SECONDARY SUCCESSION IN THE CLIMAX FOREST FORMATIONS OF NORTHERN MINNESOTA

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SECONDARY SUCCESSION IN THE CLIMAX FOREST FORMATIONS OF NORTHERN MINNESOTA [1]

Harvey Stallard
San Diego, California

Introduction

This account of secondary succession represents part of the work done by Dr. Herbert F. Bergman and the writer in a study of the vegetation of northern Minnesota during the summers of 1912–16 (inclusive). A preliminary report (Bergman and Stallard, 1916) devoted principally to primary succession has already been published. The purpose of this paper, the publication of which has been delayed for more than twelve years, is to describe and classify the secondary successions of the state and show their relations to the climax or subclimax formations. During the field work the following counties were visited: Beltrami, Koochiching, St. Louis, Cook, Hubbard, Cass, Crow Wing, Itasca, Aitkin, Carlton, Pine, Wadena and Ottertail (Fig. 1). The most detailed studies were made in Cass, Crow Wing, Hubbard and St. Louis counties, since they are the most representative areas of the northern part of the state.

The ecesis of the dominants in each stage has been studied. The effects of these dominants upon the water-content of the soil and upon the light values of the habitats have been measured with field instruments, so that as far as possible, the results of succession have been ascertained as well as the causes. This is, perhaps, the first attempt to treat all the secondary successions of a great region in this manner.

The terms and classifications used are those of Clements (1916 and 1928) according to which successions are separated into two kinds, primary and secondary (Clements, 1916: 182), a concrete primary succession being termed a *prisere*, a concrete secondary succession a *subsere*. Priseres begin on bare rock or in water; subseres begin wherever a plant community has been destroyed but without effecting a complete return to bare rock or deep water. The essential difference between the two is that of initial conditions, the former commencing where soil conditions are extremely dry or wet and devoid of plant deposits or relicts, the latter starting on soils where the water-content is less extreme, as on glacial till, drained lake bottoms, or wherever the original plants and other geological processes have ameliorated the primitive conditions of the habitat. Secondary areas usually con-

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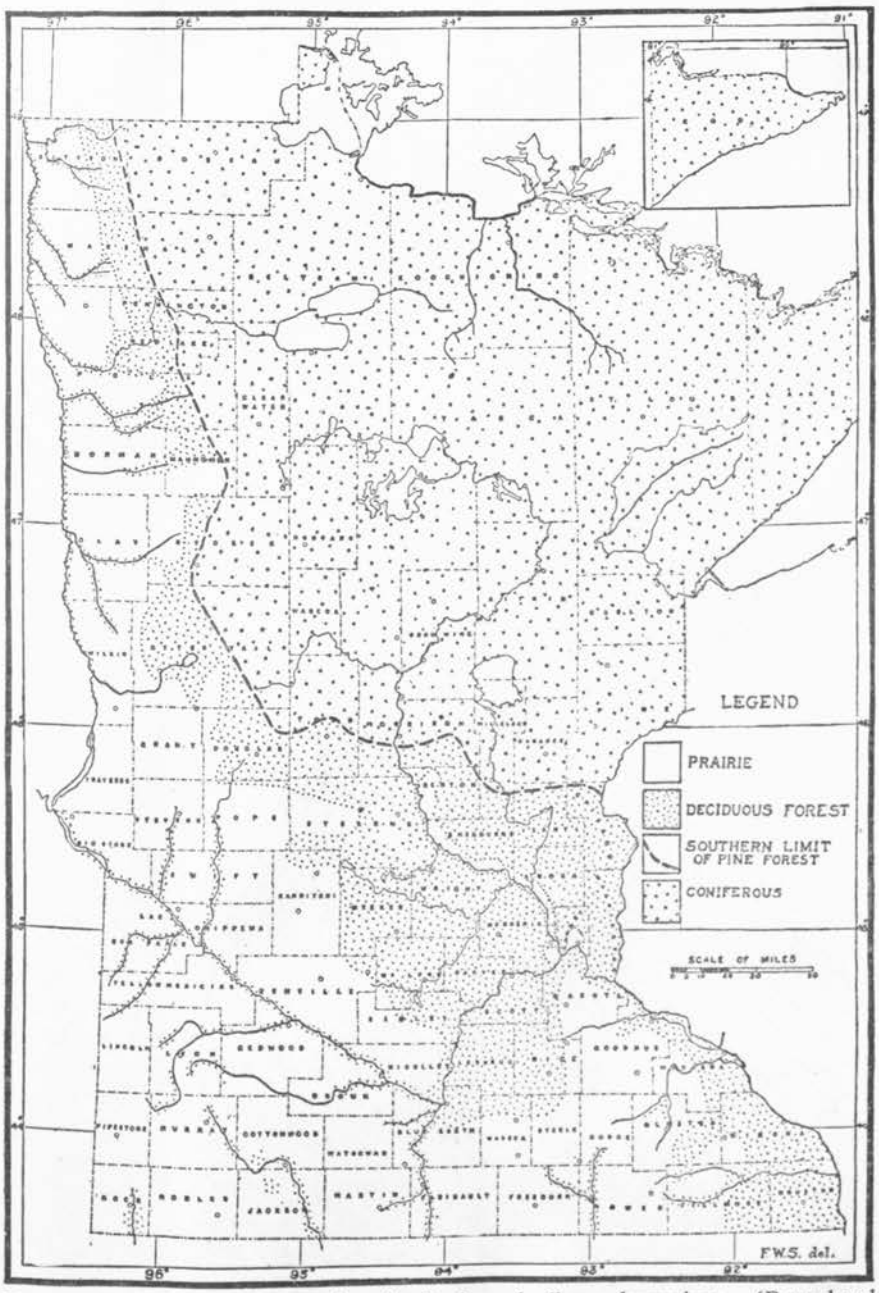


