CHAPTER 1

Preface to *Plant Succession: An Analysis of the Development of Vegetation*

Frederic E. Clements

The present book constitutes the general part of a monograph on Rocky Mountain vegetation which has been under way since 1899. It is hoped that another volume dealing with the details of the development and structure of the climax formations of the Great Plains, Rocky Mountains, and Great Basin may appear subsequently. The general principles advanced here are an outgrowth of the treatment in the "Development and Structure of Vegetation" (1904) and "Research Methods in Ecology" (1905), in which an endeavor to organize the whole field of present-day succession was made for the first time. The studies of the past decade have confirmed and broadened the original concepts, and have led irresistibly to the conclusion that they are of universal application. The summer of 1913 and the spring and summer of 1914 were spent in testing both principles and processes throughout the vegetation of the western half of the continent. The area scrutinized extends from the Great Plains to the Pacific Coast and from the Canadian Rockies to the Mexican boundary. The great climax formations of this region were traversed repeatedly, and their development and relations subjected to critical analysis and comparison.

As a consequence, it is felt that the earlier concept of the formation as a complex organism with a characteristic development and structure in harmony with a particular habitat is not only fully justified, but that it also represents the only complete and adequate view of vegetation. This concept has been broadened and definitized by the recognition of the developmental unity of the habitat. As a result, formation and habitat are regarded as the two inseparable phases of a development which terminates in a climax controlled by climate. Hence, the basic climax community is taken to be the formation, which exhibits seral or developmental stages as well as climax units. It is hardly necessary to point out that this places the study of vegetation upon a purely developmental basis, which is as objective as it is definite.

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The recognition of development as the cause and explanation of all existing climax formations forced the conclusion that all vegetation has been developmentally related; in short, that every climax formation has its phylogeny as well as its ontogeny. This led at once to the further assumption that the processes or functions of vegetation today must have been essentially those of the geological past, and that the successional principles and processes seen in existing seres hold equally well for the analysis of each eosere. As a consequence, it has been possible to sketch in bold outline the succession of plant populations in the various eras and periods, and to organize in tentative fashion the new field of paleoecology. . . .

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 (Clements 1905: 199). 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, badlands, 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.

Succession and Sere

In thorough analysis of succession it becomes evident that the use of the term in both a concrete and an abstract sense tends to inexactness and uncertainty. With the recognition of new kinds of succession it seems desirable to restrict the word more and more to the phenomenon itself and to employ a new term for concrete examples of it. In consequence, a word has been sought which would be significant, short, euphonic, and easy of combination. These advantages are combined in the word *sere,* from a root common to both Latin and Greek, and hence permitting ready composition in either. The root *ser-* shows its meaning in Latin *sero,* join, connect; *sertum,* wreath; *series,* joining or binding together, hence sequence, course, succession, lineage. In Greek, it occurs in ειρω, to fasten together in a row, and in σειρα, σηρα, rope, band, line, lineage. *Sere* is essentially identical with *series,* but possesses the great advantage of being distinctive and of combining much more readily, as in *cosere, geosere,* etc.

Sere and Cosere

A sere is a unit succession. It comprises the development of a formation from the appearance of the first pioneers through the final or climax stage. Its normal course is from nudation to stabilization. All concrete successions are seres, though they may differ greatly in development and thus make it

necessary to recognize various kinds, as is shown later. On the other hand, a unit succession or sere may recur two or more times on the same spot. Classical examples of this are found in moors and dunes, and in forest burns. A series of unit successions results, in which the units or seres are identical or related in development. They consist normally of the same stages and terminate in the same climax, and hence typify the reproductive process in the formation. Such a series of unit successions, i.e., of seres, in the same spot constitutes an organic entity. For this, the term *consere* or *cosere* (*cum,* together, *sere; consero,* bind into a whole) is proposed, in recognition of the developmental bond between the individual seres. Thus, while the sere is the developmental unit, and is purely ontogentic, the cosere is the sum of such units throughout the whole life history of the climax formation, and is hence phylogenetic in some degree. Coseres are likewise related in a developmental series, and thus may form larger groups, eoseres, etc., as indicated in the later discussion. . . .

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.

Relation of Causes

Since succession is a series of complex processes, it follows that there can be no single cause for a particular sere. One cause initiates succession by producing a bare area, another selects the population, a third determines the sequence of stages, and a fourth terminates the development. As already indicated, these four processes—initiating, selecting, continuing, and terminating—are essential to every example of succession. As a consequence, it is difficult to regard any one as paramount. Furthermore, it is hard to determine their relative importance, though their difference in role is obvious. It is especially necessary to recognize that the most evident or striking cause may not be the most important. In fact, while the cause or process which produces a bare habitat is the outstanding one to the eye, in any concrete case, it is rather less

important if anything than the others. While the two existing classifications of successions (Clements 1904; Cowles 1911) have both used the initiating cause as a basis, it seems clear that this is less significant in the life history of a climax formation than are the others. [The] same sere may result from several initial causes.

Kinds of Causes

All of the causative processes of succession may best be distinguished as initiating or initial, continuing or ecesic, and stabilizing or climatic. At first thought, the latter seems not to be a cause at all but an effect. As is shown later, however, the character of a successional development depends more upon the nature of the climatic climax than upon anything else. The latter determines the population from beginning to end, the direction of development, the number and kind of stages, the reactions of the successive stages, etc. Initial causes are those which produce a new or denuded soil upon which invasion is possible. Such are the chief physiographic processes, deposition and erosion, biotic factors such as man and animals, and climatic forces in some degree. . . .

Ecesic causes are those which produce the essential character of vegetational development, namely, the successive waves of invasion leading to a final climax. They have to do with the interaction of population and habitat, and are directive in the highest degree. The primary processes involved are invasion and reaction. The former includes three closely related processes: migration, competition, and ecesis. The last is final and critical, however, and hence is used to designate the causes which continue the development.

Proximate and Remote Causes

In dealing with the causes of development, and especially with initial causes, it must be borne in mind that forces in nature are almost inextricably interwoven. In all cases the best scientific method in analysis seems to be to deal with the immediate cause first, and then to trace its origin just as far as it is possible or profitable. Throughout a climax formation, physiography usually produces a large or the larger number of developmental areas. The influence of physiography in this respect is controlled or limited by the climate, which in its turn is determined by major physiographic features such as mountain barriers or ocean currents. These are subordinate as causes to the general terrestrial climates, which are the outcome of the astronomical relations between the sun and the earth. As a consequence, physiography may well be considered the immediate initial cause of the majority of primary successions, just as the chresard is the controlling cause of vegetation structure, though it is dependent on the one hand upon soil structure, and this upon physiography, and on the other upon the rainfall, etc.

Apart from the gain in clearness of analysis, greater emphasis upon the

proximate cause seems warranted by the fact that it is the chresard to which the plant responds, and not the soil texture or the physiography. In like manner, the invasion of a new area is a direct consequence of the action of the causative process and not of the remote forces behind it. The failure to consider the sequence of causes has produced confusion in the past . . . and will make more confusion in the future as the complex relations of vegetation and habitat come to be studied intensively. . . .

Essential Nature of Succession

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.