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NATURE AND STRUCTURE OF THE CLIMAX

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(*With Plates VI—XI*)

| CONTENTS | |
|---|------|
| | PAGE |
| INTRODUCTION | 253 |
| THE CLIMAX CONCEPT | 253 |
| NATURE OF THE CLIMAX | 254 |
| Unity of the climax | 254 |
| Stabilisation and change | 255 |
| Origin and relationship | 257 |
| Tests of a climax | 257 |
| CLIMAX AND PROCLIMAX | 261 |
| Essential relations | 261 |
| Proclimaxes | 262 |
| Subclimax | 262 |
| Disclimax | 265 |
| Prelimax and postclimax | 266 |
| Prelimax | 267 |
| Postclimax | 269 |
| STRUCTURE OF THE CLIMAX | 270 |
| Community functions | 270 |
| Roles of the constituent species: dominants | 270 |
| Influents | 271 |
| Climax and seral units | 271 |
| Climax units | 272 |
| Association | 273 |
| Consociation | 274 |
| Faciation | 274 |
| Lociation | 275 |
| Society | 275 |
| Sociation | 276 |
| Lamiation | 277 |
| Sation | 277 |
| Clan | 278 |
| Seral units | 278 |
| Serule | 280 |
| RANK AND CORRESPONDENCE OF UNITS | 280 |
| TABLE OF CLIMAX AND SERAL UNITS | 281 |
| Panclimax and eoclimax | 281 |
| Prerequisites to research in climaxes | 282 |
| REFERENCES | 283 |

INTRODUCTION

MORE than a century ago when Lewis and Clark set out upon their memorable journey across the continent of North America (1803-6), they were the first to traverse the great climaxes from deciduous woods in the east through the vast expanse of prairie and plain to the majestic coniferous forest of the north-west. At this time the oak-hickory woodland beyond the Appalachians was almost untouched by the ax except in the neighborhood of a few straggling pioneer settlements, and west of the Mississippi hardly an acre of prairie had known the plow. A few years later (1809), Bradbury states that the boundless prairies are covered with the finest verdure imaginable and will become one of the most beautiful countries in the world, while the plains are of such extent and fertility as to maintain an immense number of animals. It appears probable that at this time no other grassland in the world exhibited such myriads of large mammals belonging to but a few species.

The natural inference has been that the prairies were much modified by the grazing of animals and the fires of primitive man, and this has been reinforced by estimates of the population of each. Seton (1929) concludes that the original number of bison was about 60 million with a probable reduction to 40 million by 1800, and that both the antelope and white-tailed deer were equally abundant, while elk and mule-deer each amounted to not more than 10 million at the maximum. However, these were distributed over a billion or two acres, and the average density was probably never more than a score to the square mile. Estimates of the Indian tribes show the greatest divergence, but it seems improbable that the total population within the grassland ever exceeded a half million. The general habit of migration among the animals further insured that serious effects from overgrazing and trampling were but local or transitory, while the influence of fires set by the Indians was even less significant in modifying the plant cover. As to the forests, those of the north-west were still primeval and in the east they were yet to be changed over wide areas by lumbering and burning on a large scale.

THE CLIMAX CONCEPT

The idea of a climax in the development of vegetation was first suggested by Hult in 1885 and then was advanced more or less independently by several investigators during the next decade or so (cf. Clements, 1916; Phillips, 1935). It was applied to a more or less permanent and final stage of a particular succession and hence one characteristic of a restricted area. The concept of the climax as a complex organism inseparably connected with its climate and often continental in extent was introduced by Clements (1916). According to this view, the climax constitutes the major unit of vegetation and as such forms the basis for the natural classification of plant communities. The relation between climate and climax is considered to be the paramount one, while the intimate

bond between the two is emphasized by the derivation of the terms from the same Greek root. In consequence, under this concept climax is invariably employed with reference to the climatic community alone, namely, the formation or its major divisions.

At the outset it was recognized that animals must also be considered members of the climax, and the word *biome* was proposed for the purpose of laying stress upon the mutual roles of plants and animals (Clements, 1916*b*; Clements and Shelford, 1936). With this went the realization that the primary relations to the habitat or *ece* were necessarily different by virtue of the fact that plants are producents and animals consuments. On land, moreover, plants constitute the fixed matrix of the biome in direct connection with the climate, while the animals bear a dual relation, to plants as well as to climate. The outstanding effect of the one is displayed in reaction upon the *ece*, of the other in coaction upon plants, which constitutes the primary bond of the biotic community.

Because of its emphasis upon the climatic relation, the term climax has come more and more to replace the word formation, which is regarded as an exact synonym, and this process may have been favored by a tendency to avoid confusion with the geological use. The designation "climatic formation" has now and then been employed, but this is merely to accentuate its nature and to distinguish it from less definite usages. Furthermore, climax and biome are complete synonyms when the biotic community is to be indicated, though climax will necessarily continue to be employed for the matrix when plants alone are considered.

NATURE OF THE CLIMAX

This theme has been developed in considerable detail in earlier works (Clements, 1916, 1920, 1928; Weaver and Clements, 1929), as well as in a recent comprehensive treatment by Phillips (1935), and hence a summary account of the major features will suffice in the present place. These may be conveniently grouped under the following four captions, i.e. unity, stabilization and change, origin and relationship, and objective tests.

Unity of the climax

The inherent unity of the climax rests upon the fact that it is not merely the response to a particular climate, but is at the same time the expression and the indicator of it. Because of extent, variation in space and time, and the usually gradual transition into adjacent climates, to say nothing of the human equation, neither physical nor human measures of a climate are adequately satisfactory. By contrast, the visibility, continuity, and sessile nature of the plant community are peculiarly helpful in indicating the fluctuating limits of a climate, while its direct response in terms of food-making, growth and life-form provides the fullest possible integration of physical factors. Naturally,

both physical and human values have a part in analyzing and in interpreting the climate as outlined by the climax, but these can only supplement and not replace the biotic indicators.

It may seem logical to infer that the unity of both climax and climate should be matched by a similar uniformity, but reflection will make clear that such is not the case. This is due in the first place to the gradual but marked shift in rainfall or temperature from one boundary to the other, probably best illustrated by the climate of the prairie. In terms of precipitation, the latter may range along the parallel of 40° from nearly 40 in. at the eastern edge of the true prairie to approximately 10 in. at the western border of the mixed grassland, or even to 6 in. in the desert plains and the Great Valley of California. Such a change is roughly 1 in. for 50 miles and is regionally all but imperceptible. The temperature change along the 100th meridian from the mixed prairie in Texas to that of Manitoba and Saskatchewan is even more striking, since only one association is concerned. At the south the average period without killing frost is about 9 months, but at the north it is less than 3, while the mean annual temperatures are 70 and 33° F. respectively. The variation of the two major factors at the extremes of the climatic cycle is likewise great, the maximum rainfall not infrequently amounting to three to four times that of the minimum.

The visible unity of the climax is due primarily to the life-form of the dominants, which is the concrete expression of the climate. In prairie and steppe, this is the grass form, with which must be reckoned the sedges, especially in the tundra. The shrub characterizes the three scrub climaxes of North America, namely, desert, sagebrush, and chaparral, while the tree appears in three subforms, coniferous, deciduous, and broad-leaved evergreen, to typify the corresponding boreal, temperate, and tropical climaxes. The life-form is naturally reflected in the genus, though not without exceptions, since two or more forms or subforms, herb or shrub, deciduous or evergreen, annual or perennial, may occur in the same genus. Hence, the essential unity of a climax is to be sought in its dominant species, since these embody not only the life-form and the genus, but also denote in themselves a definite relation to the climate. Their reactions and coactions are the most controlling both in kind and amount, and thus they determine the conditions under which all the remaining species are associated with them. This is true to a less degree of the animal influents, though their coactions may often be more significant than those of plants.

Stabilization and change

Under the growing tendency to abandon static concepts, it is comprehensible that the pendulum should swing too far and change be overstressed. This consequence is fostered by the fact that most ecological studies are carried out in settled regions where disturbance is the ruling process. As a result, the

climax is badly fragmented or even absent over wide areas and subseres are legion. In all such instances it is exceedingly difficult or entirely impossible to strike a balance between stability and change, and it becomes imperative to turn to regions much less disturbed by man, where climatic control is still paramount. It is likewise essential to employ a conceivable measure of time, such as can be expressed in human terms of millennia rather than in eons. No student of past vegetation entertains a doubt that climaxes have evolved, migrated and disappeared under the compulsion of great climatic changes from the Paleozoic onward, but he is also insistent that they persist through millions of years in the absence of such changes and of destructive disturbances by man. There is good and even conclusive evidence within the limitations of fossil materials that the prairie climax has been in existence for several millions of years at least and with most of the dominant species of to-day. This is even more certainly true of forests on the Pacific Coast, owing to the wealth of fossil evidence (Chaney, 1925, 1935), while the generic dominants of the deciduous forests of the Dakota Cretaceous and of to-day are strikingly similar.

It can still be confidently affirmed that stabilization is the universal tendency of all vegetation under the ruling climate, and that climaxes are characterized by a high degree of stability when reckoned in thousands or even millions of years. No one realizes more clearly than the devotee of succession that change is constantly and universally at work, but in the absence of civilized man this is within the fabric of the climax and not destructive of it. Even in a country as intensively developed as the Middle West, the prairie relicts exhibit almost complete stability of dominants and subdominants in spite of being surrounded by cultivation (cf. Weaver and Flory, 1934). It is obvious that climaxes display superficial changes with the season, year or cycle, as in aspection and annuation, but these modify the matrix itself little or not at all. The annuals of the desert may be present in millions one year and absent the next, or one dominant grass may seem prevailing one season and a different one the following year, but these changes are merely recurrent or indeed only apparent. While the modifications represented by bare areas and by seres in every stage are more striking, these are all in the irresistible process of being stabilized as rapidly as the controlling climate and the interference of man permit.

