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THE VEGETATION OF CONNECTICUT

III. Plant Societies on Uplands*

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In the first paper of this series the writer undertook to point out and in a measure to account for certain of the broader features of the vegetation of Connecticut. In the second an account is given of the virgin forests. In the present and subsequent papers attention will be devoted primarily to the study of plant societies and their relationship both to one another and to environment. Numerous writers during the past few years have dealt with this phase of vegetation in other parts of the country, but so far as published records show very little work of this nature seems to have been accomplished in southern New England. Since it is desired that this series of studies may serve as a starting-point for further investigations, both extensive and intensive, it has seemed advisable to treat the subject matter more or less comprehensively, drawing freely upon the observations of other workers in the same field of study.

The scheme of classification which in a general way underlies the writer's treatment of the plant societies of Connecticut is the one originated some years ago by Cowles.† This classification "attempts to relate plant societies not only to water, but also to soil, and more especially to the physiography." The fundamental concept of the scheme is that "each particular

* Contribution from the Osborn Botanical Laboratory.

† Cowles, H. C. The physiographic ecology of Chicago and vicinity. Bot. Gaz. 31: 73–108, 145–182. *f. 1–35.* 1901. Reprinted with slight modifications as Bull. Geog. Soc. Chicago No. 2. 1901.

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topographic form has its own peculiar vegetation. This is due to the fact that the soil conditions upon which plants depend are determined by the surface geology and topography." And, since the nature of the topography is constantly undergoing modifications as a result of erosion and deposition, it follows that "just as there is an order of succession of topographic forms in the changing landscape," so "there must be an order of succession of plant societies. As the years pass by, one plant society must necessarily be supplanted by another, though the one passes into the other by imperceptible gradations." Such a classification, it will be seen, is at once genetic and dynamic. It aims to "group plant societies according to their relationship and their evolution."

In a more recent contribution Cowles* has defined three types of vegetative succession, regional, topographic, and biotic. Regional successions are due primarily to secular changes in climate and move with extreme slowness. In Connecticut the series of changes in vegetation that have ensued since the retreat of the continental ice sheet serve to illustrate this type of succession. Topographic successions "are associated with the topographic changes which result from the activities of such agencies as running water, wind, ice, gravity, and vulcanism." Such successions in Connecticut are seen principally along rivers and along the coast. Topographic successions take place much more rapidly than regional successions. Biotic successions are instituted by plant and animal agencies. On account of the comparative rapidity with which these agencies operate and their far-reaching influence, this type of succession must be regarded as more important than either of the two preceding. "If, in their operation, regional agencies are matters of eons, and topographic agencies matters of centuries, biotic agencies may be expressed in terms of decades."

In treating the plant societies of Connecticut and their ecological relations, it has been found convenient to group them in the following manner.*

* Cowles, H. C. The causes of vegetative cycles. Bot. Gaz. **51**: 161–183. 1911.

† Compare Cowles, 1901, op. cit.

1. Plant societies on uplands.
2. Plant societies in lowlands.
3. Plant societies along rivers and streams.
4. Plant societies along the coast.

Broadly speaking, the term lowland is here used to designate depressions of all sorts—areas occupied by lakes, swamps, etc. All other types of topography are included under uplands. In the present paper attention is confined to upland successions. By way of introduction a representative upland succession, such as may be studied along the trap ridges in the vicinity of New Haven, will be described. Then, with this as a background, differences between successions on various substrata and in different parts of the state will be considered.

Probably nowhere in this region are the environmental conditions to which vegetation is subjected more severe than on the bare surface of an exposed rock. Insolation during the daytime is intense, temperature changes are extreme, and water is absent for long periods. Add to these the difficulty, where the surface slopes and crevices are absent, of securing a foothold, and it is evident that even among xerophytes comparatively few plants are qualified to exist in such localities. Usually the first living organisms to appear on a freshly exposed trap surface are crustose lichens, *e. g.*, *Buellia petraea* and *Lecanora cinerea.* These form a black or grayish incrustation over the surface and adhere so tightly to the rock as to be practically inseparable from it. Immediately following these, but apparently dependent upon them for a foothold, frequently comes *Physcia tribacea*, a foliaceous lichen whose rosette-shaped thallus for the most part is closely adnate to the substratum. These three plants represent the pioneers of vegetation. Many crustose lichens are said to secrete acids by means of which they effect to a certain extent the disintegration of the rock on whose surface they occur. In this way, as well as by their very presence, they tend to create a substratum upon which it becomes possible for foliose and fruticose lichens and certain mosses to secure a foothold. And not only do the crustose lichens prepare the way for other plants, but by so doing they pave the way for their own destruction; for with the advent of taller, shade-producing forms they are speedily eliminated. There may be three more or less distinct lichen sub-stages, viz., crustose, foliose, and fruticose; but as a rule the last two are more or less completely telescoped into one. Of the foliose lichens the most conspicuous in the trap-rock succession is *Parmelia conspersa*, a form which often is so abundant as to almost obscure the rock surface over considerable areas. But sometimes other foliose species are equally important, notably *Dermatocarpon miniatum*, *Umbilicaria pennsylvanica*, and *Parmelia caperata;* while not infrequently *Stereocaulon paschale*, one of the most characteristic of the fruticose lichens along the trap ridges, usurps the soil prepared by the crustose lichens. Associated with these lichens, and equally capable of thriving wherever they can secure foothold, are a few mosses, *e. g.*, *Grimmia Olneyi* and *Hedwigia ciliata.*

The rapidity with which not only the changes just described, but subsequent changes as well, are brought about is influenced of course to a greater or less extent by the nature of the site—the degree of exposure to sun and wind, steepness of the rock surface, etc. Succession almost invariably proceeds more rapidly along the lower slopes of a hill than near its crest, due to the lesser exposure here. The relative abundance of seepage water as the bottom of a hill is approached, also furthers rapid succession.

Thus far observations have been restricted to the vegetation of the rock face. Attention must now be directed to another phase of the trap rock succession, viz., succession in the crevices. Crevices due to various causes are found in greater or less abundance in practically all exposed rocks. Trap rocks especially, on account of the peculiar manner in which they were formed, are characterized by the presence of numerous fissures. In these fissures, and in hollows of the rock surface, dust and sand collect, thus favoring the conservation of moisture and making it possible for plants to develop whose roots or rhizoids require a soil. The pioneer crevice plants are fruticose lichens and mosses. Of the lichens, the majority belong to the genus *Cladonia*, *e. g.*, *C. rangiferina*, *C. uncialis*, *C. furcata*, *C. sylvatica*, *C. pyxidata*. Of the mosses, *Ceratodon purpureus*, species of *Polytrichum* (*P. commune*, *P. piliferum, P. juniperinum*), *Leucobryum glaucum*, and *Dicranum scoparium* are prominent. Closely following these, and indeed often contemporaneous with them are certain Pteridophytes and the advance guard of the Angiosperms—the group which ultimately is destined to predominate. The appended list includes a few of the more conspicuous herbaceous vascular plants characteristic of crevices in trap.

Selaginella rupestris	*Danthonia spicata*
Woodsia ilvensis	*Krigia virginica*
Andropogon scoparius	*Lechea tenuifolia*
Aquilegia canadensis	*Opuntia vulgaris*
Aristida dichotoma	*Poa compressa*
Campanula rotundifolia	*Potentilla argentea*
Corydalis sempervirens	*Rumex Acetosella*
Saxifraga virginiensis	

It will be noted that most of the species here mentioned are perennial, and necessarily all are xerophytes.

Notwithstanding that crevice plants and rock face forms are contemporaneous, the crevice vegetation, for the sake of convenience, may be regarded as the second stage in the succession on trap (fig. 1). On steep slopes this condition may be protracted indefinitely. But as a rule a third stage is soon inaugurated by the encroachment of the crevice vegetation on neighboring portions of the rock face; and where, as on gentle slopes, the soil collects not only in crevices but in shallow depressions of any sort, the surface of the rock may soon become clothed with a more or less continuous plant cover. The spreading out of the crevice colonies is accelerated by the continued accumulation alongside of windblown particles of inorganic matter and fragments of vegetable debris. It is hardly necessary to more than suggest the improved condition of the rock as a habitat for plants which results from the development of a soil. The usual pioneers on such an area are the lichen and moss species already present in the crevices, and it is a common occurrence to find flat rocks and gentle slopes completely overgrown by loose masses of *Cladonia*, thin mats of *Ceratodon*, or dense colonies of *Polytrichum*. But the prestige of these lower forms is short lived, for as soon as sufficient soil has accumulated they are superseded by grasses and other vascular plants. These, by means of their interlacing roots and rhizomes bind the soil together more firmly, and in this way a sod is gradually developed. Because of their omnipresence and the abundance of their tough, fibrous roots, the bunch grass (*Andropogon scoparius*) and the wire grass (*Poa compressa*) are especially important as sod formers. The wire

