PLANT SUCCESSION, AN ANALYSIS OF THE DEVELOPMENT OF VEGETATION

Frederic E. Clements—1916

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Besides containing an account of the various forces and characteristics in succession, this monograph presents a philosophic viewpoint about the nature of the community which has prompted considerable discussion. In Clements' view, the plant community is an organic entity having attributes describable in terms of an individual (see also Braun-Blanquet, p. 147). Further controversy has arisen over his concept that all succession leads to one climax type in a given area owing to the pervading influence of climate. The major opposing viewpoint to Clements' organismic concept is expressed by Gleason (see p. 153) and Ramensky (see p. 151); Whittaker (p. 159), among others, suggests an alternate theory on the nature of the climax. Professor Clements was one of the most influential early American ecologists both as a faculty member at the Universities of Nebraska and Minnesota and as a research associate of the Carnegie Institution.

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CONCEPT AND CAUSES OF SUCCESSION

The formation an organism. The developmental study of vegetation necessarily rests upon the assumption that the unit or climax formation is an organic entity. As an organism the formation arises, grows, matures, and dies. Its response to the habitat is shown in processes or functions and in structures which are the record as well as the result of these functions. Furthermore, each climax formation is able to reproduce itself, repeating with essential fidelity the stages of its development. The life-history of a formation is a complex but definite process, comparable in its chief features with the life-history of an individual plant.

Universal occurrence of succession. Succession is the universal process of formation development. It has occurred again and again in the history of every climax formation, and must recur whenever proper conditions arise. No climax area lacks frequent evidence of succession, and the greater number present it in bewildering abundance. The evidence is most obvious in active physiographic areas, dunes, strands, lakes, floodplains, bad lands, etc., and in areas disturbed by man. But the most stable association is never in complete equilibrium, nor is it free from disturbed areas in which secondary succession is evident. An outcrop of rock, a projecting boulder, a change in soil or in exposure, an increase or decrease in the water-content or the light intensity, a rabbit-burrow, an ant-heap, the furrow of a plow, or the tracks worn by wheels, all these and many others initiate successions, often short and minute, but always significant. Even where the final community seems most homogeneous and its factors uniform, quantitative study by quadrat and instrument reveals a swing of population and a variation in the controlling factors. Invisible as these are to the ordinary observer, they are often very considerable, and in all cases are essentially

materials for the study of succession. In consequence, a floristic or physiognomic study of an association, especially in a restricted area, can furnish no trustworthy conclusions as to the prevalence of succession. The latter can be determined only by investigation which is intensive in method and extensive in scope.

Viewpoints of succession. A complete understanding of succession is possible only from the consideration of various viewpoints. Its most striking feature lies in the movement of populations, the waves of invasion, which rise and fall through the habitat from initiation to climax. These are marked by a corresponding progression of vegetation forms or phyads, from lichens and mosses to the final trees. On the physical side, the fundamental view is that which deals with the forces which initiate succession and the reactions which maintain it. This leads to the consideration of the responsive processes or functions which characterize the development, and the resulting structures, communities, zones, alternes, and layers. Finally, all of these viewpoints are summed up in that which regards succession as the growth or development and the reproduction of a complex organism. In this larger aspect succession includes both the ontogeny and the phylogeny of climax formations. . . .

Processes in succession. The development of a climax formation consists of several essential processes or functions. Every sere must be initiated, and its life-forms and species selected. It must progress from one stage to another, and finally must terminate in the highest stage possible under the climatic conditions present. Thus, succession is readily analyzed into initiation, selection, continuation, and termination. A complete analysis, however, resolves these into the basic processes of which all but the first are functions of vegetation, namely, (1) nudation, (2) migration, (3) ecesis, (4) competition, (5) reaction, (6) stabilization. These may be successive or interacting. They are successive in initial stages, and they interact in most complex fashion in all later ones. In addition, there are certain cardinal points to be considered in every case. Such are the direction of movement, the stages involved, the vegetation forms or materials, the climax, and the structural units which result. . . .

Developmental aspect. The essential nature of succession is indicated by its name. It is a series of invasions, a sequence of plant communities marked by the change from lower to higher life-forms. The essence of succession lies in the interaction of three factors, namely, habitat, life-forms, and species, in the progressive development of a formation. In this development, habitat and population act and react upon each other, alternating as cause and effect until a state of equilibrium is reached. The factors of the habitat are the causes of the responses or functions of the community, and these are the causes of growth and development, and hence of structure, essentially as in the individual. Succession must then be regarded as the development or life-history of the climax formation. It is the basic organic process of vegetation, which results in the adult or final form of this complex organism. All the stages which precede the climax are stages of growth. They have the same essential relation to the final stable structure of the organism that seedling and growing plant have to the adult individual. Moreover, just as the adult plant repeats its development, *i. e.*, reproduces itself, whenever conditions permit, so also does the climax formation. The parallel may be extended much further. The flowering plant may repeat itself completely, may undergo primary reproduction from an initial embryonic cell, or the reproduction may

be secondary or partial from a shoot. In like fashion, a climax formation may repeat every one of its essential stages of growth in a primary area, or it may reproduce itself only in its later stages, as in secondary areas. In short, the process of organic development is essentially alike for the individual and the community. The correspondence is obvious when the necessary difference in the complexity of the two organisms is recognized.