In brief, the changes due to aspection, annuation or natural coaction are superficial, fleeting or periodic and leave no permanent impress, while those of succession are an intrinsic part of the stabilizing process. Man alone can destroy the stability of the climax during the long period of control by its climate, and he accomplishes this by fragments in consequence of a destruction that is selective, partial or complete, and continually renewed.

Origin and relationship

Like other but simpler organisms, each climax not only has its own growth and development in terms of primary and secondary succession, but it has also evolved out of a preceding climax. In other words, it possesses an ontogeny and phylogeny that can be quantitatively and experimentally studied, much as with the individuals and species of plants and animals (*Plant Succession*, 1916, pp. 181, 342). Out of the one has come widespread activity in the investigation of succession, while interest in the other lingers on the threshold, chiefly because it demands a knowledge of the climaxes of more than one continent. With increasing research in these, especially in Europe and Asia, it will be possible to test critically the panclimaxes already suggested (Clements, 1916, 1924, 1929), as well as to determine the origin and relationships of the constituent formations.

This task will also require the services of paleo-ecology for the reconstruction of each eoclimax, which has been differentiated by worldwide climatic changes into the existing units of the panclimax or panformation. As it is, there can be no serious question of the existence of a great hemispheric clisere constituted by the arctic, boreal, deciduous, grassland, subtropical and tropical panclimaxes. Desert formations for the most part constitute an exception and may well be regarded as endemic climaxes evolved in response to regional changes of climate (Clements, 1935).

It is a significant fact that the boreal formations of North America and Eurasia are more closely related than the coniferous ones of the former, but this seeming anomaly is explained by the greater climatic differences that have produced the forests of the Petran and Sierran systems. The five climaxes concerned are relatively well known, and it is possible to indicate their relationships with some assurance, and all the more because of their parallel development on the two great mountain chains. In the case of deciduous forest and grassland, only a single formation of each is present in North America, and the problem of differentiation resolves itself into tracing the origin and relationship of the several associations. It has been suggested that the mixed prairie by virtue of its position, extent and common dominants represents the original formation in Tertiary times, an assumption reinforced by its close resemblance to the steppe climax (Clements, 1935). It is not improbable that the mixed hardwoods of the southern Appalachians bear a similar relation to the associations of the modern deciduous forest (Braun, 1935).

Tests of a climax

As has been previously indicated, the major climaxes of North America, such as tundra, boreal and deciduous forest, and prairie, stand forth clearly as distinct units, in spite of the fact that the prairie was first regarded as comprising two formations, as a consequence of the changes produced by over-

grazing. The other coniferous and the scrub climaxes emerge less distinctly because of the greater similarity of life-form within each group, and hence it is necessary to appeal to criteria derived from the major formations just mentioned. This insures uniformity of basis and a high degree of objectivity, both of which are qualities of paramount importance for the natural classification of biomes. In fact, entire consistency in the application of criteria is the best warrant of objective results, though this is obviously a procedure that demands a first-hand acquaintance with most if not all the units concerned and over a large portion of their respective areas.

The primary criterion is that afforded by the vegetation-form, as is illustrated by the four major climaxes. The others of each group, such as coniferous forest or scrub, are characterized also by the same form in the dominants, but this is not decisive as between related climaxes and hence recourse must be taken to the other tests. The value of the life-form is most evident where two climaxes of different physiognomy are in contact, as in the case of the lake forest of pine-hemlock and the deciduous forest of hardwoods. The static view would make the hemlock in particular a dominant of the deciduous formation, but the evidence derived from the vegetation-form is supported by that of phylogeny and by early records of composition and timber-cut to show that two different climaxes are concerned. Secondary forms or subforms rarely if ever mark distinctions between climaxes, but do aid in the recognition of associations. This is well exemplified by the tall, mid and short grasses of the prairie and somewhat less definitely by the generally deciduous character of the Petran chaparral and the typically evergreen nature of the Sierran.

As would be expected, the most significant test of the unity of a formation is afforded by the presence of certain dominant species through all or nearly all of the associations, but often not in the role of dominants by reason of reduced abundance. Here again perhaps the best examples are furnished by prairie and tundra, though the rule applies almost equally well to deciduous forest and only less so to coniferous ones because of a usually smaller number of dominants. For the prairie, the number of such species, or *perdominants*, found in all or all but one or two of the five associations is eight, namely, *Stipa comata*, *Agropyrum smithi*, *Bouteloua gracilis*, *Sporobolus cryptandrus*, *Koeleria cristata*, *Elymus sitanion*, *Poa scabrella* and *Festuca ovina*. Even when a species is lacking over most of an association, as in the case of *Stipa comata* and the true prairie, it may be represented by a close relative, such as *S. spartea*, which is probably no more than a mesic variety of it. As to the three associations of the deciduous forest, a still larger number of dominant species occur to some degree in all; the oaks comprise *Quercus borealis*, *velutina*, *alba*, *macrocarpa*, *coccinea*, *muhlenbergi*, *stellata* and *marilandica*, and the hickories, *Carya ovata*, *glabra*, *alba* and *cordiformis*.

It was the application of this test by specific dominants that led to the recognition of the two climaxes in the coniferous mantle of the Petran and

Sierran cordilleras. The natural assumption was that such a narrow belt could not contain more than one climax, especially in view of its physiognomic uniformity, but this failed to reckon with the great climatic differences of the two portions and the corresponding response of the dominants. The effect of altitude proved to be much more decisive than that of region, dominants common to the montane and subalpine zones being practically absent, though the rule for the same zone in each of the two separate mountain systems. Long after the presence of two climaxes had been established, it was found that Sargent had anticipated this conclusion, though in other terms (1884, p. 8).

As would be inferred, the dominants of related associations belong to a few common genera for the most part. Thus, there are a dozen species of *Stipa* variously distributed as dominants through the grassland, nearly as many of *Sporobolus*, *Bouteloua* and *Aristida*, and several each of *Poa*, *Agropyrum*, *Elymus*, *Andropogon*, *Festuca* and *Muhlenbergia*. In the deciduous forest, *Quercus*, *Carya* and *Acer* are the great genera, and for the various coniferous ones, *Pinus*, *Abies* and *Picea*, with species of *Tsuga*, *Thuja*, *Larix* and *Juniperus* hardly less numerous.

The perennial forbs that play the part of subdominants also possess considerable value in linking associations together, and to a higher degree in the deciduous forest than in the prairie, owing chiefly to the factors of shade and protection. Over a hundred subdominants belonging to two score or more of genera, such as *Erythronium*, *Dicentra*, *Trillium*, *Aquilegia*, *Arisaema*, *Phlox*, *Uvularia*, *Viola*, *Impatiens*, *Desmodium*, *Helianthus*, *Aster* and *Solidago*, range from Nova Scotia or New England beyond the borders of the actual climax to Nebraska and Kansas. Across the wide expanse of the prairie climax, species in common are only exceptional, these few belonging mostly to the composites, notably *Grindelia squarrosa*, *Gutierrezia sarothrae*, *Artemisia dracunculus* and *vulgaris*. On the other hand, the number of genera of subdominants found throughout the grassland is very large.

The greater mobility of the larger mammals in particular renders animal influents less significant than plants as a criterion, but several of these possess definite value and the less mobile rodents even more. The antelope and bison are typical of the grassland climax, the first being practically restricted to it, while jack-rabbits, ground-squirrels and kangaroo-rats are characteristic dwellers in the prairie, as is their chief foe, the coyote.

The remaining criteria are derived from development directly or indirectly, though this is less evident in the case of the ecotone between two associations. Here the mixing of dominants and subdominants indicates their general similarity in terms of the formation, within which range their preferences assign them to different associations. The evidence from primary succession is of value only in the later stages as a rule, since initial associates like the reed-swamp may occur in several climaxes. With subseres, however, all or nearly all the stages are related to the particular climax and such seres denote a

corresponding unity in development. This is especially true of all subclimaxes and most evidently in the case of those due to fire. More significant still are postclimaxes in both grassland and forest. For example, the associates of species of *Andropogon*, which is subclimax to the oak-hickory forest, constitutes a postclimax to five out of the six associations of the prairie. On the other hand, the community of *Ulmus*, *Juglans*, *Fraxinus*, etc., found on flood-plains through the region of deciduous forest, forms a common subclimax to the three associations.

In addition to such ontogenetic criteria, phylogeny supplies tests of even greater value. This is notably the case with the two associations of the montane and subalpine coniferous forests of the west, though perhaps the most striking application of this criterion is in connection with the lake forest of pine-hemlock. Though the concrete evidence for such a climax recurs constantly through the region of the Great Lakes to the Atlantic, it is fragmentary and there is no evident related association to the westward. However, the four genera are represented by related species in the two regions, namely, *Pinus strobus* by *P. monticola*, *P. banksiana* by *P. contorta*, *Tsuga canadensis* by *T. heterophylla*, *Larix laricina* by *L. occidentalis*, and *Thuja occidentalis* by *T. plicata*, though the last two genera have changed from a subclimax role in the east to a climax one in the west. As suggested earlier, phylogenetic evidence of still more direct nature is supplied by the mixed prairie with the other enclosing associations and by the remnants of a virgin deciduous forest that exhibits a similar genetic and spatial relation to the associations of this climax (cf. Braun, 1935).