FIG. 1. Map of Minnesota showing distribution of climax formations. (Reproduced from Fig. 14, Bulletin No. 12, Minnesota Geological Survey.)

tain propagules of one or more stages, or provide for rapid ecesis of invaders. Primary areas are not only devoid of propagules but are also unfavorable for the ecesis of invaders. Priseres develop slowly. After many years, decades, or even centuries, a prisere may reach a climax stage which will maintain itself so long as the climate remains essentially the same. A subsere more quickly restores the climax, subclimax, or any of the other preliminary stages of the prisere after denuding forces have interrupted and subsided.

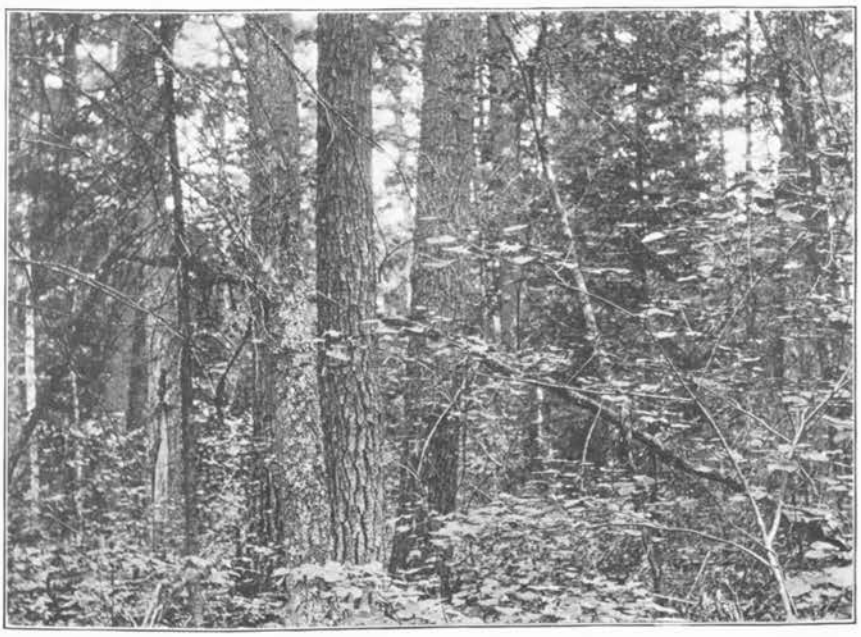
The following outline of subseres will aid the reader to comprehend the scope of this work:

I. Secondary Succession in the *Pinus-Tsuga* Climax:
   1. Subseres on Sand Outwash Plains,
   2. Subseres on Wet Clay and Wet Loam Soils,
   3. Subseres on Well Drained Clay and Loam Soils,
   4. Subseres on Rock Areas covered with Organic Soil;
      a. Humus Burned,
      b. Humus not Burned.
   5. Subseres on Rocky Clay or Loam,
   6. Subseres in Bogs:
      a. Subseres in Shallow Water,
      b. Subseres beginning with the Grass Associes,
      c. Subseres in Cut-overs,
      d. Subseres in Drained and Cultivated Bogs.
   7. Subseres in Flood-plains,
   8. Subseres beginning with Grass Stages (See 6, *b*):
   8. Subseres beginning with a Grass Stage (See 6, *b*):
      a. On Xeroid and Mesophytic Soils, Prairie and Bluegrass;
      b. The *Rhus* consocies,
      c. The Subclimaxes or Climax following *Rhus:*
         x. *Betula-Populus* Associes,
         y. *Pinus-Betula* Associes,
         z. *Quercus* Associes.