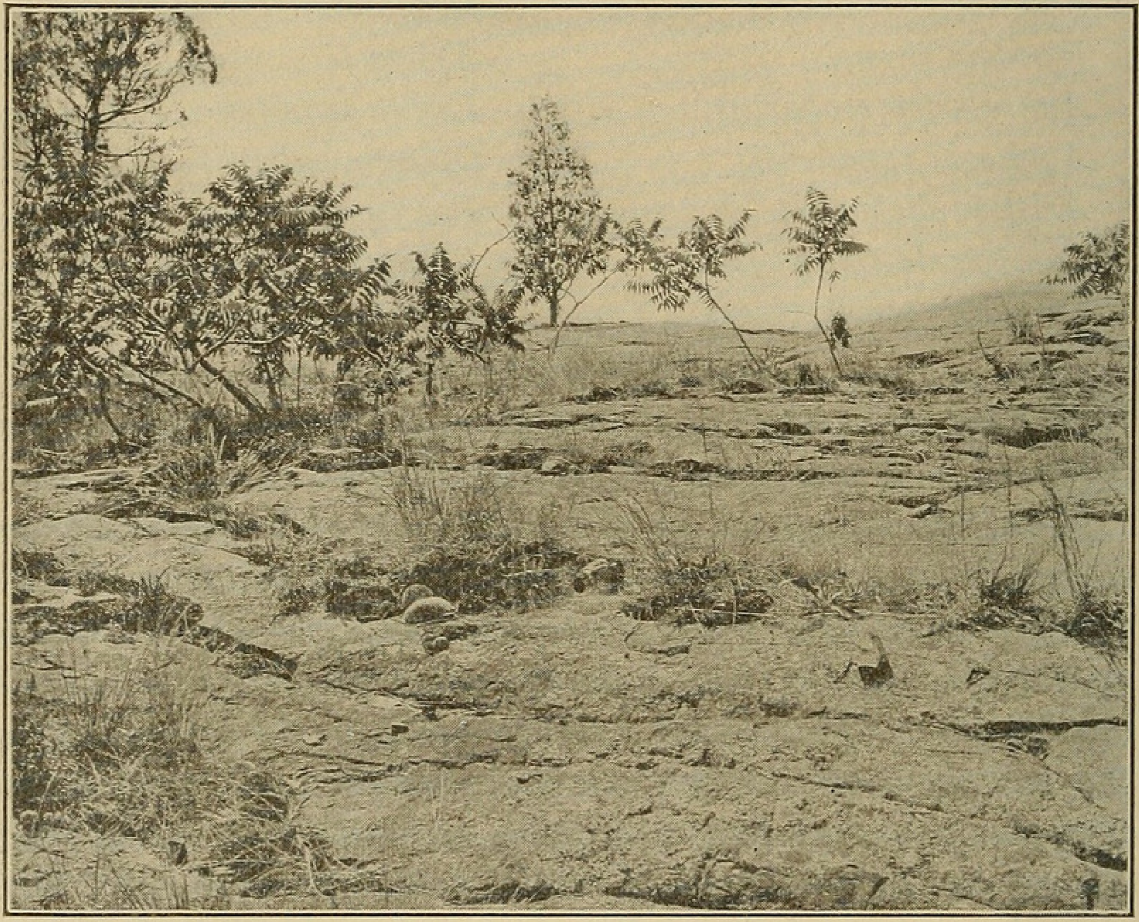

FIG. 1. Rock face and crevice vegetation on trap; near summit of West Rock, New Haven. The conspicuous lichen in the foreground is *Parmelia conspersa*. Among the crevice forms are *Leucobryum glaucum* and other mosses, *Cladonia* sp., *Woodsia ilvensis*, *Andropogon scoparius*, and *Rhus typhina*. The tree in the background is *Juniperus virginiana*.

grass possesses an additional advantage in that it develops long rhizomes which facilitate the invasion of new territory. There may thus arise a plant society characterized by the prevalence of tall, perennial grasses. Associated with the two grasses already mentioned may occur many other herbaceous plants, some of which are here noted.

Antennaria plantaginifolia
Aster linariifolius
Aster patens
Carex pennsylvanica
Cerastium arvense
Comandra umbellata
Helianthus divaricatus
Lespedeza capitata
Lespedeza Nuttallii
Liatris scariosa
Poa pratensis
Pteris aquilina
Pycnanthemum virginianum
Sericocarpus asteroides
Solidago nemoralis
Viola pedata

Up to this point in the succession herbaceous plants have predominated. But some shrubs usually appear in the crevice stage (fig. 1) and by the time the rock has become sod-covered they may have increased in number to such a degree as to become the controlling element of the vegetation. Very often it is possible to recognize a distinct shrub stage. Of the shrubs present at this time, a number may be cited as about equally characteristic, viz.

Ceanothus americanus
Gaylussacia baccata
Myrica asplenifolia
Prunus virginiana
Quercus ilicifolia
Quercus prinoides
Rhus copallina
Rhus glabra
Rhus hirta
Rosa humilis
Vaccinium pennsylvanicum
Vaccinium vacillans

The next advance toward mesophytism is seen in the advent of trees. Like the shrubs, trees begin to appear early in the series, and their presence often exerts an appreciable effect on the character of the rock face and crevice vegetation. *Polypodium vulgare*, for example, grows in crevices beneath the shelter of these scattered trees, but almost never out in the open. Many mosses are likewise restricted. Succession invariably is more rapid in the shade than in the open sunlight. Foremost in importance among the pioneer trees in the trap ridge succession near New Haven are the red cedar (*Juniperus virginiana*) and the post oak (*Quercus stellata*). The transition from the shrub stage to the pioneer tree stage is not abrupt, and, as a matter of fact, so simultaneously may the shrubs and trees make their appearance that quite as often as not the stages are telescoped into one. Both the red cedar and the post oak require plenty of sunlight, *i. e.*, they are intolerant of shade. They never give rise to dense woodlands, but always form open, almost park-like groves (fig. 2). In the sunny patches between the trees the herbaceous and shrubby vegetation of the two preceding stages persists almost unaltered, but in shaded spots there begin to appear forms which are characteristic of the subsequent stage in the succession.

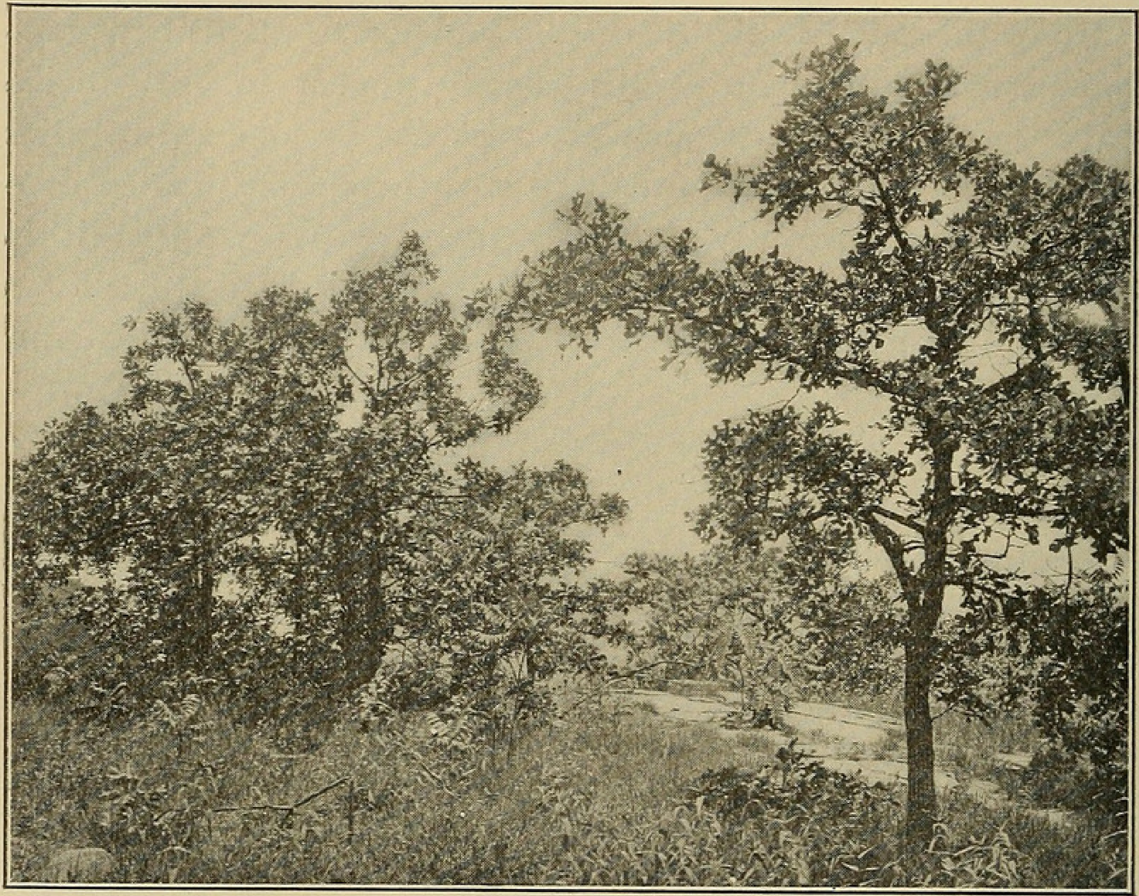

FIG. 2. Pioneer tree stage along crest of West Rock ridge, New Haven. Between the scattered trees (*Quercus stellata*) occur patches of herbaceous vegetation and shrubs. In the foreground is seen *Helianthus divaricatus*. The shrubs shown are *Rhus typhina*.

