SUCCESION

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In its widest sense the term "succession" refers to observed sequences of vegetation associations or animal groups. Some occur in space, such as a sequence of zones of grasses, shrubs, and trees on the side of many ponds; or a sequence of zones of vegetation on the side of a mountain. Other sequences occur in time, as, for example, a sequence of vegetation types occurring after an "old field" or a gravel pit is abandoned.

Definition

In ecological literature, the term succession is usually used to imply sequences in time. However, only short-term changes can be observed directly, and most descriptions of long-term changes are based on observation of spatial sequences. In order to provide a unified description on which a general theory can be based, it is necessary to assume a homology between a spatial sequence of zones of vegetation visible at one time in a landscape and a long-term sequence of vegetation types on a single site (Gleason 1927: 320 and 324). This assumption is consistent with and reinforced by the classical geomorphological theory (Davis 1909) of landscape development (for discussion see Hack & Goodlett 1960, McCormick 1968, Drury & Nisbet 1971).

Functional effects have been ascribed to the observed sequences. For example, MacArthur and Connell (1966) describe the changes in organisms on an abandoned field, in stored grain, and in a jar of water. Then they comment: "This gives us a clue to all of the true replacements of succession: each species alters the environment in such a way that it can no longer grow so successfully as others." (Italics theirs.)

Another property ascribed to succession is that the changes are progressive, that is, directional, and it is possible to predict which species will replace others in the course of a succession. MacArthur and Connell, in the same chapter (1966) say:

In the case of forest succession, each species is able to stand deeper shade than the previous one, and as the forest grows the canopy becomes thicker

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and casts an even deeper shade. In this new, deeper shade other species are more successful, ... Forests have tables of 'tolerance' of different tree species; tolerant species are those that are successful in shade. As expected, the climax forests are composed of the most tolerant species.

Hence the theory of succession allows one to predict the characteristics of those species which will replace others, and to recognize unstable or successional species. Thus, species and associations of organisms have been assigned to places in a successional order.

Succession is supposed to continue until the species combination best suited to the regional climate and the site are established. Many authors believe this reflects the development of a particularly well-adjusted configuration of species (Braun 1950, Clements 1916, 1936, Dansereau 1957, Daubenmire 1956, Odum 1959, Oosting 1958); other authors believe it to be simply running out of available species (Gleason 1926, 1927, Cooper 1926). But however the concept of succession is inseparable from that of climax (Whittaker 1953), even if it is possible to equivocate by suggesting that change continues at a very slow rate in the "climax."

The concept of climax has been used in a highly inconsistent way (Whittaker 1953), and there is a rich literature challenging, defending, and redefining climax and the nature of plant communities (see reviews by Whittaker 1953, MacIntosh 1967 and the replies in The Botanical Review 1966, and Langford & Bebb 1969). The concept of succession has seldom been critically reviewed (but see Egler 1954 and McCormick 1968).

There are several vegetational types conventionally referred to as successional. Cowles (1911) classified successions into regional, topographic, and biotic types. These include (a) the "major vegetation zones" (biomes or latitudinal and altitudinal sequences); (b) pond margins, peat bogs, and marshes, or sand dunes; (c) old fields, or changes following fire. Among other successions are included patterns of plants on floodplains, around the snouts of retreating glaciers, on landslides, and the sequences of species in the course of the history of colonization of islands and the microcosms of laboratory infusions.

The primary bases for assigning plant associations to a position in a succession are the size of the dominant plants, complexity of the vegetation structure and the number of species present. Successional series are generally recognized as extending from associations of low stature, few species and simple structure to associations of tall plants, many species and complex structure: (a) encrusting, prostrate, decumbent or emergent forms; (b) grasses and sedges; (c) perennial wildflowers and low thistles; (d) tall shrubs and scattered, taller trees, or stands of uniformly aged trees with little underbrush; (e) a canopy of trees with understorey of saplings and ground cover of several levels.

On the longest time-scale, some successions are credited to sites not previously occupied by vegetation; these are called Primary Successions. If the site has been previously occupied, the succession is called Secondary. Tansley (1935) distinguished Autogenic Successions, "in which succes-

cessive changes are brought about by the action of the plants themselves on the habitat," from Allogenic Successions, "in which the changes are brought about by external factors." Primary successions were divided by Clements (1916) into hydroseres, xeroseires, etc., according to the moisture conditions of the site.

Ponds and lakes have been put into a quasi-successional sequence from Oligotrophic (deep lakes, poor in nutrients, with little visible floating vegetation) to Eutrophic (shallow lakes, rich in nutrients, often covered with floating plants). Zones of vegetation occur in the sea below high tide and have been described on the coasts of the Pacific (Ricketts & Calvin 1968) and the Atlantic, of Europe (Yurie 1949) and the United States (Dexter 1947, Lamb & Zimmermann 1964, Stephenson & Stephenson 1954). However, we know of no assignment of such algal zones to successional stages, although the zones of emergent vegetation immediately above high tide in salt marshes are usually classified in successional terms.

**Historical Review**

Descriptions of zones of vegetation and of changes in vegetation on one site are available from Theophrastus (300 B.C.) onwards. The idea that one community of plants might alter its site and prepare the way for another is also old (Buffon 1742). Several authors during the 19th century (e.g. Kermer 1863) described zones and sequences of vegetation, but did not formulate a model for the ecological events involved. In 1853 Thoreau recognized that pine stands on upland soils in central New England were followed after logging by even-aged hardwood stands which today are the main forest type of the region. He named this trend forest succession (Spurr 1952). Hult (1885) recognized "developmental changes" in vegetation, yet it was the work of Cowles (1899, 1901, 1911) which formulated the concept of succession. Clements' brilliant and exhaustive studies (1905, 1916, 1920, 1928, 1934, 1935) appear to be responsible for its general acceptance, because he made of it the mechanism of "progress in the visionary system for plant ecology." His developmental model, in which climax was regarded as a superorganism and succession its embryonic development (Clements 1916 161) was consistent with determinist, closed system models current in several branches of earth science of that time.

Apparently it was Clements' experience in the grasslands which convinced him of the validity and integrity of grassland communities (in contrast to the previously held opinion that they were unnatural) and led him to the concept of the vital integrity of plant associations. Following Clements, ecologists were for several decades preoccupied with mapping and monitoring the natural communities of North America and discovering their structures, consistencies and inconsistencies. In this

1 In botanical usage, site refers to a place and a set of habitat conditions suitable for the growth of a particular species or vegetation association. For example, in the course of succession, "each species alters the site."
the same as the "strategy" of long-term evolutionary development of the biosphere — namely, increased control of, or homeostasis with, the physical environment in the sense of achieving maximum protection from its perturbations.

Generally agreed upon successional trends are listed in Table 1 (after Odum 1969).

Requirements of a Generalized Theory

It will be apparent from the foregoing survey that a number of different types of phenomena have been drawn together under the term succession. For the purposes of this paper, it is useful to classify successions into three broad categories.

a) Temporal sequences on one site with climate and physiography substantially stable. This category includes most of the classical types of secondary succession and perhaps some primary successions.

b) Temporal sequences on one site with the local environment changing under the influence of extrinsic factors (e.g., climatic change, erosion, deposition, changes in drainage, input of nutrients, etc.). This category (allrogenic succession of Tansey) includes many primary successions (especially successions in lakes and ponds) and some secondary successions.

c) Spatial sequences on adjacent sites. These are used to infer temporal changes, at least on the time-scale appropriate to vegetational change. Changes on a longer (geological) time-scale are not now usually included in the successional scheme.

Theories of succession are usually formulated explicitly to describe and explain temporal sequences of type (a). However, as we pointed out at the beginning of this paper, only short-term observations of such changes are available; hence most of the observational basis for the theories is derived from sequences of type (c). Accordingly the primary task of our review is to examine how well observations of type (c) and of short-term changes in type (a) conform to the generalizations of the contemporary theory.