II. In the *Acer-Fagus* Climax:
   1. Mesophytic Clay and Loams, their Conditions and Subseres,
   2. Subseres beginning with Grass Stages.

Grateful acknowledgment is due Dr. F. E. Clements for directions, criticisms and suggestions. The writer is deeply indebted to Dr. Herbert F. Bergman, who, during four of the five years, aided in every way possible to make the field tasks pleasant as well as profitable. He identified most of the difficult species and made some of the most typical quadrats and transects.

A. Photograph of red pine forest near Benedict, Minnesota. This area includes quadrat in figure 2. In such stands 200 to 250 trees occupy an acre.



B. White pine forest near Craig, Minnesota.

I. Secondary Succession in the Pine-Hemlock Climax (The Coniferous Climax)

NATURE OF THE CLIMAX

A study of the ecological behavior, the forest composition and the gross structure of red and white pines will show, the writer believes, that they are the climax dominants of Northeastern Minnesota and would ultimately

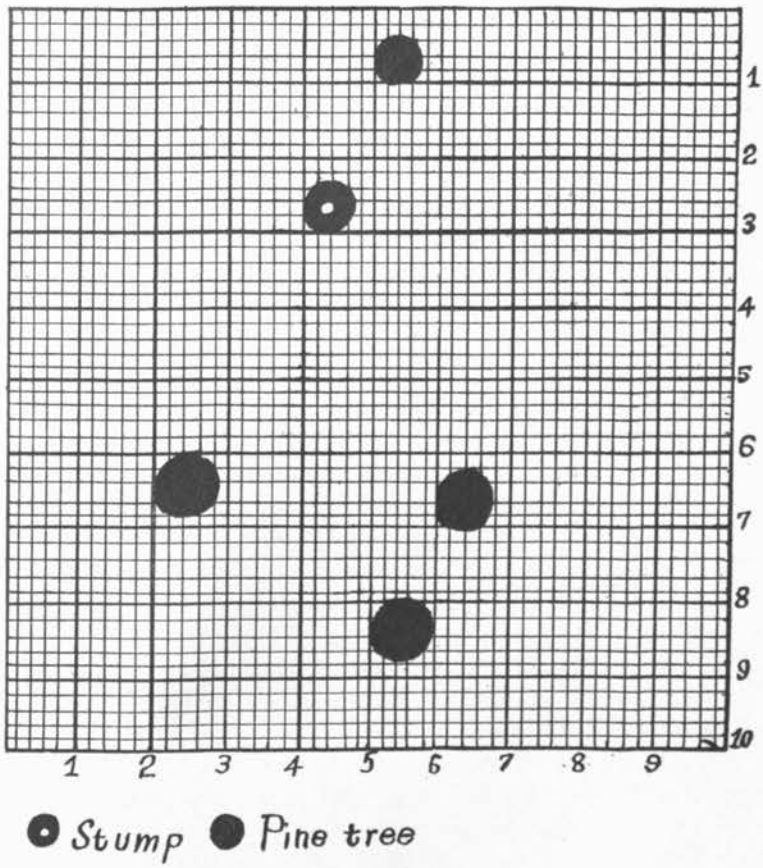


FIG. 2. A ten-meter quadrat (equivalent to .025 acre) in a forest of red pine near Benedict, Minnesota. See Plate I *A*.

occupy most of the coniferous area of the state, if the most damaging denuding forces were to subside. They are the principal representatives in the state of the pine-hemlock association. In certain districts stands of their mature trees may still be found. Although they have been burned slightly, they have been protected from the most damaging fires by such barriers as wet bogs, rivers, lakes, or by combinations of the three. On

unburned islands of Lake of the Woods and Rainy Lake these pines are the chief dominants. The uncut and unburned areas across the border in Canada are covered principally by them. In these places are found the largest and oldest trees in the northern portion of the state. They vary in diameter from 1 to 3 feet; in height, from 75 to perhaps 125 feet; and in age, from 65 to 200 years or more. Ten-meter quadrats (Fig. 2) show that 3 or 4 large trees cover an area of 100 square meters. The two species of pine are generally mixed, though either may be more abundant than the other in certain communities termed consociations.