Further significant changes in the physiognomy of the vegetation are foreshadowed by the advent of such trees as the chestnut oak (*Quercus Prinus*) and the pignut (*Carya glabra*). These species, like the red cedar and post oak, are relatively xerophytic and on some accounts they should perhaps be classed with them as pioneer trees. But they differ in two important respects, viz., they are slightly tolerant of shade, and they attain a much larger size. Red cedars and post oaks more than thirty feet high are seldom encountered, but the pignut and chestnut oak commonly grow to a height of more than fifty feet. While, then, both the chestnut oak and pignut may put in their appearance early in the series, and while often they may be conspicuous members of the pioneer tree stage, their chief importance lies in the fact that as the trees grow larger they overtop the cedar and post oak; and as they become more numerous, their crowns forming a more or less continuous canopy, the red cedar and post oak underneath, unable to endure the changed light relations, gradually succumb. And along with the trees disappear also the majority of the herbaceous and shrubby plants of the pioneer tree stage.

For a time the forest which thus originates may be dominated to so marked a degree by chestnut oak and pignut as to seem to warrant the recognition of a separate chestnut oak or chestnut oak-pignut stage in the succession.* But on the whole it seems simpler to regard this phase as merely a subdivision of a larger association which may be designated the oak-hickory stage. For, during the transition from the open, grove-like type of woodland to the closed type, other species of oak and hickory become increasingly abundant, so that the resultant forest comprises an admixture of a number of species of oak and hickory, together with certain other trees. The more important trees present in such a society are here listed.

Acer rubrum	*Quercus alba*
Carya alba	*Quercus coccinea*
Carya glabra	*Quercus Prinus*
Carya ovata	*Quercus rubra*
Pinus Strobus	*Quercus velutina*

Such a forest approximates closely the type of habitat so commonly referred to in the manuals as "dry woodlands."

The general aspect of these oak-hickory forests at their best

* It should be remarked, however, that the particular species of oak and hickory here mentioned by no means invariably play the important rôle in the inauguration of the oak-hickory stage that is here assigned them. Quite as often other species, *e. g.*, *Carya ovata*, *Carya alba*, *Quercus velutina*, *Quercus coccinea*, are more prominent at the outset.

is well brought out in fig. 3. Underneath the canopy formed by the larger trees there usually develop certain smaller arborescent species, viz., *Cornus florida, Ostrya virginiana,* and *Sassafras variifolium.* The rest of the undergrowth, with the exception of some few species like the huckleberry and the blueberries, which

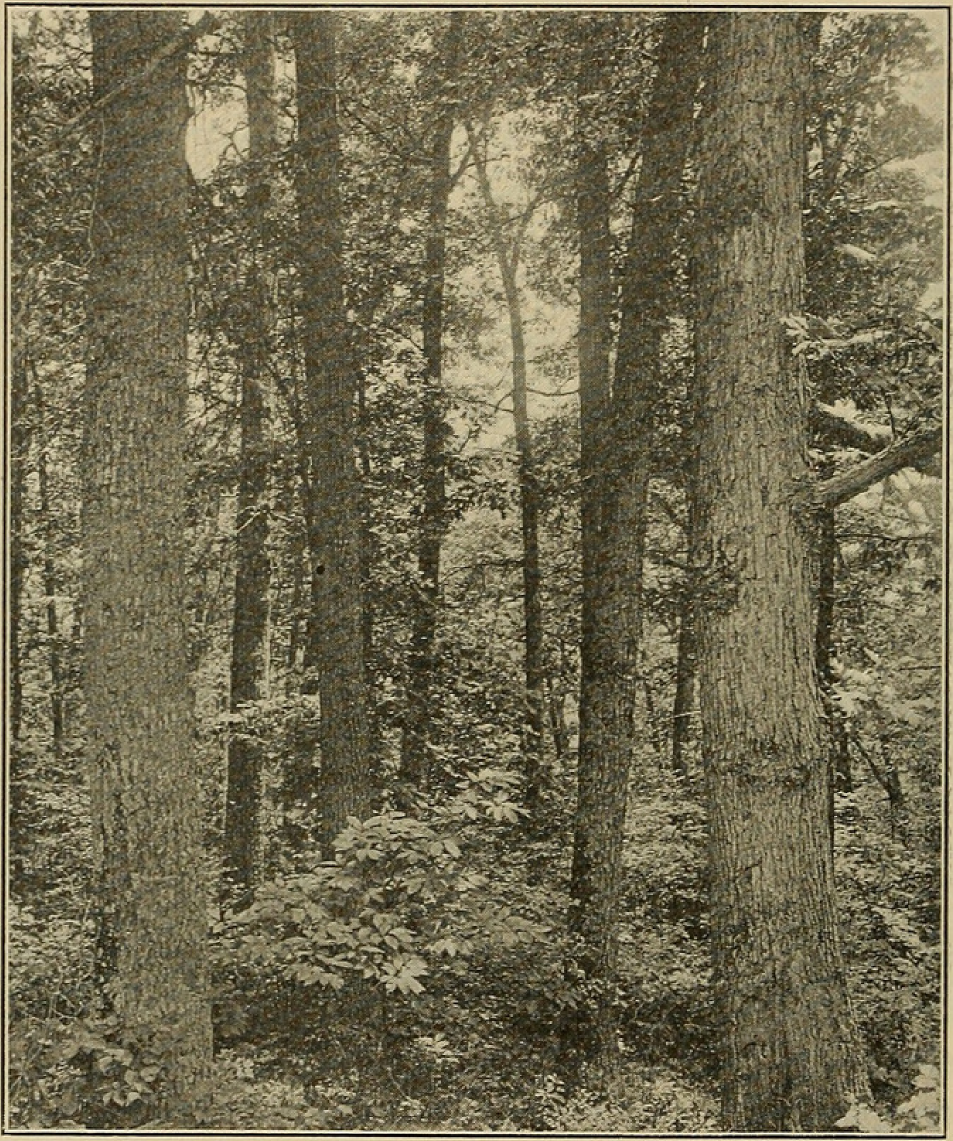

FIG. 3. An oak-hickory forest of a very mesophytic type; Salisbury. The tree in the right foreground is *Quercus alba;* most of the others are *Quercus rubra.* The undergrowth includes many of the shrubs listed on page 177. A majority of the young trees are *Castanea dentata* (i. e., in center foreground) and *Acer saccharum.*

flourish equally well in the open or in diffuse light, is made up largely of plants which heretofore either have not been present at all, or else have been poorly represented in the succession. As representative of the shrubs may be cited:

Corylus americana
Gaylussacia baccata
Kalmia latifolia
Rhododendron nudiflorum
Vaccinium pennsylvanicum
Vaccinium vacillans
Viburnum acerifolium

Prominent among the herbaceous plants of this stage are:

Aspidium marginale
Aster divaricatus
Carex virescens
Chimaphila umbellata
Cypripedium acaule
Desmodium sp.
Epigaea repens
Gaultheria procumbens
Geranium maculatum
Gerardia flava
Hepatica triloba
Hieracium venosum
Lysimachia quadrifolia
Maianthemum canadense
Melampyrum lineare
Mitchella repens
Panicum dichotomum
Pedicularis canadensis
Polystichum acrostichoides
Pteris aquilina
Pyrola americana
Pyrola elliptica
Smilacina racemosa
Solidago bicolor
Solidago caesia

Oak-hickory forests like the one here depicted constitute the most familiar type of woodland encountered along the trap ridges near New Haven, and in many sites they may represent the ultimate formation. But, under favorable conditions, such a forest is destined to give way to a still more mesophytic type. And here again the light requirement of the various trees involved seems to be an important factor in determining their behavior and in conditioning their presence or absence in the ultimate forest. For it is self evident that trees like the chestnut oak and pignut, whose seedlings are unable to develop in any but the lightest shade will tend to become less and less abundant as the forest floor becomes more deeply shaded by the ever denser foliage overhead. Conversely, it is those trees whose seedlings are best able to develop under these circumstances that will ultimately survive. Thus it comes about that the climax forest of any region is composed very largely of those native trees which are most tolerant of shade. Of course the proximate composition of the forest in any given locality is necessarily influenced by the fortuitous distribution of seeds. Moreover, the advent of the ultimate stage may be hastened or retarded by the abundance or scarcity of water in the superficial layers of the soil. Thus shade conditions in an oak-hickory forest favor the conservation of the soil water, but at the same time the demands of the trees upon the available supply may be so great as to practically exhaust the water near the surface. And where, as along the summits of the trap ridges, water is never very abundant, it is not surprising to find that while the arborescent species in the forest, with their deeply penetrating root systems, may be relatively mesophytic, the shrubs and herbaceous plants, with their shallow root systems, are quite xerophytic. The point to be emphasized in this connection is that, although the mature trees of the climax forest may be able to utilize water at some depth below the surface, their seedlings are dependent on the supply near the surface; so that, unless there is sufficient water in these surface layers to enable the climax trees to tide over the critical seedling stages, they cannot establish themselves and the oak-hickory stage may be of indefinite duration. As will be brought out in a later paragraph, the accumulation of humus may have an important bearing on the phenomena of succession, particularly during these more advanced stages.