The extent to which observations of type (b) successions are relevant to contemporary theory is less clear. They were explicitly included in the classical theories, as developmental sequences leading to the climatically determined end-point (Clements 1916, 1936). Contemporary theories, however, although recognizing control by the physical environment (see quotation from Odum 1969 above), place primary emphasis on community-controlled changes and tend to treat cases where external factors are dominant (e.g., agricultural management, or eutrophication of lakes) as exceptions to or temporary reversals of the successional process (Odum 1959, 1969). On the other hand one of the most thorough studies of changes in species diversity within developing lakes (Goulden 1969) was interpreted entirely within the framework of the contemporary theory. In this paper we take the view that external factors make at least some contribution to change in all real systems (i.e., that "pure" type (a)
successions are an abstraction), and that any acceptable generalization about succession must be able to describe adequately a reasonable number of real systems. However, for a fair test of the contemporary theory, it is necessary to consider primarily cases where the effects of external factors are relatively modest. Extreme cases of type (c) successions will be considered separately at the end of this review.

**REVIEW OF AVAILABLE FIELD EVIDENCE**

In this section we will examine the Odum-Whittaker criteria by reviewing observational studies of successional systems, and we will show that many of the observed structural or physiological characteristics of the communities do not conform to their generalization. That is, changes in species or life form are not necessarily or consistently accompanied by the other functional changes that are supposed to accompany them. We do not assume that every succession should show all the characteristics ascribed by the ideal sequence. On the other hand, we think that the counter-instances we present are sufficient to show that the Odum-Whittaker formulation of succession is not acceptable as a generalization on the basis of the informal and anecdotal arguments presented to date.

The following general comments may be a desirable introduction to this review.

We have not attempted to cover all the vast literature on vegetational sequences. For each topic under discussion, we have selected the two or three best-documented studies known to us. It is not often realized how few detailed quantitative studies have been made of even short-term changes in vegetation. While there are doubtless important studies that we have not quoted, we have not selectively omitted studies supporting the contemporary theory. Indeed, many of the studies we quote appear in Odum and Whittaker’s bibliographies.

Our review is largely restricted to studies of forest succession in areas of temperate climate (including studies of lakes and bogs in forested regions). Succession in other habitats has not been studied in comparable detail. We know of no adequate quantitative evidence for extending contemporary theories of succession to such habitats as grassland, deserts, or tundra.

We have placed emphasis on studies of old-field succession, as this is the best documented example of secondary succession. It might be argued that old fields, having been previously forested, are already “prepared” for the regrowth of the climax forest. However, the contemporary theory of succession is itself based very heavily on studies of old fields (Odum 1969, Whittaker 1970, MacArthur & Connell 1966, etc.), so it is appropriately tested by observations in them.

Although we present evidence opposing contemporary generalizations about succession we do not claim that generalizations about vegetational change are impossible. We ourselves, in concluding, present a very broad generalization as an alternative explanation. More limited generalizations...
may be possible about certain groups of species or certain floristic regions; comparison of these generalizations may give more biological insight than attempts to develop comprehensive theories.

In evaluating evidence and in our alternative explanation, we have placed some emphasis on natural selection. Natural selection has been neglected in theories of succession because most of them have been primarily concerned with adding community properties. However, natural selection must act on every species, including "successional" species, to adjust them to their environment, including the communities in which they live. In our view, generalizations about the behavior of communities should be viewed with caution unless they can be reconciled with the action of natural selection on the individual organism.

**Bioenergetics**

**Statement of Hypothesis.** Margalef (1968: 30): "Biomass increases during succession as, almost always, does primary production; however, the ratio of primary production to total biomass drops." Figure 1 (from Odum, 1969).

![Figure 1](attachment:image.png)

**Figure 1** (after Odum, 1969). Comparison of the energetics of succession in a forest and a laboratory microcosm. P_g, gross production; P_n, net production; R, total community respiration; B, total biomass.

Odum (1969: 264) illustrates the energetic changes during succession, comparing a forest with a laboratory microcosm. Both production and diversity were described as increasing toward the climax, but both reached a maximum just before the climax stage was reached. They continued at a high, but not maximum, value in the climax. At that stage community respiration is approximately equated to photosynthesis (Bormann 1969:163). Therefore production and diversity should be correlated.

**Field Evidence.** a) Old field successions have been studied in detail as illustrative of the developmental changes involved in more general cases.

Odum (1960) made a detailed study over seven years of changes in species composition and organic production in an old field in Georgia (Figure 2, from Odum 1969) about which he wrote the following paragraphs (p. 48):

If we consider that species composition and species diversity represent "structural" features of the community and that productivity is a "functional" attribute, then it is clear that structurally the "old-field" community changed gradually and continuously, but that functionally a temporary steady-state was established during the period of forb dominance. The study clearly showed that productivity does not necessarily change with change in species, nor necessarily increase with succession as has often been assumed.

The trends so far observed suggest a tentative hypothesis regarding the relationship of energy to succession. From the functional standpoint succession may involve a series of steady-states each associated with a major life form, rather than a continuous change associated with species change as is usually postulated. It may be further suggested that an increase in productivity, even if only a temporary "bloom," would be most likely to occur in transition from one life form to another since a new life form may be able to utilize accumulated limiting materials not available to the previous life form.

b) Whittaker (1965:251) cast doubts on the hypothesized correlation between increasing diversity and increasing production in the course of a successional development. In his extensive studies of plant communities, plant production, foliage insects, and birds in the Great Smoky Mountains, he has given measures of diversity (the number of vascular plant species) in quadrats and measured net production.

Variations in species diversity do not simply parallel variations in community production. In the Great Smoky Mountains, production and diversity are not significantly correlated either in vegetation samples or in samples of foliage insects. The magnificent redwood forests of the California and Oregon coasts, probably among the most productive of temperate-zone climax forests, have low species diversity.

Table 2, plotted in Figure 3, was made by combining Table 1 from Whittaker (1965) with Table VI from Whittaker (1966). It supports the conclusion that there is no demonstrated increase in production with increase in diversity.
**Table 2.** Species diversity and above ground net production, Great Smoky Mountains. (After Whittaker, 1965, 1966)

<table>
<thead>
<tr>
<th>Sample No.</th>
<th>Diversity</th>
<th>Production</th>
</tr>
</thead>
<tbody>
<tr>
<td>9</td>
<td>High mixed heath</td>
<td>8</td>
</tr>
<tr>
<td>10</td>
<td>Pine forest, Cade’s Cove</td>
<td>27</td>
</tr>
<tr>
<td>11</td>
<td>Pine forest, Pittman Center</td>
<td>32</td>
</tr>
<tr>
<td>12</td>
<td>Pine heath, Brushy Mountain</td>
<td>23</td>
</tr>
<tr>
<td>13</td>
<td>Pine heath, Greenbrier Pinnacle</td>
<td>20</td>
</tr>
<tr>
<td>14</td>
<td>Chestnut oak heath</td>
<td>23</td>
</tr>
<tr>
<td>15</td>
<td>Hemlock-beech forest</td>
<td>40</td>
</tr>
<tr>
<td>16</td>
<td>Hemlock-rhododendron forest</td>
<td>5</td>
</tr>
<tr>
<td>17</td>
<td>Spruce-rhododendron forest</td>
<td>7</td>
</tr>
<tr>
<td>18</td>
<td>Deciduous cove forest</td>
<td>43</td>
</tr>
<tr>
<td>19</td>
<td>Cove forest transition</td>
<td>44</td>
</tr>
<tr>
<td>20</td>
<td>Oak-hickory forest</td>
<td>26</td>
</tr>
<tr>
<td>21</td>
<td>Chestnut oak forest</td>
<td>27</td>
</tr>
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<td>22</td>
<td>Successional tulip forest</td>
<td>35</td>
</tr>
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<td>23</td>
<td>Upper deciduous cove forest</td>
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<td>24</td>
<td>Hemlock mixed cove forest</td>
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<td>Gray beech forest</td>
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</tr>
<tr>
<td>33</td>
<td>Fraser fir forest</td>
<td>6</td>
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</tbody>
</table>

* Column 1 — Diversity indicates the number of species in quadrat, from Table 1 in Whittaker 1965.
† Column 2 — Production equals total net above ground production, from Table 6 in Whittaker 1966.