The red pine consociation (Plate I *A*) presents a beautiful and clear forest whose trees are straight with high naturally trimmed trunks but with overlapping crowns in whose shade only the seedlings of white and red pine and certain shrubs of the forest floor can persist indefinitely. Such forests are found at Benedict near Leech Lake, near Rice Lake at Popple, west of Kelliher on the old lake beaches of Red Lake, on numerous islands of Lake of the Woods and Rainy Lake and rather extensively over the rocky areas of Lake and St. Louis counties.

Pure stands of the white pine consociation (Plate I *B*) are less frequently found now than are those of the former consociation but they do occur on islands of Lake of the Woods, the banks of the Big Fork River west of Big Fork village and also north of Craig, usually appearing on rather moist soils. The floor of such forests is usually occupied by such undershrubs as alders, dogwoods and scrub maples.

On the Red Lake peninsula, the soil of which is a light sandy loam, and on similar soils elsewhere in this part of the state, the two species are associated in about equal numbers. In many places, where white pine trees are more sparse, are found young basswoods, birches, white elms, ironwoods, or scrub maples, constituting a mictium which has replaced a local area in a damaged climax forest. This mictium is temporary, comparatively speaking, and is hardly general enough throughout the coniferous area to be regarded as a regular subclimax associes.

In the small white pine communities on the islands of Rainy Lake and Lake of the Woods are found occasional trees of white spruce, a species here regarded as a subdominant for reasons to be mentioned subsequently.

Such pine tracts as those described and illustrated above no doubt exhibit the nature and structure of the pine climax as it has existed since the glacial epochs. The general past existence of this climax forest can be traced in many communities now populated by representatives of *Pinus banksiana, Populus, Betula, Picea* or *Larix*, by means of stump relicts of trees which were destroyed by fire. This is notably true of places near Big Falls, Hubert (Pl. II, *A*), Walker, Ely, Meadowlands (Pl. II, *B*), Red Lake, Stanley and Kelliher, as well as in scores of other localities. By comparing quadrats of the old stumps with those of figure 2, it can be shown that the

A. Stumps of red pine in a jack pine forest near Hubert, Minnesota.

B. Stump of white pine, a relict of the *P. strobus* consociation, in a *Betula-Populus* associes which contains some young trees of white pine. Meadowlands, Minnesota.

pine trees formerly populated these areas as densely as those in the photograph (Pl. I, *A*). The red pine stumps in the quadrat of figure 3 are as numerous as the trees are in figure 2.

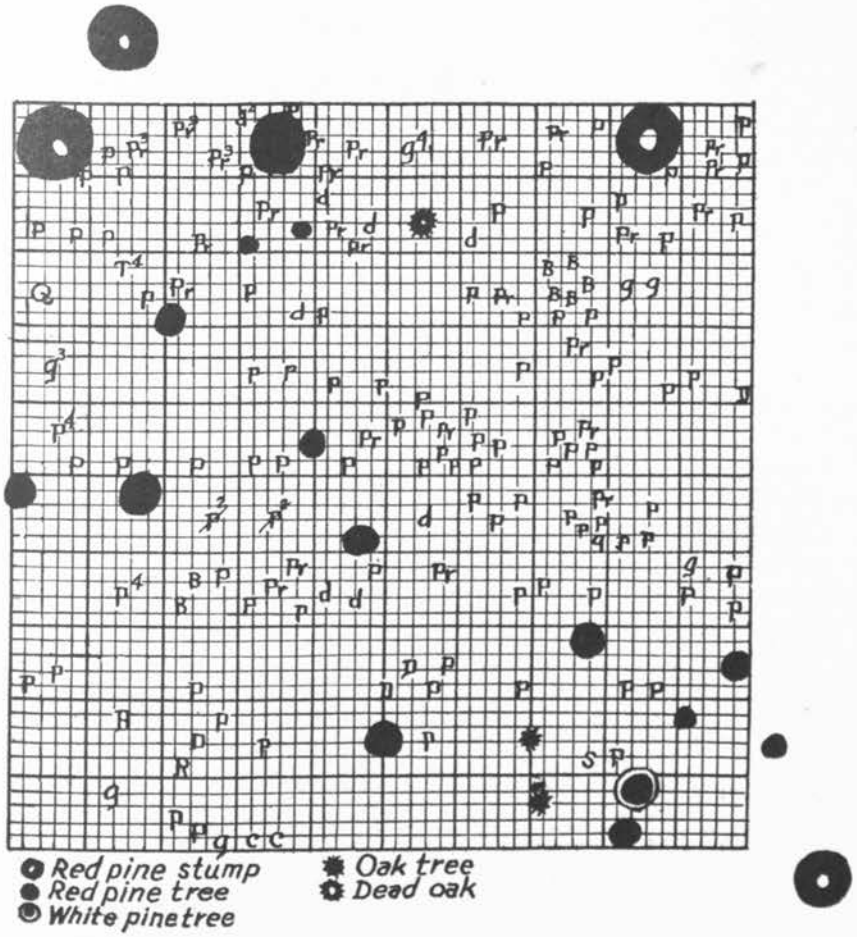


FIG. 3. Ten-meter quadrat showing, in a jack pine forest, the stumps, seedlings and young trees of white and red pine. Benedict, Minnesota.