Along the trap ridges the climax forest of this region is best developed on the lower slopes, where there is a relatively constant supply of ground water, available throughout the growing season.* By far the most abundant and most characteristic tree here is the chestnut (*Castanea dentata*). With it are commonly associated *Liriodendron Tulipifera* and some of the more mesophytic trees of the preceding stage, *e. g.*, *Quercus rubra*, *Quercus alba*, and *Acer rubrum*, while scattered through the forest, sometimes abundant locally, are other mesophytic trees, such as *Acer saccharum*, *Fagus grandifolia*, *Fraxinus americana*, *Prunus serotina*, *Tilia americana*, and *Tsuga canadensis*. As species of secondary importance may be mentioned *Carpinus caroliniana*,

* It should perhaps be remarked at this point that the slopes of the trap ridges, especially toward the base, are usually covered to a greater or less degree with glacial debris. As will be brought out in a later paragraph, this fact has an important bearing on the rapidity of the succession.

Cornus florida, Ostrya virginiana, and *Sassafras variifolium.* These are sometimes so abundant as to produce a distinct stratum of vegetation. Many of the shrubs and herbaceous plants of the oak-hickory stage are still prominent, but their number is augmented by numerous new arrivals, among which are many pronounced shade plants. Three species comprise the bulk of the shrubby undergrowth, viz., *Kalmia latifolia, Hamamelis virginiana,* and *Viburnum acerifolium.* Some of the characteristic herbaceous plants not heretofore noted are given in the subjoined list.

Adiantum pedatum	*Corallorrhiza maculata*
Aspidium noveboracense	*Epifagus virginiana*
Aspidium spinulosum	*Epipactis pubescens*
Botrychium virginianum	*Medeola virginiana*
Lycopodium lucidulum	*Monotropa uniflora*
Phegopteris polypodioides	*Polygonatum biflorum*
Arisaema triphyllum	*Sanicula marilandica*
Aster divaricatus	*Solidago latifolia*
Brachyelytrum erectum	*Trientalis americana*
Collinsonia canadensis	*Trillium cernuum*
Trillium erectum	

A series of changes in vegetation such as has been described in connection with the succession on the trap ridges is actuated almost entirely by biotic agencies and is therefore termed a biotic succession. The general manner in which biotic agencies institute succession has been admirably summarized by Cowles,* and some of his observations may be briefly stated here. All external factors which affect the plant reside either in the soil or in the air. Of the soil agencies humus is by far the most important in influencing succession. Due to its great capacity for water retention the accumulation of humus on uplands causes an increase in soil moisture; while in depressions, for obvious reasons, it has the opposite result. The change thus brought about in the water content of a soil is without doubt the most important effect of humus, and, in the opinion of Cowles, is perhaps the most significant of all factors influencing succession.

* 1911, op. cit.

Humus accumulation is associated with an increase of saprophytic soil organisms, a fact which may be of vital significance in conditioning the presence or absence of plants which are dependent on root fungi for their nitrogen supply.* The effect of humus on the toxicity of the soil, while as yet inadequately investigated, may prove to be a factor of large significance. Finally, the accumulation of humus modifies the soil temperature and the air content of the soil.

Just as the soil factors that influence succession may be summed up under humus, so the air factors may largely be included under the head of shade. Decrease in light, as already demonstrated, is favorable to species tolerant of shade, but fatal to light-requiring species. Moreover, increased shade favors the more rapid accumulation of humus; it also results in increased atmospheric humidity, and hence in decreased evaporation. This latter effect is important, not only in connection with the conservation of soil moisture, but also as it affects the transpiration of the plants themselves.

Two other biotic agencies are of greater or less importance in their effect on the trend of succession. The first of these is plant invasion. "In the long period of geologic history, plant migrations from one region to another must have played a tremendous part in the changing aspect of vegetation." But, "so imperceptibly do these migrations take place that we know of no profound change that has been wrought by this means in natural floras within historic time."† To this latter statement it may be that the chestnut blight (*Endothia gyrosa* var. *parasitica* (Murr.) Clint.) will furnish an interesting exception. For although much has been written regarding this disease from a pathological and an economic standpoint, it seems to the writer that its possible significance has been overlooked by ecologists. The chestnut is one of the most important trees in the climax forest, not only over a large part of Connecticut, but throughout much of the

* It should be noted in this connection that recent investigations of W. B. McDougall (Amer. Jour. Bot. 1: 51–74. *pl. 4–7* + *f. 1.* 1914) would seem to indicate that the benefits accruing to many trees from their association with root fungi may have been greatly overestimated.

† Cowles, 1911. *Op. cit.*, p. 179.

eastern United States. During the ten years that have elapsed since the chestnut disease was first recorded in this country—at New York—it has spread with amazing rapidity. At the present writing practically all the chestnut in southwestern Connecticut has been wiped out, and there is no part of the state which has been immune from its depredations. In the vicinity of New Haven much of the chestnut has already been exterminated and it is difficult to find a group of trees, some of which have not been affected by the ravages of the blight. And whether, as some workers think, the blight fungus is a native species, "which, because of peculiar conditions detrimental to the host, has assumed unusual virulence and widespread prominence,"* or, as others maintain, is an invader from the Old World, certain it is that from the present outlook it is destined to have a profound effect on the nature of the climax forest in the eastern United States.

The influence of man on succession is almost invariably retrogressive. Man destroys the more ultimate societies and causes them to be replaced by more primitive ones. The cutting of the forest, the introduction of grazing animals, and fire—all of these interfere with the mesotrophic trend of succession. Thus in a recently cleared area mesophytic herbaceous plants are largely superseded by the so-called " fire-weeds ", e. g., *Epilobium angustifolium*, *Erechtites hieracifolia*, *Erigeron canadensis*, *Phytolacca decandra*, and *Verbascum Thapsus;* while *Betula populifolia*, *Myrica asplenifolia*, *Populus grandidentata*, *Populus tremuloides*, *Prunus virginiana*, *Rubus allegheniensis*, *Rubus idaeus* var. *aculeatissimus*, and other woody plants not represented in the antecedent forest may be abundant here. Fire, perhaps, should be considered a natural agency, but as a rule its frequency becomes much greater with the advent of man into a region.

There is one other phase of succession on trap to which, as yet, no reference has been made, viz. succession on talus slopes. This is of peculiar interest because it differs in certain respects from the type described above. Taken as a whole the trap ranges extend from north to south. As a rule the hills dip gently toward the

* Clinton, G. P. Chestnut bark disease. Report Conn. Agr. Exp. Sta. 1912: 359–453. *pl. 21–28.* 1914.

east, and it is largely from a study of the vegetation on these slopes that the observations thus far recorded have been made. But toward the west the ridges terminate in perpendicular cliffs, at the foot of which are great masses of rocks waste (fig. 4) or talus, derived from the disintegration of the overhanging precipices, and sometimes these are so extensive as to completely bury cliffs several hundred feet in height. The upper part of such a talus slope is steep, and, except at the very foot of the cliff, is composed of large, loose blocks of rock, with practically