**Soil Development**

**Statement of Hypothesis.** Whittaker (1970:69) stated: "A number of trends or progressive developments underlie most successional processes. There is usually progressive development of the soil, with increasing depth, increasing organic content, and increasing differentiation of layers or horizons toward the mature soil of the final community. . . ."

Two points in this statement call for examination. First, the length of time involved in development, and second, the differentiation of soils into layers as they mature. Central to the argument is the idea that successive generations of plants leave their remains which are incorporated.
into the mineral soil and humified while nutrients and minerals are leached and deposited at specific depths in the process of soil formation.

a) The time scale within which progressive soil development takes place has seldom been specified explicitly. But it is clearly implied that development of a mature soil profile is conterminous with succession, and is therefore a process which approaches completion and equilibrium in the climax. Because successions are generally believed to take a very long time (Clements 1916, Braun 1950) it is clearly implied that soil development requires a very long time for its consummation. "Succession in general appears to be very slow, and the vegetational history of any particular habitat is more apt to be measured in thousands of years, or even tens of thousands, than in centuries or decades" (Gleason 1927:301). "Cowles and others cherished the hope that the old black oak dunes might eventually succeed to typical mesophytic forest even though they had not done so in all of post-glacial time— that it was merely a question of too slow a rate and too little time" (Olson 1958:155). Cowles (1901:177) blamed "the slowness of humus accumulation ... perhaps more than all else."

b) Soil development involves increasing differentiation of soil horizons, so that processes which stir up and homogenize the soil into a uniform layer must be considered to reverse the process of soil development and to run counter to successional development.

FIELD EVIDENCE. a) Time scale of soil development. Olson (1958) re-examined chronological details of soil development in the vegetation of the Indiana sand dunes studied a half-century earlier by Cowles.

The ages of the dunes and hence of the period available for development of soils upon them were derived from ages of trees or dates of subsequently buried fences on younger dunes and from radiocarbon dating of older ridges and raised shore lines. Age estimates are of course subject to error (up to 20\%) but as Olson said: "Present Great Lakes chronology is far superior to any available only a decade ago and covers a much longer period than most previous quantitative studies of succession."

Our Figure 4 (Olson 1958, Fig. 19) graphs cation exchange relations as function of time age in the process of soil development. "The cation exchange capacity of dune soils is another important variable that increases along with humus content. The exchange complex is initially saturated with calcium and other metallic ions that are valuable in plant nutrition, but gradually these basic ions are partially replaced by hydrogen ions (exchangeable acidity) as soil development proceeds under the influence of vegetation" (Olson 1958:160). Figure 4 shows rapid changes

Figure 3 (after Whittaker 1965, 1966). Community diversity is compared to community productivity in the Great Smoky Mountains vegetation. Diversity (the number of vascular plant species) in quadrat samples numbered 9-33 in Table 1 of Whittaker (1965) is compared to productivity (total above ground net production) in the same numbered quadrat samples taken from Table VI of Whittaker (1966).
in the first 1000 years, followed by many thousands of years without further development.

Olson in his summary (p. 168) concluded that:

3. Soil analyses of carbon, nitrogen, moisture equivalent, carbonates, acidity, and cation exchange relations show how most soil improvement of the original barren dune sand occurs within about a thousand years after stabilization. The pattern of change on older dunes promises little further improvement and perhaps even deterioration of fertility.

4. Low fertility favors vegetation with low nutrient requirements. But such vegetation probably is relatively ineffective in returning nutrient to the dune surface in its litter and thus aggravates low fertility. Leaching of nutrients out of the sand-dune ecosystem and the low moisture reserve of

most dune surfaces help account for the poor prospects for successional replacement of the black oak-blueberry community by the more exacting species of the mesophytic forest.

Olson's studies indicated that soil development has been rapid in terms of the ages of the present dunes. Soils on a relatively young dune surface have developed to a steady state, but those on surfaces many times older have not “progressed.” The growth of trees appeared to be in response to physical stabilization of the dune-hollow rather than soil preparation.

b) Stratification in soil development. Goodlett (1954) studied the distribution of forest tree species related to the depths and structure of soil. He found wind-throw to be an active force in determining the structure of soils in the deciduous forests of Pennsylvania:

The unplowed areas of Potter County are characterized by pronounced microlief of mounds and pits. . . . Most of the mounds are old and have resulted from the fall of trees that grew in the presettlement forest . . . .

The evidence indicates that wind-throw has disturbed the soil materials to a depth of 2 to 3 feet throughout the past 200 to 300 years, and probably since the reoccupation of the region by forest trees. Lutz and Griswold (1939) made a study of the influence of tree wind-throw in southern New Hampshire, and suggested that “all soils which bear, or in the past have borne, forest stands have been more or less disturbed.”

Disturbance of the upper parts of the surficial deposits by wind-throw over long periods of time probably produces the high degree of variability observed in soil profiles over short horizontal distances. Existing soil profiles are disturbed, inverted, or destroyed within the depth of upheaval. . . .

Lutz (1940) described the effect of uprooting trees upon the structure of the soil in southern New Hampshire, a forest vegetation which would be generally accepted as climax:

. . . as a result of disturbance, horizons may be very irregular, occasionally with long tongues forming the upper layers penetrating deeply into the layers below. Further, horizons may be discontinuous and masses of soil material may be translocated to positions above or below those normally occupied. Frequently, material from upper and lower horizons is rather intimately mixed. The vertical and horizontal movements of rocks two or more feet in diameter is evidence of the tremendous forces involved. . . .

Farmers plowing the soil have leveled the mound-and-pit topography characteristic of the forest floor in old-growth stands. Because most of the soils of the northeastern United States have been plowed, and most studies of forests have until recently been made in that region, the real condition of the soils of the pre-Colonial “climax” forests has not been examined.

These studies of soil development and modification in early and late forest successional stages indicate that soils develop rapidly in response to the vegetation types on the site. No evidence indicated that development of a profile is associated with the replacement of the vegetation type
responsible by another one. In the northeastern forest region there is evidence that the mature old-growth forest grew on soils which were immature by theoretical standards.

**Sequence of Vegetation Types**

**Statement of hypothesis.** Whittaker (1970) describes the process: "One dominant species modified the soil and microclimate in ways that made possible the entry of a second species, which became dominant and modified its environment in ways that suppressed the first and made possible the entry of a third dominant, which in turn altered its environment."

In order to understand why species compositions change, we need to know if species associations replace each other as groups; whether later communities replace early stages, or if many of the final climax species are present on the site from the start. Also, do the species of the early stages facilitate or inhibit the establishment of the species of later stages? If the early stages are removed, is the appearance of later communities delayed or accelerated? And finally, do successions always go in one direction? Do lateral and retrogressive successions occur and under what conditions?

The question — Are the early successional stages made up exclusively of species of lower life form or is it possible that most species are present as seedlings from the start and the visible successional sequences are the overt expression of sequential conspicuousness reflecting different growth rates and sizes at maturity?

In a review of old field succession Egler (1954) presented two opposed hypotheses. In his "relay floristics" one floristic group relays the site to another until some relatively stable stage is reached. This sequence would illustrate simple or classical succession.

In his "initial floristic composition," "Up to the year of abandonment, the land is receiving many species as seeds and living roots. . . . After abandonment, development unfolds from this initial flora, without additional increments by further invasion (for the purpose of this discussion)."