LEGEND: For unlettered characters see legend immediately under quadrat. Exponents denote approximate age of seedlings.

B. *Betula papyrifera,*
C. *Ceanothus ovatus,*
D. *Diervilla lonicera,*
P. *Pinus banksiana,*
Pr. *Pinus resinosa* (seedlings),
Ps. *Pinus strobus* (seedlings),
q. *Quercus coccinea* (seedlings),
Q. *Quercus macrocarpa,*
R. *Rosa blanda,*
S. *Symphoricarpos pauciflora,*
T. *Tilia americana.*

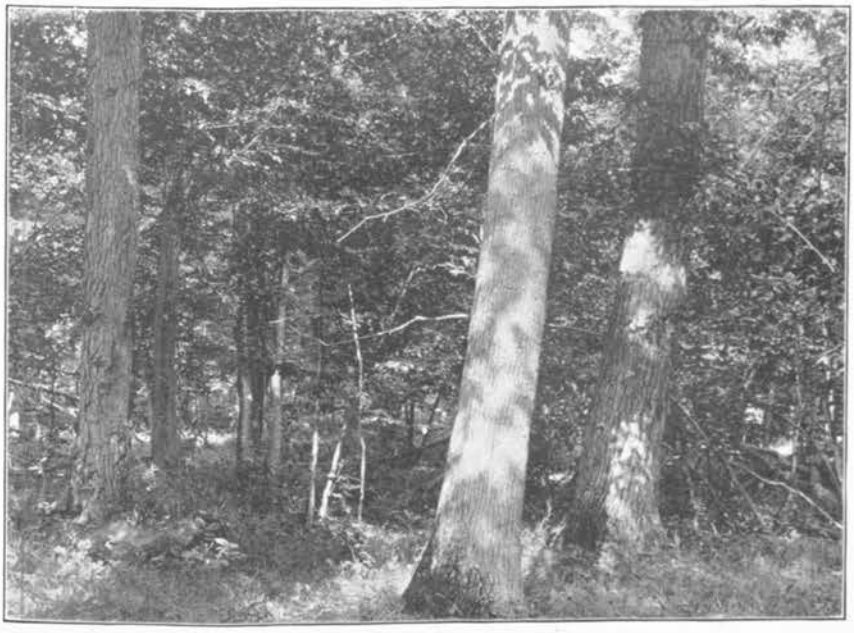
Few swamps, if any, were ever occupied formerly by pines, although it is not uncommon to find young pine groves on small partly drained bogs. A most notable example of this is a swamp north of Long Lake near Merrifield. Fire also destroys green bogs. Charcoal taken from various depths by peat samplers discloses that bogs too have been partly destroyed simultaneously with the climax forest.

By lake shores, in swamp edges, or in the bends of streams, are found towering above the trees of aspen or jack pine solitary white or red pines which have bushy tops and clear trunks just as trees usually have when grown in a uniformly populated forest. These seed bearers have had their seeds sown rather extensively throughout the surrounding areas so that seedlings and young descendents are much in evidence. The ecesis of pines, their ability to tolerate shade, their tall life-forms, and the age they attain make them superior competitors. Their charred stumps and fallen trees, frequently occurring as relicts on much of the upland in the coniferous area, show that they have been dominants. Their death was not due to competitors, but to fire, which has been and is today the principal denuding agent (Pl. II, *A, B*). A photograph (Pl. III, *A*) of a typical clearing in St. Louis County also discloses the general prevalence of white pine stumps in a field adjacent to the forest represented in Plate II, *B*.

The nature of the life-forms of the pines, the structure of their forest, the tendency of succession in the coniferous district, and the relicts, indicate that a pine climax has been established in these regions at least once, if not many times since the glacial epoch. To show that the pines no longer represent the climax dominants, it would be necessary to prove that the climate has changed to their disadvantage, which seems to be contrary to all the evidence available.