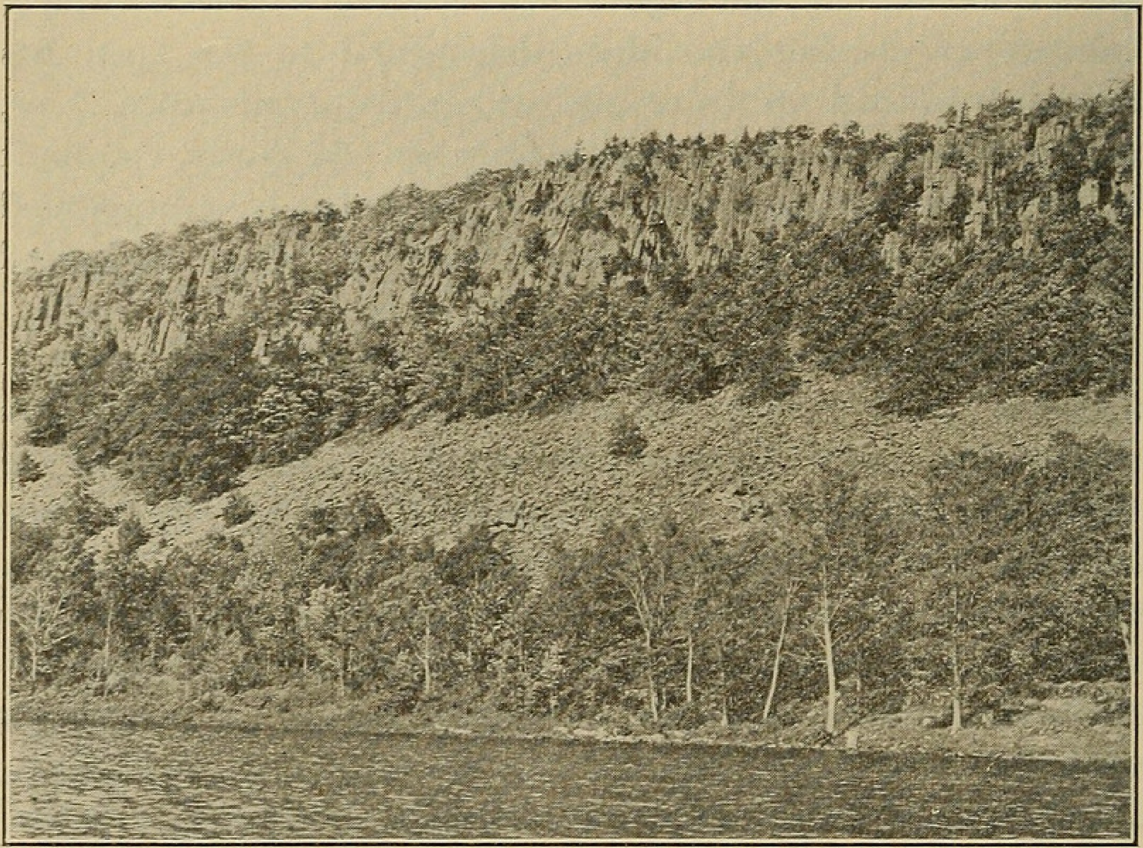

FIG. 4. Talus slope along west face of West Rock ridge, Woodbridge. A short distance to the north of where this picture was taken the talus has become completely covered with forest.

no soil between them. But as the bottom is approached the gradiant becomes gentler, the rock fragments smaller, and a rich soil collects. Here conditions are favorable for plants from the very outset, since seepage water is abundant the year round and a measure of protection from wind is afforded by the neighboring hill. Succession proceeds with great rapidity, and the pioneer associations quickly give way to forest. The mesophytism of the forests which ultimately clothe these lower slopes is attested by the presence of such trees as *Acer saccharum*, *Betula lutea*, *Tilia americana*, and *Tsuga canadensis;* also by the frequency of many mesophytic shrubs and herbaceous plants elsewhere uncommon in upland woods. Such, for example, are *Actaea rubra*, *Asarum canadense*, *Caulophyllum thalictroides*, *Dicentra Cucullaria*, *Geranium Robertianum*, *Sambucus racemosa* and *Staphylea trifolia*. A further step in the reclamation of the talus by vegetation is seen in the appearance of a belt of trees along the upper margin of the slope. Here, under the very shadow of the precipice, is usually a narrow zone where earth and finer rock particles, dislodged from the cliff overhead, collect in sufficient quantity to favor rapid colonization by plants. Moisture relations, however, are poorer than at lower levels, so that a truly mesophytic vegetation is slow to develop. The belt of forest which fringes the upper margin of the talus shown in fig. 4 consists largely of chestnut oak and black oak. But the condition shown in this photograph is by no means permanent. For, as the blocks of rock midway up the talus gradually disintegrate and soil collects, the two belts of forest encroach upon the barren area which separates them, and ultimately the entire slope becomes wooded. The first plants to appear in the talus succession are lichens, but their influence on later stages is negligible, for they are confined principally to the rock face while the transformations that culminate in the formation of forest are brought about almost entirely by crevice plants. Crevice mosses doubtless aid in the accumulation of soil and humus, and many of the crevice plants previously noted are also present here; but the first conspicuous crevice stage on talus slopes is usually dominated by vines and shrubs. The shade produced by trailing vines such as *Celastrus scandens*, *Psedera quinquefolia*, and *Rhus Toxicodendron* may be a factor of considerable significance in hastening the advent of mesophytic conditions. Characteristic pioneer shrubs are *Cornus circinata*, *Rubus odoratus* and various species of *Rhus*. The shrubs and vines are accompanied by trees, but except toward the top of the slope there may never be a xerophytic pioneer tree stage, for among the first trees to appear may be mesophytic species like *Betula lutea*, *Juglans cinerea*, *Tilia americana*, and even *Tsuga canadensis*, most of which are present in the ultimate forest.

The complexity of the surface geology of this state has been referred to in a previous paper.* Most of the underlying rocks are covered with sand, gravel, or clay; but in addition to the trap rocks—basalt and diabase—the surface outcrops include granites, gneisses, schists, quartzite, sandstone and shale, and limestone. To what extent, it may be asked, do the successional phenomena on these other types of rock correspond with, or disagree from, succession on trap? In other words, how is succession influenced by the physical or chemical nature of the substratum. In the opinion of Cowles† the most important feature of a rock, as regards its effect on succession, is its stability, *i. e.*, its degree of resistance to erosion. On stable uplands, where erosion is slow, succession is likewise slow. On unstable uplands, on the other hand, succession is rapid. Thus "in a given region a shale area may be clothed with a mesophytic forest, while a dolomite outcrop is still xerophytic, or a quartzite is scarcely more than a naked hill." The influence of the physiographic state of a region on the character of the vegetation is far more important than either the physical or chemical nature of the underlying rock. "The flora of a youthful topography in limestone more closely resembles the flora of a similar stage in sandstone than [that of] a young limestone topography resembles [that of] an old limestone topography." In other words, "rock as such, or even the soil which comes from it, is of less importance in determining succession than are the aerial conditions, especially exposure. And it is the stage in the topography that determines the exposure."

In view of Cowles's conclusions, which are based on the study of succession in various parts of the eastern United States, it is not surprising to find that in comparing successions on different types of rock in this state the resemblances are much more pro-

* Torreya 13: 109. 1913.

† Cowles, H. C. The influence of underlying rocks on the character of the vegetation. Bull. Amer. Bur. Geog. 11: 1–26. *f. 1–10.* 1901; Bot. Gaz. 31: 89, 90. 1901.

nounced than the differences. Thus a succession on granite, such as may be studied to advantage on the numerous islands that rise out of the salt marshes in the vicinity of New Haven, is strikingly similar, except in minor details, to that observed on trap.*

The effect of the chemical nature of the substratum on vegetation has been the occasion of much debate. A few years since, Fernald† made extensive investigations of arctic and alpine plants in the northern United States and Canada, and found that their distribution is controlled very largely by the preponderance in the soil of potassium, calcium, and magnesium. The plants which he studied grow mainly on the faces of cliffs, in rock crevices, or on talus slopes, localities where the soil is derived primarily from the rock in place, so that his conclusions possess unusual value. So far as the rate of succession is concerned, the chemical nature of the underlying rock would appear to be most important as it affects the rapidity of erosion. But it cannot be doubted that to a certain extent the specific composition, especially of the earlier rock face and crevice stages, is modified directly by the abundance or scarcity of certain chemical elements in the soil. In Connecticut the problem is complicated by the fact that so much of the soil is of glacial or alluvial origin, and except in a superficial way‡ this problem has not been investigated.

In physical structure unconsolidated rocks like gravel, sand, and clay contrast sharply with consolidated rocks like granite and trap. That this dissimilarity in the nature of the substratum should be reflected in the character of the vegetation is naturally to be expected; yet the differences are less marked than one might be led to anticipate. As a concrete illustration of a succession on uncompacted rock the sand plains succession has been selected. W. E. Britton§ has given an interesting account of the vegetation of the North Haven sand plains, devoting special attention to certain desert-like areas and the structural peculiarities of the

* Compare Cowles, Bull. Amer. Bur. Geog. 11: 14. 1901.

† Fernald, M. L. The soil preferences of certain alpine and subalpine plants. Rhodora 9: 149–193. 1907.

‡ See Torreya 13: 109–110. 1913.