Typological thinking (Mayr 1963) as applied to plant associations could make this contrast too black and white, but if a moderate number of the species of later stages should prove to be present as small individuals in the early successional stages, the observation would throw doubt on the purported importance of the early successional stages in modifying the environment.

**Field evidence** from several studies is cited in the paragraphs which follow.

a) Clements (1916:59, 1928:103) observed that cases of "initial floristic composition" occur:

Secondary areas such as burns, fallow fields, drained areas, etc., contain a large number of germules often representing several successive stages. In some cases it seems that the seeds and fruits for the dominants of all stages, including the climax, are present at the time of initiation.

b) Niering and Egler (1955:359), referring to plant succession along power lines in Connecticut, said:

It has been found that the majority of woody plants of the so-called later "stages" and old field "succession" have not been currently invading. To the contrary, it appears that they had invaded at the same time as or previous to the earliest stages.

c) Hack and Goodlett (1960) studying a forested valley in Virginia damaged by a flood, reported:

Sycamore and black locust trees rapidly covered the scarred areas on the valley bottoms, but six years after the flood most of the tree species characteristic of the undamaged mature forest were present.

Elsewhere these same authors reported that the tree seedlings first colonizing the landslides on the slopes were identical to the species of trees found on older, pre-Columbian forested landslides. They said:

Many of the landslides terminated in large piles of rock, soil and up-rooted trees. Old debris fans, mantled by mature trees of large diameter, indicate that similar floods have occurred in this area in the recent past, creating slides similar to those formed by the 1949 cloud-burst. The vegetation of these areas of older slides shows an adjustment of composition to topographic form.

d) Marquis (1967) reported on the vegetation composition on a site after clear cutting of an old growth stand of northern hardwoods. See Table 3 (from Marquis 1967). Tree species are identified as shade tolerant (i.e. climax), intermediate, and intolerant (i.e. sun requiring or successional). He said (p. 6):

Five years after cutting, four tolerant species comprised over half of the total numbers of stems. This proportion has increased gradually as the stand matured so that tolerant species account for 63 per cent of the stems at 30 years of age. . . . If left to mature naturally, this stand will become increasingly similar to an uneven-aged stand. . . . Red maple and white ash should survive past 100 years, but eventually they too will mature and the stand will then be dominated by the original, long-lived climax species—beech and sugar maple with small amounts of yellow birch.

Detailed studies are needed to establish at what stages "climax" species colonize a site. For example, for a critical resolution of this in Marquis's (1967) study, it would be necessary to have marked trees in the understory at the time of clear cutting. It would also of course be necessary to eliminate from consideration stump sprouts and coppice which came up after cutting. Nevertheless, this and the previous studies suggest that individual trees which make up the "climax" forest were present from the start. Hence the studies throw doubt upon the functional aspects of alteration of the environment by successional species.
Another question: Do the species of the early stages facilitate or inhibit the establishment of species of later stages?

A phenomenon called reaction, “the effect which a plant or a community exerts upon its habitat” (Clements 1916) is generally acknowledged to be central to autogenic replacement of communities. Clements (1916:79) said: “Reaction is thus the keynote to all succession, for it furnishes the explanation of the orderly progression by stages and the increasing stabilization which produces a final climax.”

Field evidence from several studies is cited here.

a) McCormick (1968:9) said:

There is no question that reactions do occur. A single plant, whether lichen or rewood, casts shade, changes the pattern of air movements, produces organic material that may become humus, and affects the site in other ways. The importance of such effects in succession, however, has not been tested adequately and certainly the generalization that these effects constitute the driving force of succession is not substantiated.

He then went on to examine the effects at an early or pioneer stage of succession on an old field and reports:

In a series of experiments initiated at the Waterloo Mills Research Station, Devon, Pennsylvania, in 1965 and repeated in 1966 and 1967, annual plants were removed as seedlings from some sections of a recently plowed field, but were allowed to grow elsewhere. According to reaction theory, an annual vegetation is necessary to “prepare the way” for perennial plants on such a site. By the end of each summer, however, perennial plants were several times as abundant on areas kept free of annuals. The biomass (dry weights) of individual perennial plants on the annual-free areas were many (15 to 82) times as great as those on areas with annuals. Many goldenrods, asters, black-eyed susans, and other perennial plants flowered on annual-free sections, but were sterile on plots covered with annuals (McCormick et al., Mss.). This experiment does not refute the general theory of the reaction mechanism. However, it does seriously question the reality of the theory and indicates that the theory was not valid for the early old field situation in which it was tested.

b) Pound and Egler (1953) found that on a fire line cleared and spike-harrowed in 1934-1936 “...the accidental absence of suitable conditions for germination and development of tree seeds and the absence of root-suckering trees allowed the formation of a dense low vegetation that has since prevented the mass invasion of trees.”

c) Niering and Egler (1955) documented the exclusion of trees of the “next successional” stage by a closed canopy of the shrub nainberry over a period of 25 years. They suggested that minor silvicultural steps could lead to more or less indefinite exclusion of trees by the closed shrub canopy once it is established.

The *Viburnum* thicket has apparently been in existence for a quarter of a century as a self-perpetuating shrub type. Some of the tallest, oldest *Vi*
burnnum stems are dead or dying, and will be replaced by younger stems, with no change in the overall height or appearance of the community. . . . The transgressives, barring accidents, would presumably grow to maturity and change at least a portion of the area into forest. . . . It seems reasonably certain, however, that the Fothernum thicket is not "permanent," and that eventually, in 30, 60 or 90 years, an occasional tree will break through and convert the area to forest. On the other hand, the number of such maturing trees of the past 25 years has been so small that economic control of them, as by artificial means, would appear to be an extremely low-cost procedure requiring attention only at intervals much greater than a decade. . . .

In most instances, it has been found that shrub-dominated vegetation tends to resist invasion by tree seedlings, whereas upland eastern grasslands are relatively open to invasion by pines, ashes, maples, elms, birches and tulip poplar.

d) Both "early" and "late" stage trees may be suppressed if overtopped. In the same way that red cedar and gray birch can be overtopped and suppressed in oak-hickory forests of southeastern New England, so seedlings of red oak, white oak, elm, white ash, sugar maple, red maple, pin oak, hickory, basswood, and beech can be found in the understory of tall forests of old field pine in central New England (Raup & Carlson 1941, Lutz & Cline 1947). While the pines are on average 90 to 100 years old (aged by counts of annual rings on increment borer samples), the hardwoods, though slender, are on average 50 to 70 years old. With the cutting of the overtopping pine, the suppressed hardwoods flourish.

e) J. A. Kadlec (in litt.) has observed in experimental game management areas in Michigan that removal of "pioneer" trees such as aspens speeded the appearance of species of later successional stages.

1) Olson (1938) observed that on the sand dunes he studied the first tree species to be established inhibited the successful colonization of the site by competitors. A closed stand of black oak-blueberry tended to regenerate itself instead of being replaced by the beech-maple "climax," because of the acid leaf litter these species produce and the low rate of return of nutrients to the soil.

g) The production by plants, through the roots or in the litter, of chemicals which inhibit the germination or growth of plants of their own or other species has received wide attention as a physiological phenomenon for many years (review by Whittaker & Feeny 1971).

That plants should release products which facilitate the growth of their own species and inhibit the growth of other species makes better sense according to natural selection than that they should alter their habitat in such a way as to facilitate the growth of other competing species. Several publications indicate that some "early successional" species do produce chemicals which inhibit the growth of later stage species.

Rice (1964) showed inhibition of nitrogen fixing and nitrifying bacteria by old field grasses which apparently gave them competitive advantage over grasses of later successional stages. Brown and Roti (1963) found that perennial goldentips produce a chemical which inhibited the germination of seeds of jack pine, a pioneer tree on old fields in Michigan. Brian (1949) and Harley (1952) showed that the shrub, ling, produced substances which inhibit mycorrhizal fungi—and, therefore, trees which require them.

An additional question: Are successions unidirectional?