Finally, it is clear that any test will gain in definiteness and accuracy of application whenever dependable records are available with respect to earlier composition and structure. These may belong entirely to the historical period, as in the case of scientific reports or land surveys, they may bridge the gap between the present and the past as with pollen statistics, or they may reach further back into the geological record, as with leaf-impressions or other fossils (Chaney, 1925, 1933; Clements, 1936). Two instances of the scientific record that are of the first importance may be given as examples. The first is the essential recognition by Sargent of the pine-hemlock climax under the name of the northern pine belt (1884), at a time when relatively little of this had been logged, by contrast with 90 per cent. or more at present (cf. also Bromley, 1935). The second is an account, discovered and communicated by Dr Vestal, of the prairies of Illinois as seen by Short in ca. 1840. This is of heightened interest since its discovery followed little more than a year after repeated field trips had led to the conclusion that all of Iowa, northern Missouri and most of Illinois were to be assigned to the true prairie,¹ a decision

¹ The true prairie is characterized by the three eudominants, *Stipa spartea*, *Sporobolus asper* and *S. heterolepis*. The presence of tall-grasses in it to-day, particularly *Andropogon furcatus* and *nutans*, is the mark of the disclimax due to the varied disturbances associated with settlement.



Phot. 1. Sierran subalpine climax: Consociation of *Tsuga mertensiana*; Crater Lake, Oregon.



Phot. 2. Proclimax of Sagebrush (*Artemisia tridentata*), a disclimax due to overgrazing of mixed prairie; climatically a preclimax.

CLEMENTS—NATURE AND STRUCTURE OF THE CLIMAX

confirmed for Illinois by Short's description, and supported by the more general accounts of Bradbury (*ca.* 1815) and Greeley (1860).

CLIMAX AND PROCLIMAX

Essential relations

In accordance with the view that development regularly terminates in the community capable of maintaining itself under a particular climate, except when disturbance enters, there is but one kind of climax, namely, that controlled by climate. This essential relation is regarded as not only inherent in all natural vegetation, but also as implicit in the cognate nature of the two terms. While it is fully recognized that succession may be halted in practically any stage, such communities are invariably subordinate to the true climax as determined by climate alone. From the very meaning of the word, there can not be climaxes scattered along the developmental route with a genuine climax at the end. There is no intention to question the reality of such pauses, but only to emphasize the fact that they are of a different order from the climax.

While it is natural to express new ideas by qualifying an old term, this does not conduce to the clearest thinking or the most accurate usage. Even more undesirable is the fact that the meaning of the original word is gradually shifted until it becomes either quite vague or hopelessly inclusive. At the hands of some, climax has already suffered this fate, and fire, disease, insects, and human disturbances of all sorts are assumed to produce corresponding climaxes (*cf.* Chapman, 1932). On such an assumption corn would constitute one climax, wheat another, and cotton a third, and it would then become imperative to begin anew the task of properly analyzing and classifying vegetation.

In the light of two decades of continued analysis of the vegetation of North America, as well as the application of the twin concepts of climax and complex organism by workers in other portions of the globe and the strong support brought to them by the rise of emergent evolution and holism (Phillips, 1935), the characterization of the climax as given in *Plant Succession*, in 1916, still appears to be both complete and accurate. "The unit of vegetation, the 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 that 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. The climax formation is the adult organism, of which all initial and medial stages are but stages of development.... A formation, in short, is the final stage of vegetational development in a climatic unit. It is the climax community of a succession that terminates in the highest life-form possible in the climate concerned."

To-day this statement would need modification only to the extent of substituting "biome" for climax or formation and "biotic" for vegetational. This characterization has recently been annotated and confirmed by Phillips' masterly discussion of climax and complex organism, as cited above, a treatise that should be read and digested by everyone interested in the field of dynamic ecology and its wide applications.

Proclimaxes

As a general term, proclimax includes all the communities that simulate the climax to some extent in terms of stability or permanence but lack the proper sanction of the existing climate. Certain communities of this type were called potential climaxes in *Plant Succession* (p. 108; 1928, p. 109), and two kinds were distinguished, namely, preclimax and postclimax. To avoid proposing a new term in advance of its need, subclimax was made to do double duty, denoting both the subfinal stage of succession, as well as apparent climaxes of other kinds. This dual usage was criticized by Godwin (1929, p. 144) and partially justified by Tansley in an appended note on the ground just given. However, this discussion made it evident that a new term was desirable and proclimax was accordingly suggested (Clements, 1934). While this takes care of the use of subclimax in the second sense noted above, it is better adapted by reason of its significance to apply to all kinds of subpermanent communities other than the climax proper. However, there is still an important residuum after subclimax, preclimax and postclimax have been recognized, and it is proposed to call these *disclimaxes*, as indicated later.

The proclimax may be defined as any more or less permanent community resembling the climax in one or more respects, but gradually replaceable by the latter when the control of climate is not inhibited by disturbance. Besides its general function, it may be used as a synonym for any one of its divisions, as well as in cases of doubt pending further investigation, such as in water climaxes. The four types to be considered are subclimax, disclimax, preclimax and postclimax.

Subclimax

As the stage preceding the climax in all complete seres, primary and secondary, the subclimax is as universal as it is generally well understood. The great majority of such communities belong to the subseres, especially that following fire, owing to the fact that disturbance is to-day a practically constant feature of most climaxes. Fire and fallow are recurrent processes in cultivated regions generally and they serve to maintain the corresponding subseres until protection or conversion terminates the disturbance. Though the subclimax is just as regular a feature of priseres, these have long ago ended in the climax over most of the climatic area and the related subclimax communities are consequently much restricted in size and widely scattered. Smallness is



Phot. 3. Fire subclimax of dwarf *Pinus* and *Quercus*; the "Plains",
New Jersey Pine-barrens.



Phot. 4. Subclimax of consociates of *Aristida purpurea* in field
abandoned 15 years; Great Plains.

CLEMENTS—NATURE AND STRUCTURE OF THE CLIMAX

naturally a characteristic of nearly all subclimaxes, the chief exceptions being due to fire or to fire and logging combined, but by contrast they are often exceedingly numerous.

Because of its position in the succession, the subclimax resembles the preclimax in some respects and in a few instances either term may be properly applied. The distinction between subclimax and disclimax presents some difficulty now and then, as the amount of change necessary to produce the latter may be a matter of judgment. This arises in part also from the structural diversity of formation and association, as a consequence of which the dominants of a particular type of subere vary in different areas. When there is but a single dominant, as in many burn subclimaxes, no question ensues, but if two or more are present, the decision between subclimax and disclimax may be less simple, as is not infrequent in scrub and grassland.

Examples of the subclimax are legion, the outstanding cases being mostly due to fire, alone or after lumbering or clearing. Most typical are those composed of "jack-pines" or species with closed cones that open most readily after fire. Each great region has at least one of these, e.g. *Pinus rigida*, *virginiana* and *echinata* in the east, *P. banksiana* in the north, *P. murrayana* in the Rocky Mountains, and *P. tuberculata*, *muricata* and *radiata* on the Pacific Slope. *Pinus palustris* and *taeda* play a similar role in the "piney" woods of the Atlantic Gulf region, as does *Pseudotsuga taxifolia* in the north-west. The characteristic subclimaxes of the boreal forest are composed of aspen (*Populus tremuloides*), balsam-poplar (*P. balsamifera*), and paper-birch (*Betula papyrifera*), either singly or in various combinations. Aspen also forms a notable subclimax in the Rocky Mountains, for the most part in the subalpine zone. Prisere subclimaxes are regular features of bogs and muskeags throughout much or all of the boreal and lake forests, the three dominants being *Larix laricina*, *Picea mariana* and *Thuja occidentalis*, often associated as zonal consociates. Where pines are absent in the region of the deciduous forest, two xeric oaks, *Quercus stellata* and *marilandica*, may constitute a subclimax, and this role is sometimes assumed by small trees, *Sassafras*, *Diospyrus* and *Hamamelis* being especially important.

Subclimaxes in the grassland are composed largely of tall-grasses, usually in the form of a consociates. In the true prairie, this part is taken by *Spartina cynosuroides* and in the desert plains by *Sporobolus wrightii*, while *Elymus condensatus* plays a similar role in the mixed prairie and in portions of the bunch-grass prairies. The function of the tall Andropogons is more varied; they are typically postclimax rather than subclimax, though they maintain the latter relation along the fringe of the oak-hickory forest and in oak openings. They occupy a similar position at the margin of the pine subclimax in Texas especially, and hence they are what might be termed "sub-subclimax" in such situations. Beyond the forest and in association with *Elionurus*, *Trachypogon*, etc., they appear to constitute a faciation of the coastal prairie. Chaparral

proper is to be regarded as a climax, but with a change of species it extends into the montane and even the subalpine zone and there constitutes a fire subclimax. In the foothills of southern California, the coastal sagebrush behaves in like manner where it lies in contact with the chaparral.