From the preceding it is clear that pines form the final stage of succession in the coniferous area, except in a few smaller places now occupied by maple and basswood (Pl. III, *B*), that white pine and red pine stands apparently will not under present climatic conditions be replaced by other dominants, and that on moist soils white pine is almost a pure dominant, while on drier soils red pine forms nearly pure stands. The wet soils are generally clays, such as are found in Cook County and along the St. Louis and White Face rivers. The dry soils are either sand having a deep water-table, as in the vicinity of Brainard, or they are thin organic soils on top of rock areas, such as occur in the northeastern part of St. Louis, Lake and Cook counties. The more mesophytic conditions exist in the well-drained loam soils of the glacial drifts, and on such the climax consists of a mixture of the pines. Theoretically, it would seem, white pine should ultimately crowd out red pine, because it is taller, its attainable age is greater, and its seedlings can grow in denser shade.

A. White pine stumps in a timothy meadow near Meadowlands, Minnesota.



B. Hardwood grove on the shore of Gull Lake, Hubert, Minnesota, consisting of hard maple, ironwood, white elm, basswood and occasional bur oak trees.

A. Effect of cutting and small grass fires in a red pine forest near Benedict, Minnesota.

B. Jack pine trees and seedlings on recently burned-over rock areas near Ely, Minnesota.

I. SUBSERES IN THE PINE CLIMAX

The following subseres occurring in the pine association have been studied:

1. Subseres on Sand Outwash Plains,
2. Subseres on Wet Clay and Wet Loam Soils,
3. Subseres on Well-drained Clay and Loam Soils,
4. Subseres on Rock Areas Covered with Organic Soil,
5. Subseres on Rocky Clay or Loam Soils,
6. Subseres in Bogs,
7. Subseres in Flood Plains,
8. Subseres beginning with a Grass Stage.

(1) *Subseres on Sand Outwash Plains*

Denudation: The simplest form of denudation, accomplished by lumbering or by wind, is the mere removal of the dominants without affecting the soil factors (Pl. IV, *A*). In large windthrows, seldom occupying extensive areas among pines, the sere initiated would be practically the same as that following cuttings. After lumbering, often the brush is burned and the area is denuded to a greater degree. Fires, especially in dry seasons, not only kill the herbs, shrubs, tree seedlings and young dominants, but they may also destroy the organic soil, usually the accumulation of decades. Organic soils lying on top of rocks are ofttimes so thoroughly destroyed that the water-content decreases almost to that of the initial stage of the prisere. However, weathering usually breaks up the surface of the rock simultaneously with the depositing of organic litter and humus, so that the soil formed is a mixture of disintegrated rock and organic debris. Unless erosion accompanies or follows denudation by fire, a complete bare area will not be produced except in small spots in the rocky areas of the state (Pl. IV, *B*). In mineral soils, denudation is never complete enough to initiate a prisere. The degree of denudation, therefore, depends not only on the agents, but directly also on the character and conditions of the soil at the time the agent acts.

Cutting annihilates individual pine trees since their stumps will not reproduce sprouts, a means of regeneration employed by many deciduous trees and shrubs. Ruthless lumbering or severe burning may kill most of the seed-bearing dominants, but no matter how extreme the fires or the processes of lumbering, the shrubs and secondary deciduous species are seldom, if ever, exterminated. Cutting increases the light values of the habitat, but does not directly affect the organic- or water-content; however, since it exposes the soil to the sun and wind, the resulting evaporation lowers the water-content and, to some extent, the inevitable oxidation following lowers the amount of organic matter. Fires directly decrease the organic soil content and hence lower the holard of the surface soil. Clearing, fol-

lowed by cultivation, completely removes the species of a forest, changing profoundly all the factors of the habitat, namely, decreasing the organic content and the holard and increasing the exposure to wind and sun. Similar conditions develop after gravel slides or in talus slopes occurring around lake shores or at the bases of high river bluffs where the erosion and slips have about the same effect as poor cultivation. Flooding of pine has been noted nowhere in the state, but there has been considerable flooding of the