Pond margins, marshes, and bogs have been generally cited as illustrations of typical successions (Smith 1966:182–191, BSCS "Green Version" 1963). The classical illustration of bog succession follows the sequence of (a) floating aquatics, (b) sedge-sphagnum floating bog which is followed by progressive compaction and humification, (c) succession of sphagnum species to produce a heath peat bog, and (d) (a hypothetical extension) a bog forest covering a peat-filled lowland.

Field evidence from several studies is cited here.

a) Several detailed studies of large bogs in the coniferous forest regions of North America and Europe have failed to find this standard sequence and led their authors to doubt even that it necessarily occurs. Drury (1956) in Alaska, and Sjörs (1948, 1950, 1955) in Sweden and the Hudson's Bay lowland drew conclusions similar to those of Heinselman in the region of Glacial Lake Agassiz of Minnesota (1963:370):

Neither the process of bog expansion nor the patterned bogs and fens of the Agassiz region fit the classical picture of succession in the Lake States. Conclusions are that: (1) Few bogs in this region are the result of a single successional stage. (2) The bog types cannot be regarded as stages in an orderly development toward mesophytism. (3) Raising of bog surfaces by peat accumulation does not necessarily mean progression toward mesophytism. Such rises often cause concurrent rises of the water table and promote site deterioration. (4) The climax concept does not contribute to understanding bog history in this region.

b) Johnson and Raup (1947) found that the peat of a peat island in a salt marsh on the Taunton River in Massachusetts gave no indication of succession of marsh grasses. The peat indicated continuous stream cutting and redeposition and most plant remains were of one type, salt-water cord-grass. Progression of vegetation types in a successional sequence was not found.

c) Walker (1970) summarized his study of the courses and rates of British post-glacial hydrosereus using peat and mud stratigraphy, amplified by pollen diagrams by saying:

... Although certain sequences of transitions are 'preferred' in certain site types, variety is the keynote of the hydrosenal succession. In spite of this, the data clearly indicated that bog is the natural 'climax' of autochthonous hydrosereous throughout the British Isles and the transition from fen to oakwood is unsubstantiated.

The term bog as referred to in this quotation is distinguished by a variety of Sphagnum species and acid tolerant plants such as Dwarf Cranberry, Sweet Gale, Cotton Grass, and Heath,
To summarize this section on the sequence of vegetation types, those cases in which detailed studies of forest succession have been made do not indicate an orderly replacement of early successional species by members of later communities. They indicate instead that in the usual case almost all species have established before the "succession starts" or that they colonize during the first few years. Hence in many cases the manifest "succession" is a sequential expression of conspicuousness which reflects the maturing of species having different speeds of growth and sizes at maturity.

In fact it appears in those cases where critical examination has been made, that early and middle successional stages suppress climax species and delay the expression of later stages. Detailed studies of events in the hydrosere indicate that successional trends are readily deflected or reversed in response to changes in water level which are externally controlled. In one case at least early successional stages (mosses) invade a forest and stimulate a rise in water table—hence reverse succession by autogenic processes. Their presence leads to replacement of the forest by heath-birch stage (Sjörs 1918, Drury 1956, Heinselman 1963).

**Diversity, Stability, and Reproductive Strategies**

**STATEMENT OF HYPOTHESIS from Margalef (1968:31):**

Diversity very often increases. Sometimes diversity increases to a certain value and then decreases again toward the final stage of succession... Fluctuations are damped and rhythms change from reactions directly induced by external agents to indirect responses to stimuli associated with ecologically significant factors; the ultimate trend is to endogenous rhythms...

In the later stages of succession, a relative constancy of numbers is achieved, and populations are not forced to reconstruct themselves rapidly after drastic and extensive destruction. The natural trend is toward a reduction in the number of offspring produced and better protection for the young.

First: **Diversity.**

**STATEMENT OF HYPOTHESIS:** Diversity in most contemporary usage refers simply to the total number of species present. The term has in the past, however, referred to all ill-defined, more complex (and more useful) concepts of community diversity including structural variety and relative frequencies of species in addition to taxonomic variety. There have been such "diverse" uses of the term that Hurlbert (1971) said: "The recent literature on species diversity contains many semantic, conceptual, and technical problems. It is suggested that, as a result of these problems species diversity has become a meaningless concept..." It is used here in its simplest sense—the number of species present.

In order to clarify the ecological significance of the increase in species diversity in the course of "successional" sequences, we need to establish which of the following statements is valid:

1. The successional sequence is the result of a process of replacement of less successful by more successful communities in which the more diverse communities are more successful.
2. The increase of species diversity is a reflection of later emergence into prominence of species which were present at the start as inconspicuous seeds and seedlings.
3. The process of succession combines (b) with progressive species enrichment (independent of modification) as a result of continuing colonization of the site. Then, species will be added first which are numerous, close at hand, and/or have highly developed means of dispersal. With the passing of time, less numerous species—those occurring at a greater distance and/or those having less effective means of dispersal—will arrive "by chance."
4. Diversity is a result of microtopographic and other special influences such as herbivore predation, and thus only partially a result of "intrinsic" processes.
5. "Diversity" is uniformly expressed in all parts of a community. Diversity in the herb layer is correlated with diversity in the shrub and tree layers, and with diversity in the insect and bird species.

Although (a) conforms to the classical descriptions of succession, contemporary ecologists consider the process of succession to result primarily from species by species replacements. Evidence of community by community replacements is inadequate.

Evidence for (b), that some successional changes result from sequential growth rates of the members of a largely complete initial floristic composition, was presented in the first part of this section. Very detailed studies which are not available at present are necessary to confirm that this is the case. Similarly, detailed studies would be necessary to eliminate the probability that (e) is a major ancillary process in most successional sequences.

Evidence that (d) plays a decisive part and that there are inconsistencies with regard to (e) would suggest that diversity is an ecological phenomenon independent of succession.

**FIELD EVIDENCE** from several studies is cited here.

a) Goulden (1969) discussed temporal changes in diversity correlated with what he called development of species associations in fresh water lakes. He based his conclusions on counts of the numbers of species found in cores of lake sediments, including the earliest stages of the lake's history. Interpreting his data from one lake, he described the sequence of events as follows:

The initial rapid immigration of species into the lake is followed by a period during which the common species become less common and the rare species less rare, which is usually associated with a change in dominant species. The sharp increase in diversity is terminated with the attainment of max-

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9 In this passage, Goulden used the term "diversity" to refer to the information-theoretic measure of weighted species abundance.
imum diversity for a given number of species. A third phase follows in which additional rare species are established.

The pattern Goulden reports is consistent with ideas presented by Darwin (1859) and Wallace (1876, 1880) and discussed in general by Darlington (1957) and in detail by MacArthur and Wilson (1967). Gleason (1917:474) emphasized that the arrival of additional species simply by migration is a major aspect of “successional” change. At first, common, widespread and well dispersed species rapidly appear. These are followed by less common, well dispersed or widespread species, which have different competitive strategies such as larger size or longer life span. With their arrival we can expect a change in dominance. Last, the widely dispersed, infrequent “rarities” appear at increasing time intervals.

b) Hack and Goodlett (1960) found in the floodplains of main valleys (i.e. higher order valleys) of the Little River in northern Virginia, a northern hardwood forest enriched by many species “extremely rare or absent in the northern hardwood forests of the hollows. . . .” The number of non-tree species is generally larger than in the northern hardwood stands of first order valleys.” In other words the floodplain, subject to repeated ravages and destruction by high water, and therefore the youngest, most unstable surface, supports the most diverse forests. The hollows, which for geomorphic reasons are subject to a higher rate of creep than most slopes, also support a relatively diverse northern hardwood forest, and the noses, the most stable surfaces of the area, support forests of the lowest diversity.

c) Oberved diversity may indeed reflect external circumstances more than the actual number of species present, as has been shown by some experiments carried out in old fields in an originally forested area of Britain (Harper 1969:49):

Generalizing from the controlled experiments and the results of post Myxomatosis surveys, the effects of rabbit removal appear to be (i) the release and demonstration of hitherto unsuspected floristic riches in the rabbit-grazed communities: species which in the past had been regularly nibbled and suppressed, flowered and showed their true identity. . . .