The disposition of seral stages below the subclimax that exhibit a distinct retardation or halt for a longer or shorter period is a debatable matter. It is entirely possible to include them among subclimaxes, but this would again fail in accuracy and definiteness and hence lead to confusion. The decision may well be left to usage by providing a term for such seral or sub-subclimax communities as persist for a long or indefinite period because of continued or recurrent edaphic control or human disturbance. By virtue of its significance, brevity and accord with related terms, the designation "serclimax" is suggested, with the meaning of a seral community usually one or two stages before the subclimax, which persists for such a period as to resemble the climax in this one respect. For reasons of brevity and agreement, the connecting vowel is omitted, but the *e* remains long as in *sere*.

For the most part, serclimaxes are found in standing water or in saturated soils as a consequence of imperfect drainage. The universal example is the reed-swamp with one or more of several consociates, such as *Scirpus*, *Typha*, *Zizania*, *Phragmites* and *Glyceria*: this is typical of the lower reaches of rivers, of deltas and of certain kinds of lakes, the great tule swamps of California affording outstanding instances. Another type occurs in coastal marshes in which *Spartina* is often the sole or major dominant, while sedge-swamps have a wider climatic range but are especially characteristic of northern latitudes and high altitudes. The Everglades of Florida dominated by *Cladium* constitute perhaps the most extensive example of the general group, though *Carex* swamps often cover great areas and the grass *Arundinaria* forms jungle-like cane-brakes through the south. Among woody species, *Salix longifolia* is an omnipresent consociate of sand-bars and river-sides, but the most unique exemplar is the cypress-swamp of the south, typified by *Taxodium*. In boreal and subalpine districts the distinctive serclimax is the peat-bog, moor or muskeg, more or less regularly associated with other seral communities of *Carex* and usually of *Larix* or *Picea* also in the proper region.

Frequent burning may retard or prevent the development of the normal fire subclimax and cause it to be replaced by a preceding stage. This may be a scrub community or one kept in the shrub form by repeated fires, but along the Atlantic and Gulf Coasts it is usually one of *Andropogon virginicus*, owing to its sufferance of burning. The so-called "balds" of the southern Appalachians are seral communities of heaths or grasses initiated and maintained primarily by fire. Finally, there are serclimaxes of weeds, especially annuals, in cultivated districts, and a somewhat similar community of native annuals is characteristic of wide stretches in the desert region.



Phot. 5. Serclimax of *Taxodium*, *Nyssa* and *Quercus* forming a cypress swamp; Paris, Arkansas.



Phot. 6. Disclimax of *Bouteloua*, *Muhlenbergia* and *Opuntia*, due to overgrazing of mixed prairie, Great Plains.

CLEMENTS—NATURE AND STRUCTURE OF THE CLIMAX

Disclimax

As with the related concepts, the significance of this term is indicated by a prefix, *dis-*, denoting separation, unlikeness or derogation, much as in the Greek *dys*, poor, bad. The most frequent examples of this community result from the modification or replacement of the true climax, either as a whole or in part, or from a change in the direction of succession. These ensue chiefly in consequence of a disturbance by man or domesticated animals, but they are also occasionally produced by mass migration. In some cases, disturbance and the introduction of alien species act together through destruction and competition to constitute a quasi-permanent community with the general character of the climax. This type is best illustrated by the *Avena-Bromus* disclimax of California, which has all but completely replaced the bunch-grass prairie.¹ A similar replacement by *Bromus tectorum* has more recently taken place over large areas of the Great Basin, while *Poa pratensis* has during the last half-century steadily invaded the native hay-fields and pastures of the true prairie, an advance first noted by Bradbury in 1809. An even more striking phenomenon is the steadily increasing dominance of *Salsola* over range and crop land in the west, and this is imitated by *Sisymbrium* and *Lepidium* in the north-west. It is obvious that all cultivated crops belong in the same general category, but this point hardly requires consideration.

Probably the example most cited in North America is that of the short-grass plains, which actually represent a reduction of the mixed prairie due to overgrazing, supplemented by periodic drouth. Over most of this association, the mid-grasses, *Stipa*, *Agropyrum*, etc., are still in evidence, though often reduced in abundance and stature, but in some areas they have been practically eliminated. Similar though less extensive partial climaxes of short-grasses characterise pastures in the true and both pasture and range in the coastal prairie, the dominants regularly belonging to *Bouteloua*, *Buchloe* or *Hilaria*. Of essentially the same nature is the substitution of annual species of *Bouteloua*

¹ The grassland climax of North America comprises six well-marked associations (*Plant Indicators*, 1920; *Plant Ecology*, 1929). The mixed prairie, so-called because it is composed of both mid-grasses and short-grasses, is more or less central to the other five and is regarded as ancestral to them. To the east along the Missouri and Mississippi Rivers, it has become differentiated into the true prairie formed by other species of mid-grasses pertaining mostly to the same genera, and this unit is flanked along the western margin of the deciduous forest by a proclimax of tall grasses, chiefly *Andropogon*. Southward the true prairie is replaced by coastal prairie, which in the main occupies the Gulf region of Texas and Mexico and is constituted by similar dominants but of different species. The desert plains are characterized primarily by species of *Bouteloua* and *Aristida*, which range from western Texas to the edge of the deserts of Mexico and Arizona. In the north-west the short-grasses disappear and the Palouse prairie of eastern Washington and adjacent regions is formed by mid-grasses of the bunch-grass life-form, among which *Agropyrum spicatum* is the eudominant. The same life-form signalizes the California prairie, found from the northern part of the state southward into Lower California, but its especial character is derived from endemic species of *Stipa*. As indicated in the discussion, the short-grass plains, composed of *Bouteloua*, *Buchloe*, and *Carex*, are not climatic in nature, and this statement applies likewise to the tall-grass meadows of *Andropogon* mentioned above.

and *Aristida* in the desert plains for perennial ones of the same genera, which is a case of short-grasses being followed by still shorter ones.

In other instances, the effect of disturbance is to produce a community with the appearance of a postclimax, when the life-form concerned is that of an undershrub or tall grass. This is notably the case in the mixed prairie when overgrazing is carried to the point of breaking up the short-grass sod and permitting the dominance of *Artemisia frigida* or *Gutierrezia sarothrae*. In essence, the wide extension of sagebrush (*Artemisia tridentata*) and of creosote-bush (*Larrea tridentata*) is the same phenomenon, though each of these is a climax dominant in its own region. In the case of *Opuntia*, the peculiar life-form suggests an important difference, but the numerous species behave in all significant respects like other shrubs, though with the two advantages of spines and ready propagation.

The communities of tall-grasses formed by species of *Andropogon* originally presented some difficulty, since these naturally have all the appearance of a postclimax to the prairie. Probably the greater number are to be assigned to this type, but the evidence from reconnaissance and record indicates that in the true prairie and especially the eastern portion, *Andropogon furcatus* in particular now constitutes a disclimax due to pasturing, mowing and in some measure to fire also (Clements, 1933). A characteristic disclimax in miniature is to be found in the "gopher gardens" of the alpine tundra, where coaction and reaction have removed the climax dominants of sedges and grasses to make place for flower gardens of perennial forbs. "Towns" of prairie-dogs and kangaroo-rats often produce similar but much more extensive communities.

Selective cutting not infrequently initiates disclimaxes, as may likewise the similar action of other agents such as fire or epidemic disease. The most dramatic example is the elimination of the chestnut (*Castanea dentata*) from the oak-chestnut canopy, but of even greater importance has been the extreme reduction and fragmentation of the lake forest through the overcutting of white pine. Finally, what is essentially a disclimax may result from climatic mass migration, such as in the Black Hills of South Dakota has brought together *Pinus ponderosa* from the montane climax of the Rocky Mountains and *Picea canadensis* from the boreal forest.

Preclimax and postclimax

These related concepts were first advanced in *Plant Succession* (1916, 1928) and have since been discussed in *Plant Ecology* (1929) and in the organisation of the relict method (1934). They are both direct corollaries of the principle of the clisere, the spatial series of climaxes that are set in motion by a major climatic shift, such as that of the glacial epoch with its opposite phases. The clisere is most readily comprehended in the case of high ranges or summits, such as Pikes Peak where the entire series of climaxes is readily visible, and is what Tournefort described on Mount Ararat in his famous journey of 1700.

However, this is but an expression of the continental clisere in latitude, which achieves perhaps its greatest regularity in North America. A similar relation is characteristic of the longitudinal disposition of climaxes in the temperate zone between the two oceans, the portion from deciduous forest through prairie to desert being the most uniform.

With the exception of the two extremes, arctalpine and tropical, each climax has a dual role, being preclimax to the contiguous community of so-called higher life-form and postclimax to that of lower life-form. This may be illustrated by the woodland climax, which is postclimax to grassland and preclimax to montane forest. The arctic and alpine tundras exhibit only the preclimax relation, to boreal and subalpine forest respectively, since a potential lichen climax attains but incomplete expression northward or upward. While the general primary relation is one of water in terms of rainfall and evaporation, temperature constantly enters the situation and at the extremes may be largely controlling, as in the tundra especially. However, in our present imperfect knowledge of causal factors it is simpler and more definite to determine rank by position in the cliseral sequence, each community higher in altitude or latitude being successively preclimax to the preceding one. This relation is likewise entirely consistent in the clisere from deciduous forest to desert, as it is among the associations of the same climax, though in both these cases the zonal grouping may be more or less obscured.