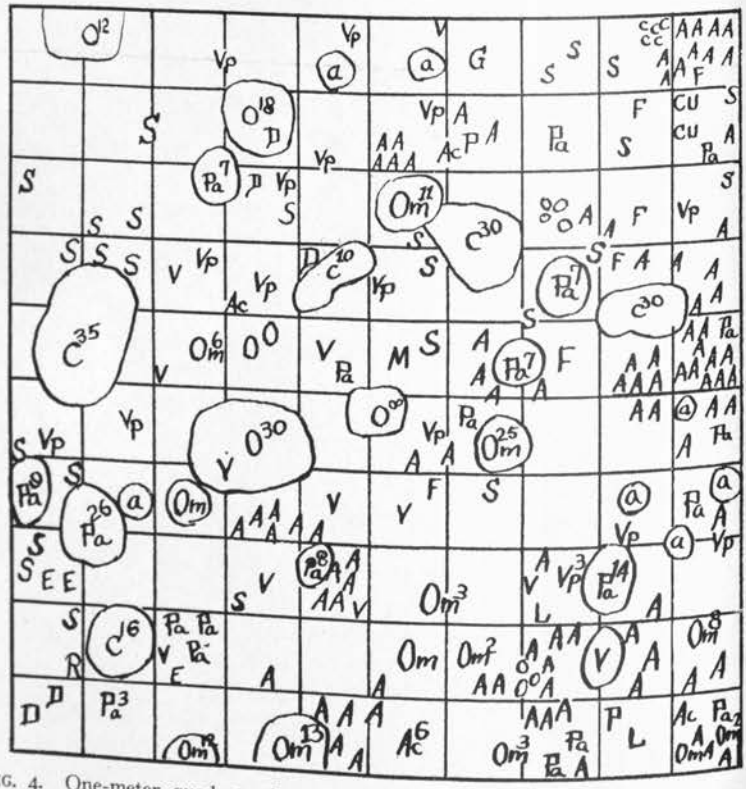


FIG. 4. One-meter quadrat of the herbs and small shrubs living on the floor of the red pine forest near Benedict, Minnesota. Exponents indicate the number of plants found in the inscribed areas.

LEGEND:

A. *Antennaria canadensis,*
a. *Agrostis hiemalis,*
Ac. *Aster cordifolius,*
C. *Carex backii,*
Cu. *Chimaphila umbellata,*
D. *Diervilla lonicera,*
E. *Erigeron canadensis,*
F. *Fragaria virginiana,*
G. *Gaultheria procumbens,*
L. Lichens,
M. *Maianthemum canadense,*
O. *Oryzopsis juncea,*
Om. *Oryzopsis micrantha,*
P. *Pteris aquilina,*
Pa. *Panicum pubescens,*
R. *Rubus strigosus,*
S. *Senicio balsamitae,*
V. *Viola conspersa,*
Vp. *Vaccinium pennsylvanicum.*

subclimax stages in the Leech Lake and Gull Lake basins, where the water-level has been raised by government dams made for the purpose of storing water for the Mississippi River.

Seres initiated by cutting become mature more quickly than those started by destructive fires. Annual or frequent burning holds the sere in an herbaceous stage, provided a previous denuding force destroyed the trees and shrubs. An area subjected to such disturbances permits the development of a prairie, a bluegrass stage, or a wet meadow, depending upon the nature of the habitat. When cultivation is neglected or stopped altogether, a meadow or grass stage of some sort usually develops. The seres passing through a grass stage require the longest time to restore a tree climax, since repeated partial denudation necessary to produce the opportunity for grass kills trees and shrubs, and since forest trees and shrubs invade unburned exposed sod with difficulty.

The secondary species of the red pine consociation are apt to be sparse in number yet abundant enough to provide seeds and propagules for increasing the herb and shrub population when the light is intensified by a removal of the forest (Fig. 4).

Societies are formed by the following species: *Anemone quinquefolia, Aralia nudicaulis, Aster cordifolius, A. laevis, A. macrophyllus, Falcata comosa, Fragaria virginiana, Lathyrus ochroleucus, L. venosus, Maianthemum canadense, Pteris aquilina, Sanicula marilandica* and *Viola conspersa.*

The following herbs usually appear in clans: *Antennaria canadensis* (Fig. 4), *Carex backii, C. pennsylvanica, Chimaphila umbellata, Chiogenes hispidula, Gaultheria procumbens, Oryzopsis micrantha, O. juncea, Pyrola americana, P. secunda* and *Polygala senega.*

The following secondary species are scattered among the other species mentioned above: *Convolvulus repens, Halenia deflexa, Houstonia purpurea, Nabalus alba, Trientalis americana* and *Vicia americana. Comptonia peregrina* forms societies in the pine consociation in the rock areas of the northeastern part of the state.

The following shrubs may appear individually or in societies: *Arctostaphylos uva-ursi* (Figs. 6 and 7), *Corylus americana, C. rostrata, Diervilla lonicera, Rubus strigosus, Rosa blanda, Vaccinium canadense* and *V. pennsylvanicum* (Fig. 5). *Ceanothus ovatus* is a dominant shrub in sand dunes and outwash plains, particularly in the vicinity of Hubert.

A subsere during its development on any upland soil in the pine association usually displays three distinct stages, namely, an herbaceous, a shrub and a tree subclimax associes. It is evident that many of the dominants of the first two stages are found among the species in the lists given above. The dominants of the tree subclimax for the most part migrate from surrounding areas bordering denuded vicinities, or even from more remote territories.