§ Bull. Torrey Bot. Club 30: 571–620. *pl. 23–28.* 1903.

plants inhabiting them, but except in a general way the subject of plant societies was not considered. These sand plains are a conspicuous feature of the central lowland of Connecticut. From a physiographic standpoint they represent outwash plains, developed during the final retreat of the continental glaciers, and now considerably dissected by stream erosion. One series of these plains stretches northward from New Haven, along the

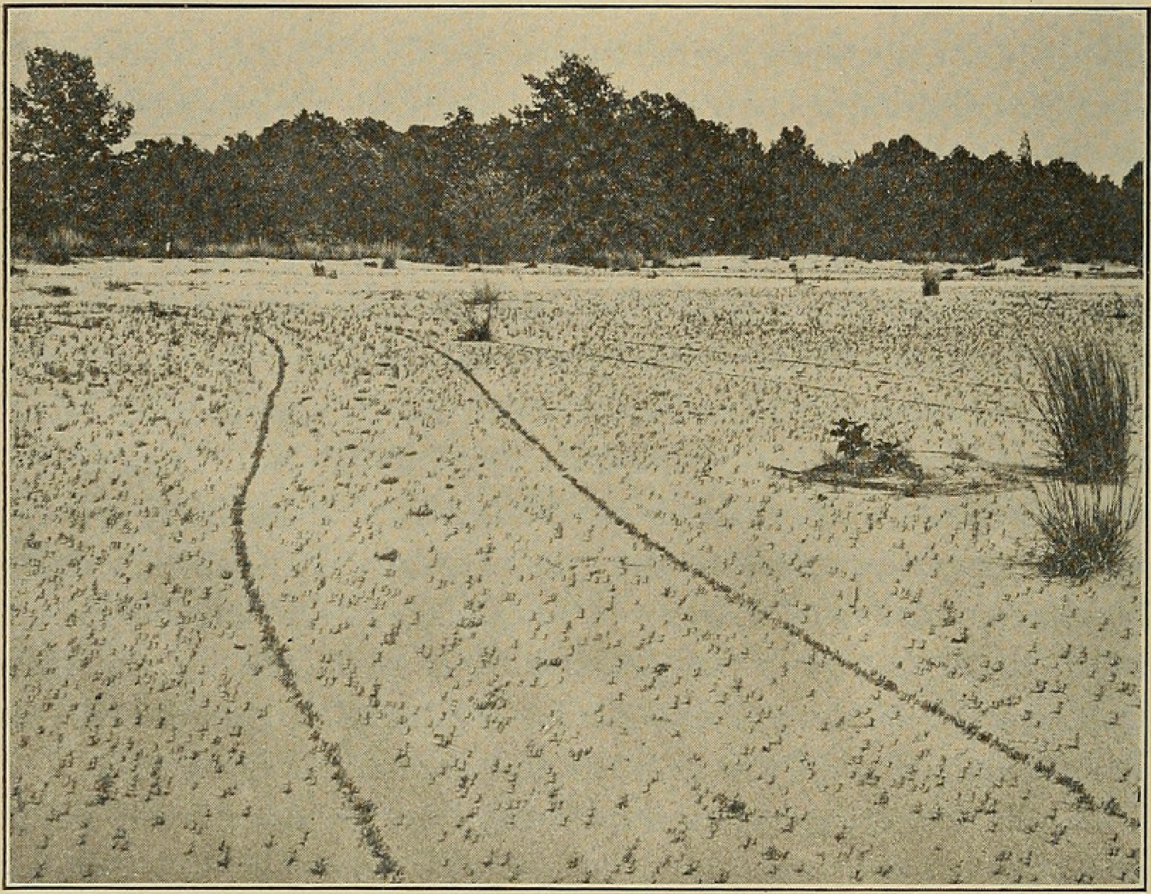

FIG. 5. Vegetation of sand plains in late summer, North Haven. The plant so common on the sand here is the annual, *Trichostema dichotoma*. Note the greater abundance of this plant in the wagon ruts—perhaps due to more favorable moisture relations there. In the right foreground are *Andropogon scoparius* and *Asclepias syriaca*.

east side of the Quinnipiac River, for about sixteen miles. The soil varies in texture from sand of medium fineness to coarse gravel. Moisture is more or less abundant throughout the year at a short distance below the surface, but, except in moist weather, the superficial soil layers are dry. This latter fact, coupled with wind sweep, the burning heat of the sun on the sand, and the high rate of evaporation, hinders the establishment of vegetation.

The greatest divergence in plant succession on such an area from, *e. g.*, succession on trap is seen in the earlier, pioneer stages. Crustose and foliose lichens are never present—a statement which holds true for unconsolidated rocks in general. The first stage in the sand plain series may not inappropriately be termed an edaphic desert. The soil lacks humus and the vegetation is very open, the plants growing scattered about over the otherwise bare, sandy soil (figs. 5, 6); and since the distinctive species are either annuals or rhizome perennials (or biennials), there are seasons of the year when to all appearances these tracts are almost des-

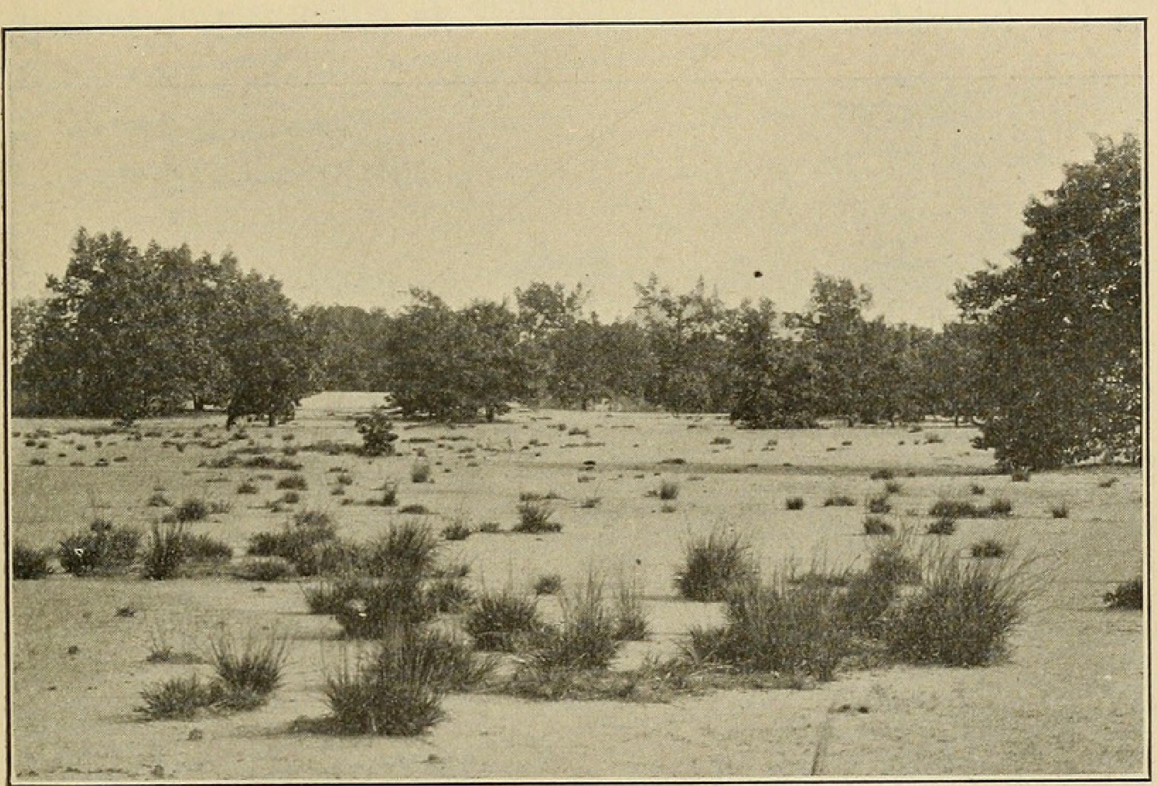

FIG. 6. Sand plains with scattered tufts of *Andropogon scoparius;* North Haven. Most of the trees are black oaks. Photograph after W. E. Britton.

titute of vegetation. Here and there, however, distributed at irregular intervals over the surface of the plain, are trees (most commonly *Quercus velutina*) whose presence may doubtless be attributed to the activities of squirrels since, despite the abundance of seeds with which the ground underneath the trees is strewn every fall, they exhibit no tendency to spread.*

* The acorns "fall upon the sand under the trees, probably germinate and dry up before the radicles can reach a sufficient depth to obtain the necessary water. In some unpublished investigations Prof. J. W. Toumey has found that in hard soil the radicle is not able to work its way into the soil, but on account of the lightness of the acorn it is tumbled about on the sand" (Britton, op. cit., pp. 578, 579).

Two annual species are especially characteristic of such areas, viz. *Hypericum gentianoides* and *Trichostema dichotomum.* Associated with these may grow *Asclepias syriaca, Baptisia tinctoria, Helianthemum majus, Lespedeza capitata, Oenothera biennis, Polygonella articulata, Stenophyllus capillaris* and occasional representatives of the succeeding stage in the succession. These barren tracts are often quite extensive, one area near North Haven, according to Britton, covering from 80 to 90 acres.