Wherever concrete preclimaxes or postclimaxes occur, either between climaxes or within a single one, they are due to the compensation afforded by edaphic situations. The major examples of the latter are provided by valleys, especially gorges and canyons, long and steep slope-exposures, and by extreme soil-types such as sand and alkali. The seriation is a series of communities produced by a graduated compensation across a valley and operating within a formation or through adjacent ones, while the ecocline embraces the differentiation brought about by shifting slope-exposures around a mountain or on the two sides of a high ridge. In the case of such soils as sand or gravel at one extreme and stiff clay at the other, the edaphic adjustment may sometimes appear contradictory. Thus, sand affords a haven for postclimax relicts in the dry prairie and for preclimax ones in the humid forest region, while the effect of heavy soils is just the reverse. However, this is readily intelligible when one recalls the peculiar properties of such soils in terms of absorption, chresard and evaporation (Clements, 1933).

Preclimax

Since they occupy the same general antecedent position with respect to the climax, it is necessary to distinguish with some care between subclimax and preclimax, especially in view of the fact that they often exhibit the same life-form. However, this is not difficult when the priseres and subseres have been investigated in detail, as the actual composition and behavior of the two

communities are usually quite different. Moreover, in the first, reaction leads to the entry of the climax dominants with ultimate conversion, while in the second the compensation by local factors is rarely if ever to be overcome within the existing climate, short of man-made disturbance.

Preclimaxes are most clearly marked where two adjacent formations are concerned, either prairie and forest or desert and prairie. Examples of the first kind are found in the grassy "openings" and oak savannahs of the deciduous forest and in the so-called "natural parks" along the margin of the montane and boreal forests. They are also well developed on warm dry slope-exposures or xeroclines in the Rocky Mountains. In the one, compensation is usually afforded by a sandy or rocky soil, in the other by a local climate due to insolation. Desert climaxes regularly bear the proper relation to circumjacent grassland, but this is somewhat obscured by the shrub life-form, which would be expected to characterize the less xeric formation. This may be explained, however, by the wide capacity for adaptation shown by such major dominants as *Larrea tridentata* and *Artemisia tridentata*, a quality that is lacking in most of their associates. Left stranded as relict communities in desert plains and mixed prairie by the recession of the last dry phase, they have profited by the overgrazing of grasses to extend across a territory much larger than that in which they are climax. Here they have all the appearance of a postclimax, especially in the case of *Larrea*, which commonly attains a stature several times that found in the desert. However, since this is the direct outcome of disturbance in terms of grazing, it is better regarded as a disclimax, particularly since the climax grasses still persist in it to some degree.

Within the same formation, the more xeric associations or consociations are preclimax to the less xeric ones. This is the general relation between the oak-hickory and beech-maple associations of the deciduous forest, the former occupying in the latter the warmer drier sites produced by insolation or type of soil. A similar relation may obtain in the case of faciatiions, the *Quercus stellata-marilandica* community often being a border of marginal preclimax to the more mesic oak-hickory faciatiions. Such preclimaxes naturally persist beyond the limits of the association proper as relicts in valleys or sandy soils and then assume the role of postclimaxes to the surrounding grassland, a situation strikingly exemplified in the "Cross Timbers" of Texas. In the montane forest of the Rockies, the consociation of *Pinus ponderosa* is preclimax to that of *Pseudotsuga taxifolia*, and a similar condition recurs in all forests where there is more or less segregation of consociations.

In the mixed prairie, fragments of the desert plains occur all along the margin as preclimaxes, the most extensive one confronting the Colorado Valley, where it is at the same time postclimax to the desert. The mixed prairie constitutes relicts of this type where it meets the true prairie. The most frequent examples are provided by *Bouteloua gracilis* and *Sporobolus cryptandrus*, though as with all the short-grasses in this role, grazing has played some part.



Phot. 7. Postclimax of *Quercus*, *Juglans*, *Ulmus*, *Fraxinus*, etc., Canadian River, near Oklahoma City.



Phot. 8. Postclimax of tall-grasses, *Andropogon*, *Calamovilfa* and *Panicum* in sandhills; Thedford, Nebraska.

CLEMENTS—NATURE AND STRUCTURE OF THE CLIMAX

Postclimax

As a general rule, postclimax relicts are much more abundant than those that represent preclimaxes, owing in the first place to the secular trend toward desiccation in climate and in the second to the large number of valleys, sandhills and sandy plains, and escarpments in the grassland especially. Postclimaxes of oak-hickory and of their flood-plain associates, elm, ash, walnut, etc., are characteristic features of the true and mixed prairies, holding their own far westward in major valleys but limited as outliers on ridges and sandy stretches to the eastern edge. However, the compensation afforded by the last two is incomplete as a rule and the postclimax is typically reduced to the savannah type. The latter is an almost universal feature where forest, woodland or chaparral touches grassland, owing to the fact that shrinkage under slow desiccation operates gradually upon the density and size of individuals. Savannah is derived from the reduction of deciduous forest along the eastern edge of the prairie, of the aspen subclimax of the boreal forest along the northern, and of the montane pine consociation, woodland or chaparral on the western and southern borders, recurring again on the flanks of the Sierras and Coast Ranges in California. On the south, the unique ability of the mesquite (*Prosopis juliflora*) to produce root-sprouts after fire, its thorniness, palatable pods and resistant seeds have permitted it to produce an extensive savannah that often closely simulates a true woodland climax.

As would be expected, a point is reached in the reduction of rainfall westward in the prairie where sand no longer affords compensation adequate for trees. In general this is along the isohyet of 30 in. in the center and south, and of about 20 in. in the north. Southward from the parallel of 37° the further shrinkage of the oak savannah may be traced in the "shinry", which dwindles from four or five feet to dwarfs only "shin" high. With these are associated tall-grasses, principally *Andropogon* and *Calamovilfa* in the form *gigantea*. To the north of this line, the shin oaks are absent and the tall-grasses make a typical postclimax that extends into Canada, though the compensatory influence of sand is still sufficient to permit an abundance of such low bushes as *Amorpha*, *Ceanothus*, *Artemisia filifolia* and *Yucca*, as well as depauperate hackberry and aspen. In the vast sandhill area of central Nebraska, the tall-grass postclimax attains its best development, which is assumed to reflect the climate when the prairies were occupied by the Andropogons and their associates some millions of years ago. The gradual decrease to the rainfall of the present has led to the tall-grasses finding refuge in all areas of edaphic compensation, not only in sand but likewise on foothills and in valleys, and in addition along the front of the deciduous forest.

STRUCTURE OF THE CLIMAX

Community functions

The nature of community functions and their relation to the structure of climax and sere have been discussed in considerable detail elsewhere (*Plant Succession*, 1916, 1928; *Plant Ecology*, 1929; *Bio-ecology*, 1936), and for the present purpose it may well suffice to emphasize the difference in significance between major or primary and minor or secondary functions. The former comprise aggregation, migration, ecesis, reaction, competition, cooperation, disoperation, and coaction, together with the resulting complexes, invasion and succession. Any one of these may have a profound effect upon community structure, but the driving force in the selection and grouping of life-forms and species resides chiefly in reaction, competition, and coaction. Migration deals for the most part with the movement and evolution of units under climatic compulsion, and succession with the development and regeneration of the climax in bare or denuded areas.

In contrast to these stands the group of minor functions that are concerned with numbers and appearance or visibility as it may be termed. The first is annuation, in accordance with which the abundance of any species may fluctuate from dry to wet phases of the various climatic cycles or the growth differ in terms of prominence, the two effects not infrequently being combined. For the grassland, a season of rainfall more or less extreme in either direction often emphasizes one dominant at the expense of others, though the balance is usually redressed by the following year, while in the desert in particular the swing in number of annuals may be from almost complete absence to seasonal dominance, again with one or few species taking the major role. Aspection is mainly the orderly procession of societies through each growing season, more or less modified by changes in number ensuing from annuation. Hibernation and estivation merely affect seasonal appearance and are forms of aspection, with the temporary suspension of coaction effects. While usually applied to the animal members of the biome, it is obvious that plants exhibit certain responses of similar nature. Diurnation is likewise best known in the case of animals, especially nocturnal ones, but it is exhibited also by the vertical movement of plankton and in different form by the opening and closing of flowers and the "sleep" movements of leaves.

Roles of constituent species: dominants

The abundant and controlling species of characteristic life-form were long ago termed dominants (Clements, 1907, 1916), this property being chiefly determined by the degree of reaction and effective competition. In harmony with the concept of the biome, it has become desirable to consider the role of animals likewise; since their influence is seen chiefly in coaction by contrast to the reaction of plants, the term *influent* has been applied to the important

species of land biomes (cf. Clements and Shelford, 1936). It is an axiom that the life-form of the dominant trees stamps its character upon forest and woodland, that of the shrub upon chaparral and desert, and the grass form on prairie, steppe and tundra. There are seral dominants as well as climax ones, and these give the respective impresses to the stages of prisere and subsere. Finally, there are considerable differences in rank or territory even among the dominants of each formation. The most important are those of wide range that bind together the associations of a climax; to these the term *perdominant* (*per*, throughout) may well be applied. In contrast to these stand the dominants more or less peculiar to each association, such as beech or chestnut in their respective communities and *Sporobolus asper* in the true and *Stipa comata* in the mixed prairie, for which *eudominant* may be employed.

Subdominants regularly belong to a life-form different from that of the dominants and are subject to the control of the latter in a high degree, as the name indicates. They are best exemplified by the perennial forbs, though biennials and annuals may serve as seral subdominants; all three may be actual dominants in the initial stages of succession and especially in the subsere. The term *codominant* has so far had no very definite status; it is hardly needed to call attention to the presence of two or more dominants, since this is the rule in all cases with the exception of consociation and consociates. In contrast to the types mentioned stands a large number of secondary or accessory species that exhibit no dominance, which may be conveniently referred to as *edominants*, pending more detailed analysis.