When protection from grazing was continued over a long period, in controlled experiments using fertilizers and fenced plots on native hill pastures in central Wales: “The effect of this long period of freedom from grazing in each year was to reduce the number of species present, and the normal result was virtually exclusive development of one or two species of grass. . . .” These results show that “unrestricted stock access was a conservative force on the vegetation and only controlled (heavy) but intermittent grazing allowed the richer flora to develop.” They further show that complete removal of grazing was also a conservative force in some cases, while in other cases there was a “later return of a new diversity associated with the entry of species belonging to phases of succession towards scrub. . . .” (Milton 1940, 1947).

1973] DRURY & N. DET. SUCCESSION

According to these field studies, the number of species in a plant association may reflect primarily special circumstances of soil, microtopography, disturbance, or predation by grazing mammals (and release from grazing) which allow certain species a local differential advantage and which suppress the tendency of some species to become dominant and exclude other species.

d) Whittaker (1965:251, 252), referring to his own field experience, said:

Diversity is as high in the disturbed, immature forests as in mature stable forests of corresponding environments. Tree-stratum diversities increase from high elevations toward low. Diversities of herb and shrub species show no clear relation to elevation below 1400 meters in the Smokies. In both the Siskiyou and Santa Catalina Mountains herb diversities increase from low to middle elevations and decrease from these to high elevations. Along the moisture gradient in the Smokies, the highest tree diversities are in intermediate sites, the highest shrub diversities are in intermediate-to-dry sites, and the highest herb densities are in moist sites. Diversities of the three strata are scarcely correlated, and numbers of insect and bird species are not simply correlated with numbers of plant species.

Hence diversity is inconsistently expressed and increased diversity is by no means an exclusive property of the later stages of vegetation succession.

Second: Stability.

Statement of Hypothesis. No generally accepted definition of stability in ecological systems is available (Brookhaven Synopsis in Biology No. 22, 1969). It is not clear whether the term means dampened fluctuations of numbers or long survival until extinction. We know of no comparative study which has confirmed the generally accepted idea that all or the majority of species populations fluctuate less in areas of greater ecological diversity. It is in fact clear that some animal species vary greatly in numbers (squirrels, rabbits, mice, chickadees, foxes) in some complex habitats, while others in the same habitats do not. On the other hand, not all species in the “simple ecosystems” in the north show the periodic spectacular changes in numbers which successional theory predicts.

Third: Reproductive strategies.

Statement of Hypothesis. Wynne-Edwards (1959, 1962) argued in general that reproductive rates are adjusted to mortality rates in order to avoid overexploitation of food supplies and consequent crashes. MacArthur and Connell (1966) rephrased the argument and applied it specifically to climax habitats. Adjustment of reproductive rate to mortality rate also appears inherent in the concept of “K-selection,” at least in its original formulation for closed populations on islands (MacArthur & Wilson 1968:149).

Field evidence.

Adjusted reproduction has been demonstrated only in specially formulated genetic models and there is no evidence that they correspond
to natural populations. It seems extremely improbable in plants, which produce vast quantities of seed and in any case do not overexploit their "food supply" or suffer crashes.

In animals, overproduction has been demonstrated even in a climax species by Kuyver and Tinbergen (1953); Kuyver (1966) demonstrated by experiment in the same species that mortality was adjusted to reproduction and not vice versa. However, the subject is still debated (Lack 1966, Skutch 1967). It is indeed likely that animals raise more young in areas where net production is very high (Crook 1965), but this can be understood as a response to variable food supplies within the context of r-selection (Lack 1966, 1968).

**Allogenic vs. Autogenic — Sand Dunes, Ponds and Marshes, Flood Plains, and Moraines**

**Statement of hypothesis.** One of Odum's (1969) hypotheses about succession is that the process is community controlled. Olson (1958:132) put it that change of an ecosystem could proceed as a function of time *even if all other variables remained constant*. If, however, vegetation changes occur in response to site changes produced by extrinsic events, then the "sequences" are not developmental but simply reflect the ecological truism that different species require different habitats.

**Field evidence** from several studies is cited here.

a) Excavations in Alaskan bogs (Drury 1956) indicated that the "late successional" bog forests were simply perched upon a thick peat composed of species of emergent mosses mixed with alluvial and aeolian silt. Where the water table had been locally lowered by deposition of silt, forest had grown up. Where the water table had risen, the forest had been replaced by bog. Other studies of bogs (Sjörs 1955, Heinselman 1963) also indicate that the observed changes are not developmental. Johnson and Raup's (1947) excavations at Grassy Island gave no indication of succession in the sediment record, but instead showed evidence of a continuing process of stream erosion and deposition, with plants colonizing newly deposited banks and being destroyed as the river's meanders migrated across the marsh.

b) Moraines abandoned below mountain glaciers have been used to illustrate primary succession from bare soil through tundra and willow-alder shrubs to needle-leaved forest. Cooper's work in Glacier Bay (1923) and Sigalos and Hendrick's on Mt. Rainier (1969) suggest on the contrary that moraine vegetation is generally at equilibrium with the present conditions. In fact, where local conditions are suitable, vegetation of an "advanced successional stage" grows on or next to the ice. In 1948 and 1950 Drury found a spruce forest 50-60 feet tall growing on the moraine, underlain by ice, of the stagnant Matanuska Glacier in Alaska. In Iceland at the edge of Vatnajökull Glacier, birch grows next to the ice and on sites covered by ice as recently as 1934 (Lindroth 1970).

**SKETCH OF AN ALTERNATIVE EXPLANATION**

In these extreme habitats, a site's edaphic and microclimate conditions differ according to topography and geomorphic changes beyond the control of (although influenced by) the vegetation. At each site various species whose propagules are already available or are constantly reaching the site are able to become established. Hence each vegetation type or zone appears to be in equilibrium with the present environment, in the same way as the several zones of vegetation on a mountainside.

**Point of departure.** The starting-point for such an explanation is three sets of observations on succession in forested regions 4 which we believe to be widely accepted.

1) On sites which are cleared but initially free of seeds, certain kinds of plant species (usually those of depressed life forms) tend to appear first; others (including those of successively larger and more complex life forms) appear later. Sites illustrating this sequence ("primary succession") are rare in nature: examples include exposed sandbanks, volcanic deposits, receding glaciers and mine tailings. Although many textbooks give hypothetical accounts of such successions, very few cases have been actually observed and only the early stages in succession have been described. Evidence about later stages in primary succession is conflicting (e.g., Olson 1958) or lacking.

2) On sites which are cleared but not initially free of seeds, there is usually a similar vegetational sequence, often apparently involving the same kinds of plants, but usually taking place more rapidly ("secondary

4In our opinion there are as yet insufficient precise observations on successional sequences in non-forested ecosystems to support any generalizations about them, or to incorporate them into a comprehensive theory.
succession”). Again most published studies are of the early stages in succession and accounts of the later stages are largely hypothetical. The evidence summarized in this paper suggests that the later stages of succession are not consistently unidirectional, and that forest succession is better represented by the lower half of Figure 1 than by the upper half.

3) Spatial gradients of several kinds of stress (climatic, chemical or radiological) give rise to similar sequences in space of life forms and vegetation. The congruence between sequences produced by different kinds of stress is reasonably well documented (see review by Woodwell 1970), although few detailed descriptions are available for any but climatic stresses.

The main task in constructing a theory of forest succession is to explain the apparent congruence between the stress-induced sequences and the early and middle stages of primary and secondary successions.