Tufts of bunch grass (*Andropogon scoparius*) are always more or less in evidence on these barrens. At first widely scattered,

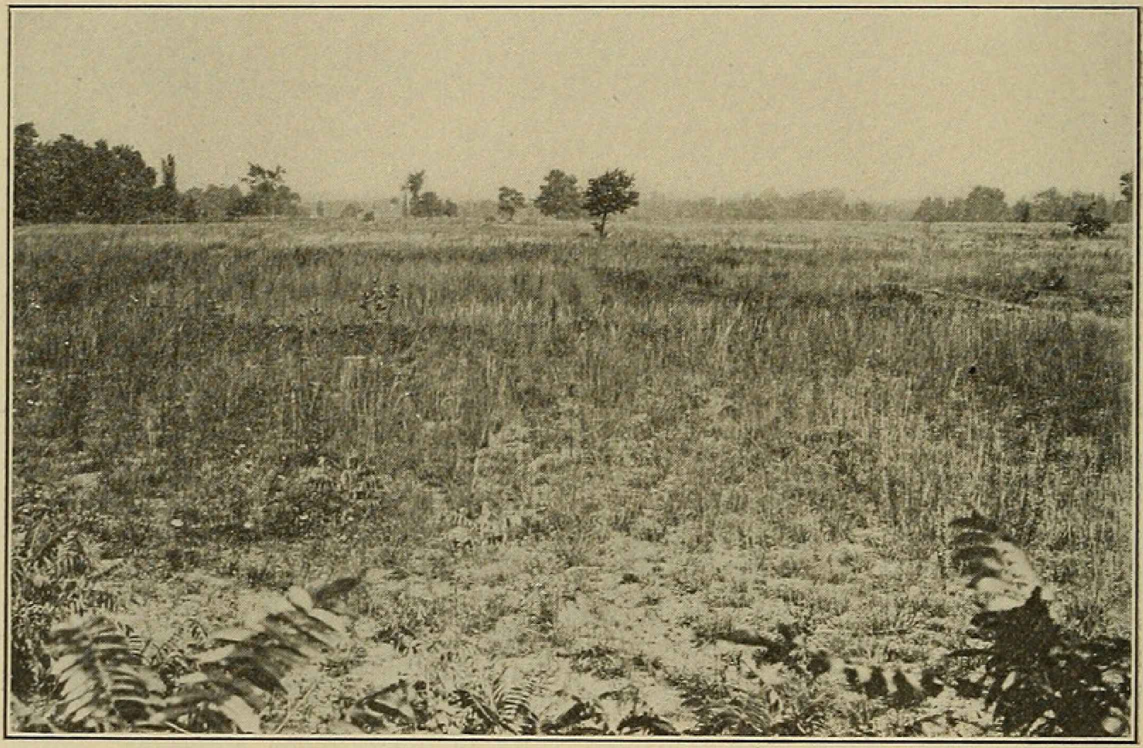

FIG. 7. Edaphic prairie; North Haven. The predominating plant is *Andropogon scoparius*. The dark patches near the center of the picture are shrubs—*Myrica asplenifolia* and *Myrica carolinensis*. All of the herbaceous species listed on page 189 could probably be found here.

they may gradually become more numerous (fig. 6) so that eventually, as more and more soil is preempted, a permanent plant cover is established. Other plants beside the bunch grass may fulfil an important role in the reclamation process, notably the moss, *Polytrichum piliferum*, and species of *Cladonia* (*e. g.*, *C. sylvatica*, *C. papillaria*). These usually appear in company with the bunch grass, occupying the soil between the tufts; but sometimes mosses or lichens alone may reclaim considerable tracts.* The second stage in the sand plains succession is dominated by the bunch grass, and not infrequently the areas controlled by this grass are so large, and the tenacity with which this control is retained so great, that, in the opinion of the writer, they should be recognized as edaphic prairies (fig. 7). Except for their smaller size they resemble the well known natural prairie of western Long Island.†

Beside the bunch grass and some of the species already mentioned the vegetation of these prairies includes many other herbaceous forms, nearly all of which are perennial. The following species are perhaps as representative as any:

Artemisia caudata
Asclepias verticillata
Aster linariifolius
Carex Muhlenbergii
Cyperus filiculmis var. *macilentus*
Desmodium canadense
Eragrostis pectinacea
Erigeron canadensis
Fragaria virginiana
Lupinus perennis
Lysimachia quadrifolia
Panicum depauperatum
Poa compressa
Potentilla canadensis
Pteris aquilina
Rumex Acetosella
Sericocarpus asteroides
Solidago nemoralis
Viola fimbriatula

Also two low shrubs, *Myrica asplenifolia* and *Rubus villosus*, are almost invariably present and seem to form a constituent part of the prairie vegetation.

Sooner or later grassland is destined to be replaced by forest. Sometimes a short-lived shrub stage intervenes, but quite as often shrubs and trees appear at about the same time. Most of the shrubs listed in connection with the shrub stage of the trap rock succession are represented in the corresponding phase of the sand plains succession, while several species not there mentioned may also be prominent, *e. g.*, *Juniperus communis*, *Kalmia angustifolia*, *Myrica carolinensis*, and *Rhus Toxicodendron*. The pioneer trees include *Juniperus virginiana*, *Betula populifolia*, *Pinus rigida*, and *Robinia Pseud-Acacia*. The last named species

* See Britton, op. cit., p. 579.

† See Harper, R. M. The Hempstead Plains of Long Island. Torreya **12**: 277–286. *f. 1–7.* 1912; also Bull. Am. Geog. Soc. **43**: 351–360. *f. 1–5.* 1911.

is native farther south, but in Connecticut has become thoroughly established on the sand plains and elsewhere. It is the only example known to the writer of a recently introduced tree which can be considered of ecological importance. It spreads quickly, largely by means of root suckers, grows rapidly, and frequently forms light forests over considerable areas. As a rule, however, the red cedar, gray birch, and pitch pine are the first arborescent forms to appear. These may come in together, giving rise to a mixed growth; or one or another, according to chance, may predominate.* Red cedar, as along the trap ridges, usually forms rather open groves. Gray birch (*Betula populifolia*) may form dense stands, but the trees never attain a large size. Pitch pine alone, of the three, is capable of developing forests, and where this species predominates, the pioneer tree stage is apt to be of much longer duration than otherwise. Fig. 8 shows a pitch pine stand near Farmington. Some of the trees here are over 18 inches in diameter. The slight shade produced by the foliage overhead here is not sufficient to exclude from the ground underneath many of the herbaceous and frutescent forms characteristic of the preceding stages, but along with these occur some species which attain their optimum development under more mesophytic conditions. The ultimate fate of a forest like this is suggested by the predominance on the forest floor of oak seedlings and the scarcity of pitch pine seedlings. As a matter of fact, owing to the ability of the pitch pine to endure fire, this particular forest, which is situated along the railroad, will probably continue indefinitely in its present condition. But under normal conditions oak and hickory would succeed the pitch pine, and there seems to be no reason to doubt that under favorable circumstances the forest might at some future time become quite as mesophytic as the climax type described in connection with the trap rock succession.

* According to R. C. Hawley and A. F. Hawes (Forestry in New England, p. 352. New York. 1912), "gray birch is a species which requires a bare soil for a seed bed, while red cedar can start well under more adverse conditions, even in a thick sod. This difference in the habits of the two species explains why pure stands now of one species and then of the other are met with on old fields."

The sand plains succession may be regarded as fairly representative of succession on unconsolidated rocks. It differs in some respects from succession on gravel and clay, but so far as the sequence and composition of stages is concerned the resemblances are greater than the differences. Just as was found in the

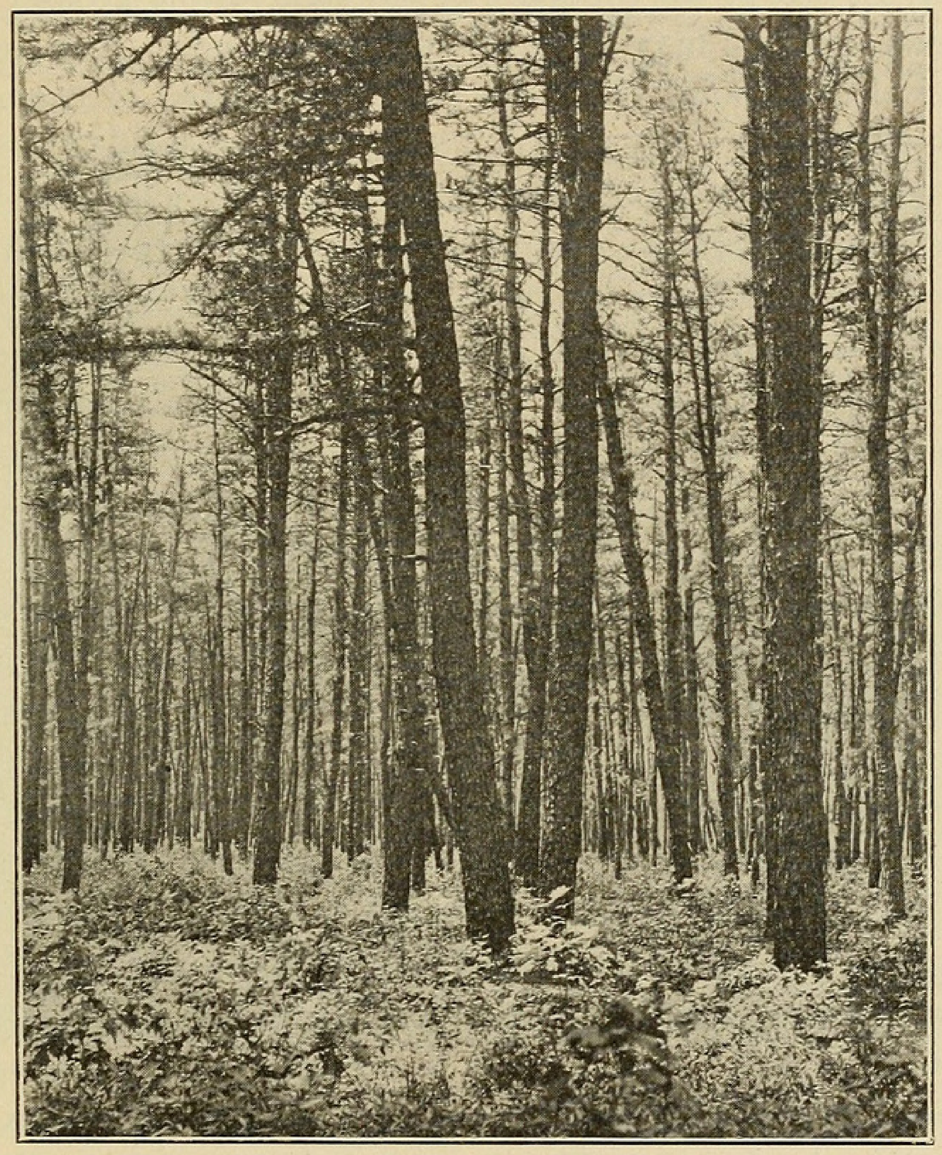

FIG. 8. Pitch pine forest; Farmington. The undergrowth is largely xerophytic, common shrubs being *Ceanothus americana, Corylus americana, Myrica asplenifolia, Quercus ilicifolia* and *Rhus glabra*.