Influents

As indicated previously, the designation of *influent* is applied to the animal members of the biome by virtue of the influence or coaction they exert in the community. The significance of this effect depends much upon the life-form and to a large degree upon the size and abundance of the species as well, and is seen chiefly in the coactions involved in food, material, and shelter. Influents may be grouped in accordance with these properties, or they may be arranged with respect to distribution and role in climax or sere, or to time of appearance (Clements and Shelford, 1936). For general purposes it is perhaps most convenient to recognize subdivisions similar to those for dominants and with corresponding terms and significance. Thus, a *perfluent* would occur more or less throughout the formation, while the *eufluent* would be more or less typical or peculiar to an association. *Subfluents* would mark the next lower degree of importance, roughly comparable to that of subdominant, while minute or microscopic influents of still less significance might well be known as *vefluents*.

Climax and seral units

No adequate analysis of vegetation or of the biome is possible without taking full account of development. As the first step, this involves a distinction between climax communities proper and those that constitute the

successional movement toward the final stages. The two groups differ in composition, stability, and type of control, but they agree in the possession of dominants, subdominants, and influents. These primary differences made it desirable to recognize two series of communities, viz. climax and seral and to propose corresponding terms, distinguished by the respective suffixes, *-ation* and *-ies* (Clements, 1916). These have gradually come into use as the feeling for dynamic ecology has grown and bid fair to constitute a permanent basis for all such studies. It is not supposed that they embrace all the units finally necessary for a complete system, but their constant application to the great climaxes of North America for nearly two decades indicates that they meet present needs in the matter of analysis.

Not all communities can be certainly placed in the proper category at the outset, but the number of doubtful cases is relatively small and few of these present serious difficulty under combined extensive and intensive research. This statement, however, presupposes an experience sufficiently wide and long to permit distinguishing between climaxes and the various types of proclimax, as well as recognizing the characteristic features of subclimaxes in particular. Comparative studies over a wide region are indispensable and the difficulties will disappear to the degree that this is achieved. While ecotones and mictia necessarily give rise to some questions in this connection, these in turn are resolved by investigations as extensive as they are detailed.

Climax units

In the organization of these, four types of descending rank and importance were distinguished within the formation, namely, association, consociation, society, and clan. Like the formation itself, the first two were based upon the dominant and its life-form, while the last were established upon the subdominant and its different life-form. It was recognized at the time that the association contained within itself other units formed by the dominants (cf. *Plant Indicators*, 1920, pp. 107, 276), and two further divisions, *faciation* and *lociation*, with corresponding seral ones, *facies* and *locies*, were suggested and submitted to Prof. Tansley for his opinion as to their desirability. These have been tested in the course of further field studies and have now and then been used in print, though the complete series was not published until 1932 (cf. Shelford, 1932). The climax group now comprises the following units, viz. association, consociation, faciation, lociation, society, and clan. At the beginning, it was intended to replace society by *sociation* for the sake of greater uniformity in terms, but the former had attained such usage that the idea was relinquished. However, the use of society in quite a different sense by students of social relations, especially among insects, again raises the question of the desirability of such a substitution, in view of the growing emphasis upon bioecology (cf. also Du Rietz, 1930; Rübel, 1930).



Phot. 9. Association of mixed prairie, *Stipa*, *Agropyrum*,
Bouteloua, etc.: Monument, Colorado.



Phot. 10. Foothill faciation of the desert-plains association, *Bouteloua*
eriopoda, *B. gracilis*, *B. hirsuta*, *B. filiformis*, etc.: Safford, Arizona.

CLEMENTS—NATURE AND STRUCTURE OF THE CLIMAX

Association.

Under the climax concept this represents the primary division of the biome or formation, and hence differs entirely from the generalized unit of the plant sociologists, for which the term *community* is to be preferred. Each biome consists regularly of two or more associations, though the lake forest and the desert scrub embody two apparent exceptions, each seeming to consist of one association only. However, these are readily explained by the fact that the western member of the former has been obscured by the expansion of montane and coast forests in the north-west, while one or more additional associations of the desert climax occur to the southward in Mexico, and apparently in South America also.

The number of associations in a particular formation is naturally determined by the number of primary differences and these in turn depend upon the presence of eudominants. Just as the unity of the formation rests upon the wide distribution of several major dominants or perdominants, so the association is also marked by one or more dominants peculiar to it, and often as well by differences in the rank and grouping of dominants held in common. Thus, in the true prairie association, the eudominants are *Stipa spartea*, *Sporobolus asper* and *heterolepis*; for the desert plains, *Bouteloua eriopoda*, *rothrocki* and *radicosa* and *Aristida californica*, while *Stipa comata* and *Buchloe* take a similar part in the mixed prairie. In the deciduous climax, the characteristic dominants of one association are supplied by the beech and hard maple, of a second by chestnut and chestnut-oak, though the oak-hickory association, of wider range and greater complexity, is comparatively poor in eudominants by contrast with the number of species.

The structural and phyletic relations of the associations of a climax are best illustrated by the grassland, which is the most highly differentiated of all North American formations, largely as an outcome of its great extent. The most extensive and varied unit is the mixed prairie, which occupies a generally median position with respect to the other five associations of this climax. Originally, it derived its dominants from three separate regions, *Stipa*, *Agropyrum* and *Koeleria* coming from Holarctica, *Sporobolus* from the south, and the short-grasses from the Mexican plateaux, and it still exhibits the closest kinship with the Eurasian steppe. It contains nearly all the genera that serve as dominants in the related associations, while many of the eudominants of these have all the appearance of direct derivatives from its species, as is shown by *Stipa*, *Sporobolus*, *Poa*, and *Agropyrum*. The evolution of both species and communities is evidently in response to the various subclimates, that of the true prairie being moister, of the coastal warmer as well; the desert plains are hotter and drier, the California prairie marked by winter rainfall and the Palouse by snowfall.

Consociation.

In its typical form the consociation is constituted by a single dominant, but as a matter of convenience the term is also applied to cases in which other dominants are but sparingly present and hence have no real share in the control of the community. It has likewise been convenient to refer in the abstract to each major dominant of the association as a consociation, though with the realization that it occurs more frequently in mixture than by itself. In this sense it may be considered a unit of the association, though the actual area of the latter is to be regarded as divided into definite faciations. Consociation dominants fall into a more or less regular series with respect to factor requirements, especially water content, and often exhibit zonation in consequence. This is a general feature of mixed prairie where *Agropyrum smithi* and *Stipa comata* are the chief mid-grasses, the former occupying swales and lower slopes, the latter upper slopes and ridges.

The consociation achieves definite expression over a considerable area only when the factors concerned fluctuate within the limits set by the requirements of the dominant or when the other dominants are not found in the region. The first case may be illustrated by *Pinus ponderosa* in the lower part of the montane forest and by *Adenostoma fasciculatum* in the Sierran chaparral, while the second is exemplified by *Picea engelmanni* in the Front Range of Colorado, its usual associate, *Abies lasiocarpa*, being absent from the district. In rolling terrain like that of the prairie, each consociation will recur constantly in the proper situation but is necessarily fragmentary in nature. Such behavior is characteristic of dominants with a postclimax tendency, as with *Stipa minor* and *Elymus condensatus* in swales and lower levels of the mixed prairie.

Faciation.

This is the concrete subdivision of the association, the entire area of the latter being made up of the various faciations, except for seral stages or fragments of the several consociations. Each faciation corresponds to a particular regional climate of real but smaller differences in rainfall/evaporation and temperature. It may be characterized by one or two eudominants, such as *Hilaria jamesi* and *Stipa pennata* in the southern mixed prairie, but more often it derives its individuality from a sorting out or a recombination of the dominants of the association. As is evident, the term is formed from the stem *fac-*, show, appear, as seen in *face* and *facies*, and the suffix *-ation*, which denotes a climax unit.

During the past decade, much attention has been given to the recognition and limitation of faciations on the basis of the presence or absence of a eudominant, such as *Hilaria*, *Buchloe*, or *Carex*, or a change in the rank or grouping of common dominants, like *Stipa*, *Agropyrum*, *Sporobolus* or *Bouteloua*. In the prairie this task has been complicated by overgrazing, cultivation and related disturbances, while selective lumbering and fire have added to the

difficulties, in the deciduous forest especially. In general, temperature appears to play the leading part in the differentiation of faciations, since they usually fall into a sequence determined by latitude or altitude, though rainfall/evaporation is naturally concerned also. The mixed prairie exhibits the largest number, but it is approached in this respect by the deciduous forest as a consequence of wide extent and numerous dominants. Over the Great Plains from north to south, the successive faciations are *Stipa-Bouteloua*, *Bouteloua-Carex*, *Stipa-Agropyrum-Buchloe*, *Bouteloua-Buchloe*, *Hilaria-Stipa-Bouteloua*, and *Agropyrum-Bouteloua*. However, the short-grass communities are to be regarded as disclimaxes wherever the mid-grasses have been eliminated or nearly so, a condition that fluctuates in relation to dry and wet phases of the climatic cycle.

Lociation.