Functional aspect. The motive force in succession, *i. e.*, in the development of the formation as an organism, is to be found in the responses or functions of the group of individuals, just as the power of growth in the individual lies in the responses or functions of various organs. In both individual and community the clue to development is function, as the record of development is structure. Thus, succession is preeminently a process the progress of which is expressed in certain initial and intermediate structures or stages, but is finally recorded in the structure of the climax formation. The process is complex and often obscure, and its component functions yield only to persistent investigation and experiment. In consequence, the student of succession must recognize clearly that developmental stages, like the climax, are only a record of what has already happened. Each stage is, temporarily at least, a stable structure, and the actual processes can be revealed only by following the development of one stage into the succeeding one. In short, succession can be studied properly only by tracing the rise and fall of each stage, and not by a floristic picture of the population at the crest of each invasion. . . .

Stabilization. The progressive invasion typical of succession everywhere produces stabilization. The latter is the outcome of greater occupation due to aggregation and migration and of the resulting control of the habitat by the population. In other words, stabilization is increase of dominance, culminating in a stable climax. It is the mutual and progressive interaction of habitat and community, by which extreme conditions yield to a climatic optimum and life-forms with the least requirements are replaced by those which make the greatest demands, at least in the aggregate. So universal and characteristic is stabilization that it might well be regarded as a synonym of succession. It has the advantage of suggesting the final adult stage of the development, while succession emphasizes the more striking movement of the stages themselves.

Causes of stabilization. The essential cause of stabilization is dominance. The latter is partly due to the increasing occupation of a bare area, but is chiefly the result of the life-form. The occupation of annuals in an initial or early stage of a secondary sere is often complete, but the dominance is usually transient. Effective dominance can occur only when the prevailing life-form exerts a significant reaction, which holds the population in a certain stage until the reaction becomes distinctly unfavorable to it, or until the invasion in force of a superior life-form. Dominance is then the ability of the characteristic life-form to produce a reaction sufficient to control the community for a period. Dominance may mean the control of soil factors alone, primarily water-content, of air factors, especially light, or of both water and light. Initial life-forms such as algæ, lichens, and mosses are characteristic but not dominant, since the reaction they produce prevents control rather than gives it. This is the essential difference between the initial and the final stages of succession. While both react upon the habitat, the reaction of the one favors invaders, that of the other precludes them. The reactions of the intermediate stages tend to show both effects. At first the reaction is slight and favors the

aggregation of occupants; then it becomes more marked and produces conditions more and more favorable to invasion. On the other hand, when the reaction is distinctly unfavorable to the occupants, the next stage develops with greater rapidity. Each stage is itself a minor process of stabilization, a miniature of the increasing stabilization of the sere itself. Reaction is thus the cause of dominance, as of the loss of dominance. It makes clear the reason why one community develops and dominates for a time, only to be replaced by another, and why a stage able to maintain itself as a climax or subclimax finally appears. Thus, reaction furnishes the explanation of stabilization, as it does of the successive invasions inherent in succession.

Relation to the climax. The end of the process of stabilization is a climax. Each stage of succession plays some part in reducing the extreme condition in which the sere began. It reacts to produce increasingly better growing conditions, or at least conditions favorable to the growth of a wider range of species. This is equivalent to reducing an excess of water-content or remedying a lack of it. The consequence is that the effect of stabilization on the habitat is to bring it constantly nearer medium or mesophytic conditions. Exceptions to this occur chiefly in desert regions, though they may occur also in water areas, where processes of deposit and erosion alternate. The effect upon the plant population is corresponding. The vast majority of species are not pioneers, *i. e.*, xerophytes and hydrophytes, but mesophytes with comparatively high but balanced requirements for ecesis. For this reason the number of species and individuals grows larger in each succeeding stage, until the final dominance of light, for example, becomes restrictive. At the same time the life-forms change from those such as lichens and submerged plants with a minimum of aggregate requirements to forms with an increasingly high balanced need. The period of individual development increases as annuals are succeeded by perennials and the latter yield to dominant shrubs and trees. The final outcome in every sere is the culmination in a population most completely fitted to the mesophytic conditions. Such a climax is permanent because of its entire harmony with a stable habitat. It will persist just as long as the climate remains unchanged, always providing that migration does not bring in a new dominant from another region. . . .