Stress gradients. Vegetational sequences on stress gradients are reasonably well understood (Woodwell 1970). Each species appears to be specialized to a certain type of site and is competitively superior within a limited range of conditions, so that different species are dominant at different points along environmental gradients (MacIntosh 1967, Whittaker 1953). Plants of higher life form dominate under low stress conditions, but are unable to withstand higher stresses. The contrasting selection pressures have been considered by Raunkiaer (1934), who classified plants into life forms according to the location of their protected growing points. Those plants, geophytes, whose buds are well protected in the ground must grow their photosynthetic structures each year. They are readily overtopped. Tall, dominant plants, phanerophytes, have competitive advantages but their buds are vulnerable to drying winds, ice, fire, and radiation. Chamaephytes, whose buds are within a couple of meters of the ground, are intermediate in adaptations.

Woodwell (1970) emphasized that plants of higher life form usually have a larger ratio of supportive structures to productive structures: hence they have a smaller margin of reserve productive capacity to repair damage and are more susceptible to stress. Thus much of the observed correlation between stress gradients and vegetational sequences can be related to the problems of organization of a complex organism, together with the competitive pressure for plant species to evolve specializations to a limited range of environments.

Secondary successions. Turning to secondary successions, most of the studies cited in this paper suggest that the early stages in secondary successions can be understood adequately in terms of differential growth. Changes in the later stages are not consistently unidirectional and appear to be influenced primarily by external factors such as grazing, stream cutting, and storm damage, which recur on a time-scale shorter than that required for intrinsic development. Whereas the classical and contemporary theories of succession place primary importance on the role of early successional plants in modifying their environment and permitting later vegetational stages to become established, the studies cited in this paper suggest that modifications of the environment by plants act frequently or generally to delay succession. The mechanisms involved include competition for nutrients, shading, pH modification and allelopathy (allotoxicity).

The studies of secondary successions cited in this paper suggest that the plants dominant in the later stages were present either from the beginning, or at least from a very early stage. Their in conspicousness in the early stages appears to be a consequence of their slow growth and/or their suppression by other species (and, to some extent, to the preoccupation of botanists with the dominant species). That is, most of the detailed observations are consistent with the “initial floristic composition” model of secondary succession (Egler 1954).

Cases in which one species, or a group of species of the same life-form, succeed in dominating the vegetation and maintaining a quasi-stationary state for a time, do not necessarily provide good evidence for the “relay floristics” model. The data of Olson (1958), Niering and Egler (1955), Raup and Carlson (1941), McCormick (1968), and Brown and Roti (1963) suggest that they should be interpreted as delays in the growth sequence, effected by successful suppression of growing subdominant plants by the temporarily dominant species. The replacement of the dominant plants by species of the next higher life form may require external disturbance (Niering & Egler 1955, Olson 1958, Raup & Carlson 1941). In the contemporary theory of succession, this replacement is in part explained as a consequence of continued high net productivity. In fact, however, net productivity is relatively low during the quasi-stationary periods and increases rapidly when a new set of plants becomes dominant (Odum 1960). These flushes of productivity are most easily explained by the hypothesis of release from suppression by the previously dominant plants.

Primary successions. Genuine observations on primary successions are meager. It seems to be generally accepted that primary succession takes place more slowly than secondary succession, but the relative roles of soil development, external supply of nutrients, exposure, and seed immigration in controlling the rate of development remain largely hypothetical.

6 Autotoxicity constitutes a limited exception to this generalization. There is at least one well documented case in which autotoxicity in a herbaceous annual appeared to accelerate or at least permit its rapid replacement in a grassland succession (Wilson & Rice 1968). However, even in this case the autotoxic chemicals were also allotoxic (see also Parenti & Rice 1969). The importance of autotoxicity in successions needs to be investigated further, but its explanation should be sought within the framework of natural selection theory. Tentatively, we suggest that autotoxicity might be a by-product of selection for producing allotoxic chemicals whose primary function would be in interspecific competition. Autotoxicity would not be selected against in species whose individuals disperse their seeds beyond the range of their own toxins, and might even serve a function in intraspecific competition in such species. To interpret its function as facilitating the establishment of other species would be teleological.
The observations quoted in this paper of “late successional” trees growing on stagnant glaciers and close behind retreating glaciers suggest that the role of soil development in primary successions has been exaggerated, and that species of later stages can become established within a few years of initial exposure. The rapid growth of forest on Krakatoa and the dominance of phanerophytes there from the very start (Richards 1952) suggests the same conclusion. The data of Olson (1958) suggest that the availability of water and nutrients may be more important limiting factors on the rate of establishment of species than the age, thickness, or organic content of the soil. Tentatively, however, we also ascribe importance to the rate of dispersal of seeds, since “early successional” species tend also to have adaptations for rapid dispersal.

Congruence of temporal and spatial sequences. Species dominant in early stages of secondary or primary successions are those characteristic of high-stress sites (Woodwell 1970). According to the present interpretation, they achieve early dominance primarily because they grow faster than species adapted to lower-stress sites. A generalized explanation for the differential growth is given in the arguments of Raunkier and Woodwell summarized above. The early dominant species maintain dominance for as long as possible by suppressing competitors, but are replaced because in general they live less long and grow less tall than their successors. In primary successions (but to a much lesser extent in secondary successions) the establishment of the low-stress species may be delayed by delays in immigration and by physical stresses.

According to this highly generalized explanation, therefore, most of the phenomena of succession should be understood as resulting from the differential growth, differential survival, and perhaps differential dispersal of species adapted to grow at different points on stress gradients. The appearance of orderly replacement of “communities” of successively higher life forms results, at least in part, from the temporary dominance of certain species over their successors. Net productivity remains high throughout succession simply because the plants are growing, and it is reduced during the periods at which full-grown plants suppress their potential successors. Net productivity rises when larger plants replace smaller plants, but this is a consequence of the growth of the larger plants and is not a cause of the replacement (as the contemporary theories imply).

Under this interpretation, succession on a single site usually involves a sequence of species (rather than simply the growth of the ultimately dominant species) because no one species can dominate the vegetation throughout the period of growth. In other words the basic cause of the phenomenon of succession is the known correlation between stress tolerance, rapid growth, small size, short life, and wide dispersal of seed. The few exceptions to this general correlation— mangroves, redwoods, coconut palms, Douglas firs—are also exceptions to the generalization of succession: they are both “early successional” and “climax” species.

Adaptations to diverse sites. Contemporary theories of geomorphological development (e.g. Chorley 1962) emphasize the continuity of the processes of uplift and erosion (in contrast to the classical concepts of cycles of erosion (Davis 1909) on which the classical theory of plant ecology was based (Clements 1936; for discussion see Drury & Nisbet 1971}). As a consequence, gradients of exposure, soil type, moisture, and other stresses can be assumed to exist continuously in essentially every geographic region. This permits the specialization of different species to different points along the stress gradients, under the pressure of interspecific competition. One extreme evolutionary strategy is to occupy sites at the extreme upper end of the stress gradient, and to grow and reproduce rapidly (during the favorable growing season) before fluctuations in weather make the site intolerable. The other extreme strategy is to occupy the most sheltered sites, to dominate the vegetation by growing as large as possible, and to live as long as possible. Species which adopt these extreme strategies may be equally well adapted to their own environments: there is no need to suppose that the species adapted to the exposed sites are “immature” or “less fit.” In geological terms, the sheltered sites are as transitory as the exposed sites.

When new unvegetated sites become exposed, plants adapted to exposed sites are pre-adapted to occupy them and to grow well, provided that they can colonize them before they are occupied by competing species. Thus efficient seed dispersal will give a competitive advantage to individuals of the stress tolerant species. This advantage would contribute to the evolution of efficient dispersal mechanisms in these species.

Essential hypothesis. To place these arguments into a deductive framework, it is necessary to formulate the following hypotheses which differ at least in emphasis from those in contemporary theories of succession.

1) Gradients of soil conditions and exposure to stress exist continuously in essentially every geographic region, as a result of continuous geological processes of uplift and erosion.

