severe (i.e. low-resource) environments (Fig. 1 bottom). For example, moisture fluctuations affect colonization of dunes (van der Maarel et al. 1985) and granite outcrops (Shure and Ragsdale 1977); flooding determines colonization patterns on riverbanks (Johnson et al. 1976, Menges and Waller 1983, Walker et al. 1986). In dry environments the stochastic occurrence of fire influences species change (Noble and Slatyer 1980). In very late succession, when old individuals become senescent, stochastic occurrence of drought or other stresses increase the probability of insect or pathogen attack (see below). Facilitation appears to be important only in severe environments (e.g. deserts and primary succession) and primarily in the stages of colonization and early community development (Lawrence et al. 1967, Connell and Slatyer 1977, Finegan 1984). In contrast, competition may be a more widespread process that structures most successional sequences (Parrish and Bazzaz 1982, Connell 1983, Schoener 1983, Tilman 1985). Competition may become critical earlier and to a greater degree in favorable than in severe environments (Grime 1979).

Life history traits differ in their importance in distinct environments and stages of succession and are well described by Noble and Slatyer (1980). Mode of arrival has been discussed above. Maximum potential growth rate affects changes in species composition in early to mid succession in all situations, but is particularly important in favorable environments where abundant resources are available to support rapid growth (Hosner and Minckler 1963, Uhl and Jordan 1984). Differential longevity may explain changes in species dominance in mid to late succession in many communities (e.g. van der Valk 1981, Hibbs 1983), yet more long-term studies are needed. Mycorrhizae may be important in all successional stages in severe environments, but less important in colonization of highly fertile sites (Harley and Smith 1983).

Insect herbivory and pathogens can be important causes of tree mortality in late succession, particularly in areas of nutrient or drought stress (Matson and Boone 1984, Waring and Pitman 1985). In contrast, mammalian herbivores appear to be more important in species changes in early to mid succession (Davis et al. 1985, Bryant and Chapin 1986). In favorable environments insect herbivores may affect species changes in both early (McBrien et al. 1983, Brown 1985) and late (Schowalter 1981) succession. Studies are needed to determine the role of plant pathogens in early succession.

In summary, we suggest that succession is a complex process driven by many processes acting simultaneously in any given situation. Recent research allows predictions of the types of environments and successional stages where each process may be particularly important. However, experimental studies are necessary to test these predictions and to determine the nature of interactions among processes that cause successional change.

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