In its turn, the lociation is the subdivision of the faciation, the term being derived from *locus*, place, as indicating a general locality rather than a large region. Nevertheless, a lociation may occupy a relatively extensive territory up to a hundred miles or more in extent, by comparison with several hundred for the faciation. It is characterized by more or less local differences in the abundance and grouping of two or more dominants of the faciation. These correspond to considerable variations in soil, contour, slope-exposure or altitude, but all within the limits of the faciation concerned. As a consequence, lociations are very often fragmented, recurring here and there as alternates with each other, and frequently with proclimaxes of various types. Like most climax units, they have been modified by disturbance in some degree, and this fact must be constantly kept in mind in the task of distinguishing them from subclimax or disclimax.

A detailed knowledge of the faciation is prerequisite to the recognition of the various lociations in it. The number for a particular faciation naturally depends upon the extent of the latter and the number of dominants concerned. Consequently, lociations are more numerous in the faciations of the mixed prairie and desert plains, of the chaparral and the oak-hickory forest. As would be expected, they are often most distinct in ecotones and in districts where there is local intrusion of another dominant. In correspondence with their local character, it is important to eliminate or diminish superimposed differences through restoration of the original cover by means of protection enclosures and thus render it possible to disclose the true composition.

Society.

This term has had a wide range of application, but by dynamic ecologists it has generally been employed for various groupings of subdominants, of which those constituted by aspects or by layers are the most important. In addition, there is a host of minor communities formed by cryptogams in the ground layer or on host-plants and other matrices. The soil itself represents a

major layer, divisible into more or less definite sublayers. Animals regularly assume roles of varying importance in all of these, especially the insects, arachnids and crustacea, and hence most if not all societies comprise both subdominant plants and subinfluent animals. It is doubtful whether animals form true societies independently of their food-plants or those used for materials or shelter, but this is a question that can be answered only after the simplest units, namely, family and colony, have been recognized and coordinated in terms of their coactions.

In view of what has been said previously, it seems desirable to employ society as the general term for all communities of subdominants and sub-influents above the rank of family and colony, much as community is the inclusive term for all groupings of whatsoever rank. This then permits carrying out the suggestion made two decades ago that the major types of societies be set apart by distinctive names. In accordance, it is here proposed to call the aspect society a *sociation* and the layer society a *lamiation*, while the corresponding seral terms would be *sociés* and *lamies*. Many of the societies of cryptogams and minute animals would find their place in these, particularly so for those of the surface and soil layers, but many others take part in a miniature sere or *serule*, such as that of a moldering log, and may best receive designations that suggest this relation.

Sociation. Wherever societies are well developed, they regularly manifest a fairly definite seasonal sequence, producing what have long been known as aspects (Pound and Clements, 1898). As phenomena of the growing season, these were first distinguished as early spring or prevernal, vernal proper, estival, and serotinal or autumnal, but there may also be a hiemal aspect, especially for animals, in correspondence with an actual and not merely a calendar winter as in California.

Sociations are determined primarily by the relation between the life cycle of the subdominants and the seasonal march of direct factors, temperature in particular. So far as the matrix of plants is concerned, the constituent species may be in evidence throughout the season, but they give character to it only during the period of flowering, or fruiting in the case of cryptogams. They are present largely or wholly by sufferance of the dominants, and they are to be related to the reactions of these and competition among themselves rather more than to the habitat factors as such. In grassland and desert, they are often more striking than the dominants themselves, sometimes owing to stature but chiefly as an effect of color and abundance, and they may also attain much prominence in woods with the canopy not too dense.

Sociations are usually most conspicuous and best developed in grassland, four or even five distinct aspects occurring in the true prairie from early spring to autumn. In the mixed prairie these are usually reduced to three, and in the desert plains and desert proper, to two major ones, summer and winter, in which however there may be subspects marked by *sations*, as indicated



Phot. 11. Sociation of *Erigeron* and *Psoralea*, estival aspect; Belmont Prairie, Lincoln, Nebraska.



Phot. 12. Lamiation of mid-herbs, *Laportea*, *Physostegia*, *Impatiens*, etc., in Oak-Hickory forest.

CLEMENTS—NATURE AND STRUCTURE OF THE CLIMAX

later. Short seasons due to increasing latitude or altitude afford less opportunity, and the tundra, both alpine and arctic, usually exhibits but two aspects, the sociations however taking a conspicuous role as in the prairie. In woodland the number and character of the sociations depend largely upon the nature of the canopy, and for deciduous forest the flowery sociations regularly belong to the spring and autumn aspects, when the foliage is either developing or disappearing.

It is convenient to distinguish sociations as simple or mixed with respect to the plant matrix in accordance with the presence of a single subdominant or of two or more. However, when animals are included in the grouping, such a distinction appears misleading and may well be dropped. The word "mixed" would be more properly applied to plant-animal societies were it not for the fact that this appears to be the universal condition. Since seasonal insects are legion, many of the societies in which they take part are best denoted as sations.

Lamination. The term for a layer society is derived from the stem *lam-*, seen in lamina and lamella. As is well known, layers are best developed in forests with a canopy of medium density, so that under the most favorable conditions as many as five or six may be recognized above the soil. In such instances, there are usually two shrub stories, an upper and lower, often much interrupted, followed by tall, medium and low forb layers, and a ground community of mosses, lichens and other fungi, and usually some delicate annuals (cf. Hult, 1881; Grevillius, 1894). The soil population is perhaps best treated as a single unit, though it may exhibit more or less definite sublayers. When the various layers beneath the dominants are distinct, each is regarded as a lamiation, but in many cases only one or two are sufficiently organized to warrant designation, e.g. shrub or tall-herb lamiation.

Layers are often reduced to a single lamiation of low herbs in the climax forest, especially of conifers, and even this may be entirely lacking in dense chaparral. Two or three layers of forbs may be present in true prairie in particular, the upper lamiation being much the most definite and often concealing the grass dominants in the estival aspect, but the structure of grassland generally reflects the greater importance of sociations. Climaxes of sagebrush and desert scrub exhibit no proper lamiations, owing to the interval between the individual dominants, but the herbaceous societies of the interspaces show something of this nature.

As a rule, well-developed lamiations also manifest a seasonal rhythm, corresponding to aspects or to subaspects. These constitute recognizable groupings in the lamiation and for the sake of determination and analysis may be termed *sations*. This word is a doublet of season, both being derived from the root *sa-*, sow, hence grow or appear. Because of the frequent interplay of aspects and layers, the sation may for the present be employed for the subdivision of both sociation and lamiation, and especially where seasonal species of invertebrates play a conspicuous role.

Clan. This is a small community of subordinate importance but commonly of distinctive character. It is marked by a density that excludes all or nearly all competing species, in consequence of types of propagation that agree in the possession of short offshoots. Extension is usually by bulb, corm, tuber, stolon or short rootstock, each of which produces a more or less definite family grouping; in fact, most clans are families developed in the climax matrix and sometimes with a blurred outline in consequence. Clans of a particular species such as *Delphinium azureum* or *Solidago mollis* are dotted throughout the respective sociation, often in large numbers, and contribute a distinctive impress much beyond their abundance. Like all units, but small ones especially, they are subject to much fluctuation with the climatic cycle, as a result of which they may pass into societies or be formed by the shrinkage of the latter.

Seral units.

The concepts of dominance and subdominance apply to the sere as they do to the climax, as does that of influence also, and the corresponding sets of units bear the same general relation to each other. Each of the four major units is the developmental equivalent of a similar community in the climax series and this is likewise true of the various kinds of societies. They constitute the successive stages of each sere, both primary and secondary, including the subclimax, where they often achieve their best expression. It has also been customary to employ seral terms for preclimax and postclimax, and this appears to be the better usage for disclimax and proclimaxes in general. From the fragmentary nature of bare areas and suitable water bodies in particular, seral communities are often but partially developed and one or more units will be lacking in consequence. Thus, the reed-swamp associates is frequently represented by a single one of its several consociates and the minor units are even more commonly absent.

The associates is the major unit of every sere, the number being relatively large in the prisere and small in the subsere. The universal and best understood examples are those of the hydrosere, in which *Lemna*, *Potamogeton*, *Nuphar*, *Nymphaea*, *Nelumbo* and others form the consociates of the floating stage, and *Scirpus*, *Typha*, *Phragmites*, etc., are the dominants of the reed-swamp or amphibious associates. As already indicated, every consociate may occur singly and often does when the habitat offers just the proper conditions for it or the others have failed to reach the particular spot. When the ecial range is wider, various combinations of two or three dominants will appear, to constitute corresponding facies. Locies are less definitely marked as a rule, except in swamps of vast extent, but are to be recognized by the abundance of reed-like dominants of lower stature, belonging to other species of *Scirpus*, to *Heleocharis*, *Juncus*, etc. Both facies and locies seem to be better developed in sedge-swamp with its larger number of dominants, though the Everglades with the single consociates of *Cladium* form a striking exception.

The tree-swamps of the south-eastern United States contain a considerable number of consocieties, such as *Taxodium distichum*, *Nyssa aquatica*, *biflora* and *ogeeche*, *Carya aquatica*, *Planera aquatica*, *Persea palustris* and *borbonia*, *Magnolia virginiana*, *Fraxinus pauciflora*, *profunda* and *caroliniana*, and *Quercus nigra*. These are variously combined in several different facies, though a more detailed and exact study of the swamp sere may show the presence of two woody associates, distinguished by the depth or duration of the water. As with other scrub communities, the heath associates of peat-bog and muskeg comprises a large number of dominants and presents a corresponding wealth of facies and locies.