2) Different species are specialized to grow under different site conditions, under the pressure of interspecific competition.

3) Individual plants already growing on a site generally have a competitive advantage over seedlings and immigrant individuals, but the advantage is often reduced by disturbance.

4) Dispersal mechanisms and tolerance of physical stress are correlated (together they constitute colonizing ability).

5) Colonizing ability and growth rate tend to be inversely correlated with size at maturity and with longevity.

Hypothesis (1) is geologically trivial, but it needs to be stated explicitly because it conflicts with the classical concept of landscape stability which underlay classical succession theory. Hypotheses (2) and (3) are biologically trivial, but represent the explicit introduction of natural selection into succession theory, in which it is customarily neglected.
Hypotheses (4) and (5) are the key statements underlying our explanation of succession. They amount to the assertion that certain adaptive strategies are mutually exclusive: species whose seeds travel far and grow fast in harsh conditions cannot also grow large and live long. There is a well-known correlation between size, longevity, and low growth-rate. We suggest that this correlation, together with the Raunkiaer-Woodwell argument, comprise a sufficient explanation of the broad features of succession.

An explanation of the correlation might be sought either in theories of senescence, or in theories of the organization of organisms. In any case, we suggest that a complete theory of vegetational succession should be sought at the organismic, physiological or cellular level, and not in emergent properties of populations or communities. The former approach seems more consistent with the theory of natural selection.

SUMMARY

In contemporary usage the term succession refers to a sequence of changes in the species composition of a community, which is supposed to be associated with a sequence of changes in its structural and functional properties. The term succession is generally used for temporal sequences of vegetation on the same site, but only the early stages in the sequence can be observed and the later stages are usually inferred from observations on spatial sequences on adjacent sites. The term is customarily applied to sequences in many types of environment, although few detailed studies have been reported except for temperate forested regions. Contemporary theories of succession in general ascribe the observed phenomena to the action of the community itself in changing the environment.

This paper discusses a number of detailed studies of succession in forested regions, and shows that most of them do not conform to the contemporary generalization. The changes in structural and functional properties are not consistently associated with changes in species composition; the later stages in succession are not consistently unidirectional; and the effects of species already on the site appear frequently to delay rather than facilitate successional replacement.

An alternative explanation is outlined which is based on the observed congruence between temporal sequences of vegetation and spatial sequences along environmental gradients. According to this explanation, most of the phenomena of succession can be understood as consequences of differential growth, differential survival (and perhaps also differential colonizing ability) of species adapted to growth at different points on environmental gradients. The appearance of successive replacement of one "community" or "association" by another results in part from interspecific competition which permits one group of plants temporarily to suppress more slowly growing successors. The structural and functional changes associated with successional change result primarily from the known correlations in plants between size, longevity, and slow growth. A comprehensive theory of succession should be sought at the organismic or cellular level, and not in emergent properties of communities.

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SCIENTIFIC NAMES OF PLANT SPECIES
REFERRED TO IN THE TEXT

Balsam fir
Fraser fir
Hemlock
Spruce
White pine
Jack pine
Red cedar
Redwood
Douglas fir
Salt-water cord-grass
Cotton grass
Coconut palm
Greenbrier
Quaking aspen (Aspen)
Sweet Gale
Pignut hickory
Yellow birch
Gray birch
Paper birch
Beech
White oak
Chestnut oak
Red oak
Black oak
American elm
Tulip poplar
Sycamore
Pin cherry
Black locust
Striped maple
Sugar maple
Red maple
Basswood
Dwarf cranberry
Blueberry
Heath
Abies balsamea (L.) Mill.
Abies Fraseri (Pursh.) Poir.
Tsuga canadensis (L.) Carr.
Picea spp.
Pinus Strobus L.
Pinus Banksiana Lamb.
Juniperus virginiana L.
Sequoia sempervirens (Lamb.) Endl.
Pseudotsuga taxifolia (Poir.) Britt.
Sportula alteriflora Loisel.
Eriophorum sp.
Cocos nucifera L.
Smilax sp.
Papulus tremuloides Michx.
Myrica Gale L.
Carya glabra (Mill.) Sweet
Betula intera Michx.
Betula populifolia Marsh.
Betula papyrifera Marsh.
Fagus grandifolia Ehrh.
Quercus alba L.
Quercus Primus L.
Quercus rubra L.
Quercus velutina Lam.
Ulmus americana L.
Liriodendron Tulipfera L.
Platanus occidentalis L.
Pinus pinyponiana L. f.
Robinia Pseudo-Album L.
Acier pinyponianum L.
Acier saccharum Marsh.
Acier rubrum L.
Tilia americana L.
Vaccinium Oxyccocos L.
Vaccinium spp.
Erica Tetralix L.
Ling calluna vulgaris (L.) hull
White ash Fraxinus americana L.
Nannyberry Viburnum Lentago L.
Goldenrod Solidago spp.
Solidago altissima Nutt.
Solidago juncea Ait.
Aster sp.
Black-eyed Susan Rudbeckia serotina Nutt.

LITERATURE CITED


1926. The fundamentals of vegetational change. Ibid. 7: 391-413.


1911. The causes of vegetative cycles. Ibid. 51: 161-193.


1973] DRURY & NISBET, SUCCESSION 365


— 1926. The individualistic concept of the plant association. Ibid. 53: 7-26.


CHROMOSOME COUNTS IN CULTIVATED JUNIPERS

Marion T. Hall, Aparna Mukherjee, and Webster R. Crowley

Sax and Sax (1933) showed the base chromosome number in the gymnosperms, with the exception of the Gnetales, to be \( n(x) = 12 \). Variations from the base number were postulated to be the results of gain of a chromosome by duplication \((n = 13 \text{ Pseudotsuga})\), loss of a chromosome and autopolyploidy \((n = 22 \text{ Pseudolarix})\), and loss of a chromosome following translocation of segments in the Cupressaceae and Taxodiaceae \((n = 11 \text{ in Juniperus, Taxodium, and Taiwania})\). Further variations in number are the result of polyploidy, presumably autopolyploidy, but to only a minor extent. Sax and Sax studied either somatic or meiotic chromosomes in 53 species and 16 genera of Coniferales.

Mehra and Khusoo (1956) briefly reviewed the cytology of the conifers and presented chromosome counts and other observations from somatic and meiotic preparations for 41 species in 14 genera in the Pinaceae, Taxodiaceae, and Cupressaceae. Their conclusions were generally in agreement with Sax and Sax: moreover they were careful to determine number and positions of secondary constrictions and the regularity of meiosis in Juniperus phoenicea, J. bermudiana, and J. scopulorum. They showed counts for Cunninghamia and Cryptomeria \((n = 11)\) for the Taxodiaceae and numbers (\(n = 12\)) for Actinostrobus, Calitris, Wilddringtonia, Tetraclinis, Thuja, Cupressus in the Cupressaceae. They supplied counts for Juniperus procera, J. phoenicea, and J. bermudiana \((n = 11)\).

In a recent paper Evans and Rasmussen (1971) illustrated a compilation of documented chromosome counts for Juniperus L. In their Table I they show nine species (or 10 if J. virginiana var. scopulorum is considered to be J. scopulorum), and they list the count by Jensen and Levant, 1941, for J. squamata 'Meyeri' \((2n = 44)\) for a total of 11 species or cultivars of species.

We are surveying the cultivated junipers of the Morton Arboretum for chromosome counts. Those currently documented are shown in Table 1 where they are arranged by sections. In section Oxycedrus we show counts of chromosomes for two species, two varieties, and four cultivars. In section Sabina we present counts for two varieties and ten cultivars.

Materials and Methods

The 20 different plant taxa listed in Table 1 are a small portion of the living juniper collections at the Arboretum. We believe that spring wood after adequate hardening is best for use as propagation material from junipers. Therefore, the cuttings were taken in mid-summer and propagated...