case of consolidated rocks, the chief difference between various uncompacted rocks in their effect on succession concerns the quickness or slowness with which mesophytic conditions are attained. The presence of clay in a soil increases its ability to retain water and thereby favors the more rapid advent of mesophytism. The most favorable of all soils in Connecticut, from a standpoint of natural vegetation, are the heterogeneous deposits of gravel, sand, and clay known as till. On such soils succession progresses so rapidly that, except where conditions have been modified by human interference, pioneer associations are seldom encountered. It should also be mentioned at this point that frequently, due to the influence of soil structure or ground water relations, swamps may be developed on uplands. But from an ecological standpoint these are better considered in connection with lowlands.

Several allusions have been made to the effect on vegetation of human interference. Unfortunately for the ecologist this is a factor which too often must be reckoned with. There is one type of succession resulting from man's activities which is deserving of special mention because of its widespread occurrence, viz., ruderal succession.* Whenever a plowed field is allowed to lie fallow for a year, a ruderal association arises. At first the plant population of such an area is composed largely of weeds, many of which are annuals. Of these, *Ambrosia artemisifolia* is almost omnipresent, but it is hardly worth while to attempt a representative list of the others. It may be noted in passing, however, that among the mosses some forms like *Funaria hygrometrica* and *Physcomitrium turbinatum* should be classed as weeds. If a field is permanently abandoned perennial herbaceous plants soon form a sod, so that annual species are largely excluded, and woody plants begin to assert themselves. In this way there may originate the type of vegetation known to the forester as the "old field type." This type is a common one in abandoned pastures, constituting one of the most familiar features of a Connecticut landscape. The characteristic trees are usually gray birch and red cedar, with which are associated low juniper and many other pioneer shrubs (fig. 9). If left to themselves such areas, in the course of time, may become clothed with mesophytic forests.

Taken as a whole, the observations recorded in the preceding paragraphs are applicable to upland vegetation in any part of Connecticut, but there are a few noteworthy discrepancies. The earlier stages in the succession are essentially alike everywhere,

* See Clements, F. E. Research methods in ecology, p. 253. Lincoln. 1905.

although there may be some divergence in the shrub stage, due to the local abundance or scarcity of particular species. But the tree stages in different sections exhibit some appreciable dissimilarities. Reference has been made in previous papers* to variations in the composition of the climax forest. The earlier tree stages as well manifest certain differences. Gray birch is a common pioneer tree in all sections, but post oak is confined to

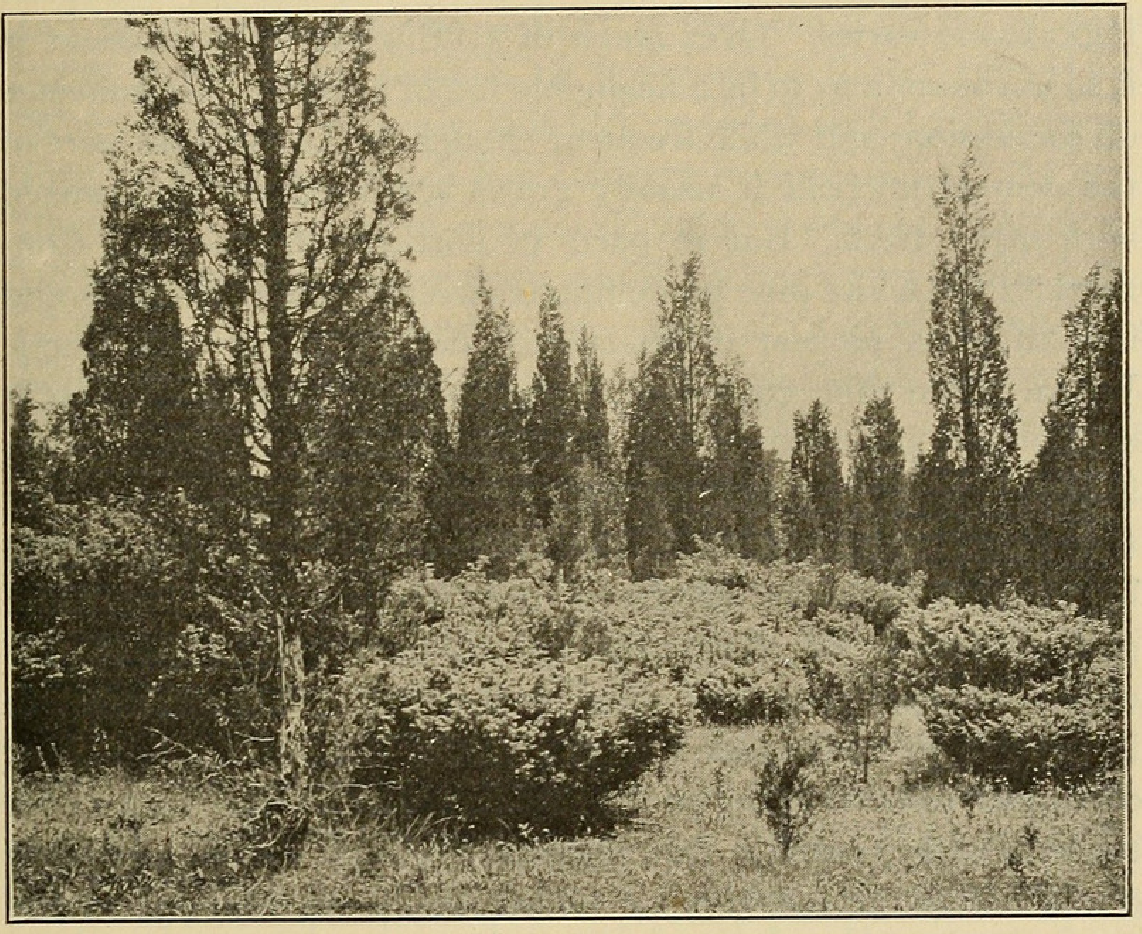

FIG. 9. A typical "old field" society in an abandoned pasture; New Haven. *Juniperus virginiana* and *Juniperus communis* var. *depressa*.

the proximity of the coast, and even here it is quite restricted in its distribution. Red cedar and pitch pine are relatively rare in northwestern Connecticut, but they are common elsewhere. Of the two, red cedar is the more usual pioneer in the southwestern part of the state; in the central lowland and in eastern Connecticut both are locally important. The aspens (*Populus tremuloides, P. grandidentata*) are of sporadic occurrence throughout, especially in areas recently burned over, but they

* Torreya **13**: 99, 101; 199–215. 1913; Bot. Gaz. **56**: 143, 144. 1913.

are perhaps more conspicuous as pioneers in northwestern Connecticut than elsewhere. The paper birch (*Betula alba papyrifera*), also, is not an infrequent pioneer in Litchfield County and along the trap ridges toward the north, but is rare near the coast. The most striking departure, however, from any type of succession heretofore described is seen where the pioneer tree is the white pine (*Pinus Strobus*). The white pine is widely distributed throughout the state, but its ecological importance varies. Over much of southwestern Connecticut it is so uncommon as to be a negligible factor as regards its influence on succession; and while frequent enough in the southern part of the central lowland it usually grows scattered and intermixed with other trees. But in parts of northern and eastern Connecticut the white pine predominates over considerable areas and is a common pioneer in abandoned fields and cut-over tracts. Where white pine comes in strongly—frequently forming, as it does, nearly pure stands—the oak-hickory stage in the succession is often completely eliminated. There may thus be only two tree stages, pine remaining dominant until largely superseded by the more tolerant species of the climax forest. The white pine may even be represented in this ultimate forest, in this respect differing from any other pioneer tree. The undergrowth in evergreen, coniferous forests is much sparser than that of deciduous forests, owing to the dry carpet of needles with which the ground is littered. But practically all the shrubs and herbs characteristic of oak-hickory forests are to be found in many white pine forests. On the whole, therefore, it seems appropriate to regard such forests as ecologically equivalent to the oak-hickory forests developed elsewhere.

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