In the hydrosere of the deciduous forest, the typical subclimax is that of the flood-plain associates, composed of species of *Quercus*, *Ulmus*, *Fraxinus*, *Acer*, *Betula*, *Juglans*, *Celtis*, *Platanus*, *Liquidambar*, *Populus* and *Salix* for the most part. There are at least three well-marked facies, namely, northern, central and southern, each with a number of more or less distinct locies. The swamp associates or subclimax of the lake and boreal forests consists of *Larix laricina*, *Picea mariana* and *Thuja occidentalis*, occurring often as consocieties but generally in the form of zoned facies. A large number of fire subclimaxes appear in the form of consocieties, as with many of the pines, but associates are frequent along the Atlantic Coast, as they are in the boreal climax, where aspens and birches are chiefly concerned. The number of shrubs and small trees that play the part of seral dominants in the deciduous climax is much larger, producing not merely a wide range of associates but of facies and locies as well. More than a dozen genera and a score or so of species are involved, chief among them being *Sassafras*, *Diospyrus*, *Asimina*, *Hamamelis*, *Prunus*, *Ilex*, *Crataegus* and *Robinia*. The subclimax of the xerosere is constituted for the most part by species of *Quercus*, forming an eastern, a south-eastern and a western associates, the last with two well-marked facies, one of *stellata* and *marilandica*, the other of *macrocarpa* and *Carya ovata*.

Among postclimax associates, those of grassland and scrub possess a large number of dominants and exhibit a corresponding variety of facies and locies, together with fairly definite consocieties. In the sandhills of Nebraska, the tall-grasses concerned are *Andropogon halli*, *furcatus* and *nutans*, *Calamovilfa longifolia*, *Eragrostis trichodes*, *Elymus canadensis* and *Panicum virgatum*; some of these drop out to the northward and others to the south, thus producing at least three regional facies. The mesquite-acacia associates of the south-west possesses a larger number of dominants and manifests a greater variety of facies through its wide area, and this is likewise true of the coastal sagebrush of California.

With reference to seral societies, it must suffice to point out that these are of necessity poorly developed in the initial stages of both hydrosere and xerosere, as the dominants are relatively few. Even in the reed-swamp, true layers are the exception, being largely restricted to such subdominants as

Alisma, *Pontederia*, *Hydrocotyle* and *Sagittaria*, which are found mostly in borders and intervals. However, in extensive subclimaxes and postclimaxes the situation is quite different. The tall-grass associates of sandhills is often quite as rich in saties and lamies as the true prairie, while the various subclimaxes of the several great forest types may equal the latter in the wealth of subdominants for each season and layer, the actual communities being very much the same.

Serule.

This term, a diminutive of *sere*, has been employed for a great variety of miniature successions that run their short but somewhat complex course within the control of a major community, especially the climax and subclimax. They resemble ordinary seres in arising in bare spots or on matrices of different sorts, such as earth, duff, litter, rocks, logs, cadavers, etc. Parasites and saprophytes play a prominent and often exclusive role in them, and plants and animals may alternate in the dominant parts. The organisms range from microscopic bacteria and worms to mites, larvae and imagoes on the one hand and large fleshy and shelf fungi on the other. The most important of these in terms of coaction and abundance are known as *dominules* (Clements and Shelford, 1936), with *subdominule* and *edominule* as terms for the two degrees of lesser importance. On the same model are formed *associiule*, *consociiule*, and *sociiule* in general correspondence with the units of the sere itself. In addition there are families and colonies of these minute organisms, which are essentially similar to those of the initial stages of the major succession. Up to the present, little attention has been devoted to the development and structure of serules, but they are coming to receive adequate consideration in connection with bio-ecological problems. Many of the coactions, however, have long been the subject of detailed research in the conversion of organic materials.

RANK AND CORRESPONDENCE OF UNITS

The following table exhibits the actual units of climax and sere, as well as their correspondence with each other. However, for the complete and accurate analysis of a great climax and especially the continental mass of vegetation, it is necessary to invoke other concepts, chiefly that of the proclimax and of communities mixed in space or in time. The several proclimaxes have been characterized (pp. 262-8), and the ecocline and seration briefly defined (p. 267). To these are to be added the *ecotone* and *mictium*, both terms of long standing, the former applied to the mixing of dominants between two units, the latter to the mixed community that intervenes between two seral stages or associates. Finally, there will be the several types of seres in all possible stages of development, the prisere in the form of hydrosere, xerosere, halosere or psammosere in regions less disturbed and a myriad of subseres in those long settled.

TABLE OF CLIMAX AND SERAL UNITS

| <i>Climax</i> | Eoclimax Panclimax | <i>Sere</i> |
|---------------|-----------------------|--------------|
| | Climax (formation) | |
| Association | | Associes |
| Consociation | | Consocieties |
| Faciation | | Facies |
| Lociation | | Locieties |
| Sociation | | Societies |
| Lamiation | | Lamies |
| Sation | | Saties |
| Clan | | Colony |
| | | Family |
| | <i>Serule</i> | |
| | Associule | |
| | Consociule | |
| | Sociule | |

As indicated previously, the word *community* is employed as a general term to designate any or all of the preceding units, while *society* may well be used to include those of the second division, i.e. sociation, etc. These are characterized by subdominants in contrast to the dominants that mark the first group. It has also been pointed out that the entire area of the association is divided into faciations and that the consociation is the relatively local expression of complete or nearly complete dominance on the part of a single species. The clan corresponds to the family as a rule, but in some cases resembles the colony in being formed by two species.

Families and colonies may also appear in climax communities, but this is regularly in connection with the serule.

Panclimax and eoclimax

The comprehensive treatment of these concepts is reserved for the succeeding paper in the present series, but it is desirable to characterize them meanwhile. The *panclimax* (παν, all, whole) comprises the two or more related climaxes or formations of the same general climatic features, the same life-form and common genera of dominants. The relationship is regarded as due to their origin from an ancestral climax or *eoclimax* (ἑως, dawn), of Tertiary or even earlier time, as a consequence of continental emergence and climatic differentiation. In the past, eoclimaxes formed a series of great biotic zones in the northern hemisphere with the pole as a focus, and this zonal disposition or clisere is still largely evident in the arrangement of panclimaxes at the present. It is striking in the case of the arctic tundra and taiga or boreal forest, fairly evident for deciduous forest and prairie-steppe, and somewhat obscure for woodland and chaparral-macchia, while the position of deserts is largely determined by intervening mountain ranges. This is true likewise of grassland in some degree, and taken with the former broad land connection between North and South America explains why both prairie and desert panclimax contain at least one austral formation.

In the light of what has been said earlier, it is readily understood that panclimax and panformation are exact synonyms, as are eoclimax and eoformation. Panbiome and eobiome are the corresponding terms when the biotic community is taken as the basis for research.

Prerequisites to research in climaxes

It would be entirely superfluous to state that the major difficulty in the analysis of vegetation is its complexity, were it not for the fact that it is too often taken as the warrant for the static viewpoint. This was embodied in the original idea of the formation as a unit in which communities were assembled on a physiognomic basis, quite irrespective of generic composition and phyletic relationship. It is not strange that this view and its corollaries should have persisted long past its period of usefulness, since this is exactly what happened with the artificial system of Linnaeus, but the time has come to recognize fully that a natural system of communities must be built just as certainly upon development and consequent relationship as must that of plant families. Complexity is an argument for this rather than against it, and especially in view of the fact that the complexity discloses a definite pattern when the touchstone of development is applied to it.

Though the mosaic of vegetation may appear to be a veritable kaleidoscope in countries long occupied by man, the changes wrought upon it are readily intelligible in terms of the processes concerned. As emphasized previously, the primary control is that of climate, in a descending scale of units that correspond to formation, association, and faciation. Upon this general pattern are wrought the more circumscribed effects of physiography and soil, and both climatic and edaphic figures are overlaid and often more or less completely obscured with a veneer applied by disturbance of all possible kinds. Even above this may be discerned the effect, transient but nonetheless apparent, of such recurrent changes as annuation and aspection. Moreover, the orderly pattern of climate is complicated by great mountain ranges so that such climaxes as tundra and taiga occur far beyond their proper zone, and the effect is further varied by the relative position of the axis.

The migrations of climaxes in the past are a prolific source of fragmentary relicts, the interpretation of which is impossible except in terms of dynamics. This is likewise true of savannah, which represents the shrinkage of forest and scrub under a drying climate and is then usually further modified by fire or grazing. Fragmentation from this and other causes is characteristic of every diversified terrain and reaches its maximum when human utilization enters the scene upon a large scale. Somewhat similar in effect though not in process is the reduction of number of dominants by distance, with the consequence that an association of several may be converted into a consociation of one. Such a shrinkage naturally bears some relation also to climate and physiography, especially as seen in the glacial period, and finds its best illustration in the

general poverty of dominants in the coniferous and deciduous climaxes of Europe, by contrast with those of eastern Asia and North America. A similar contrast obtains between the grassland of Asia and of North America, the latter being much richer in dominants, while South America approximates it closely in this respect.

On the part of the investigator, the difficulties in the way of an extensive and thoroughgoing study of climaxes are usually more serious. They arise partly from the handicap too often set by state or national boundaries and partly from the limitations of funds and time. They are also not unrelated to the fact that it is easiest to know a small district well and to assume that it reflects larger ones with much fidelity. As a consequence, it is impossible to lay too much stress upon the need for combining intensive and extensive methods in the research upon climaxes, insofar as their nature, limits and structure are concerned. The detailed development in terms of primary and secondary succession lends itself much more readily to local or regional investigation, but even here a wider perspective is essential to accurate generalization.

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