The Herb Associes: The herb associes naturally varies in structure, duration and composition so much that it is impossible to assign a definite group of dominants for any extensive area. The variations depend partly upon the degree of denudation and the number of times the destructive agents have acted and partly upon the migration and ecesis of the invaders.

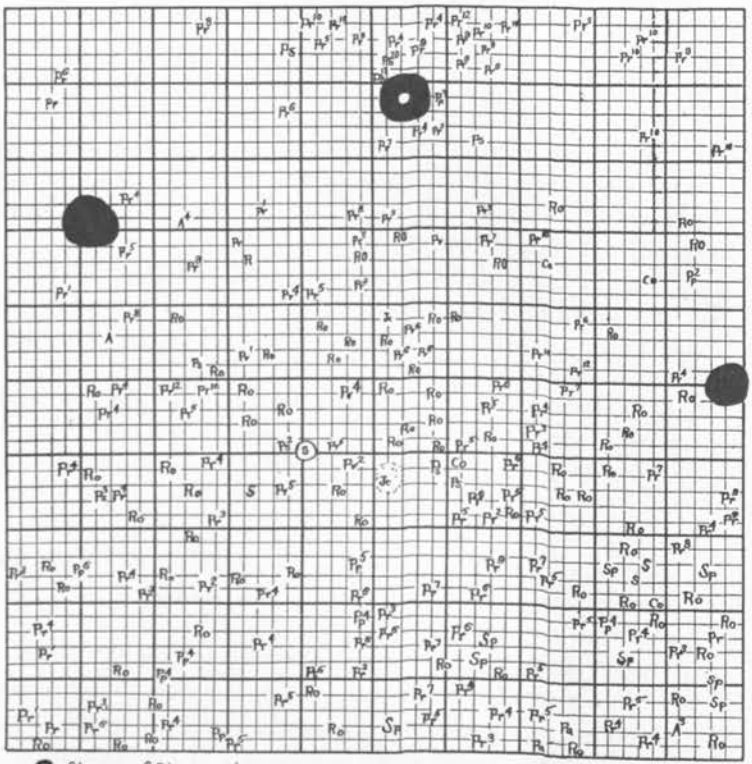
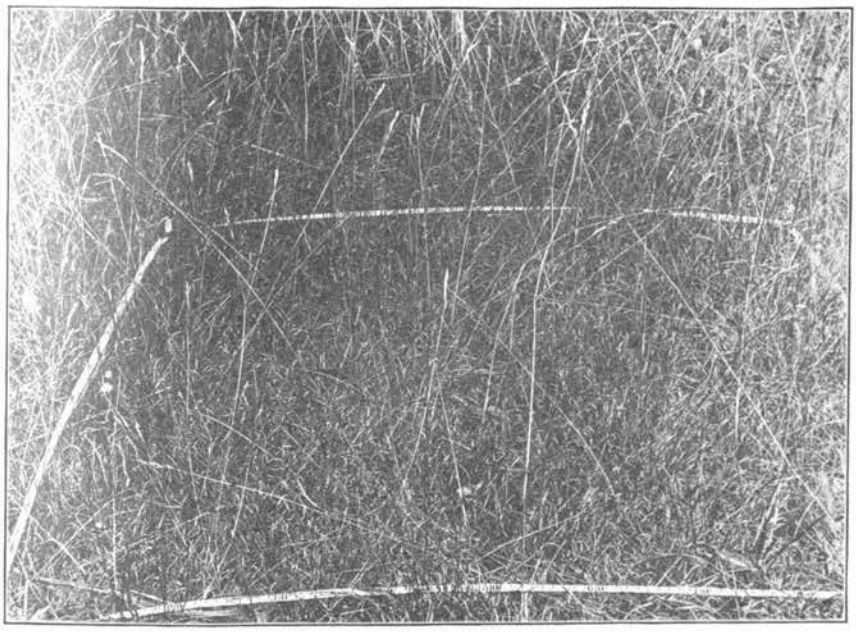


FIG. 5. A ten-meter quadrat of shrubs underneath red pine trees near Benedict, Minnesota. Made by H. F. Bergman. Exponents indicate approximate height, in feet, of the trees and seedlings.

LEGEND:

A. *Amelanchier canadensis,*
Co. *Corylus americana,*
Jc. *Juniperus communis,*
Pa. *Prunus pumila,*
Pb. *Pinus banksiana,*
Pr. *Pinus resinosa* (seedlings),
Ps. *Pinus strobus,*
Pv. *Prunus virginiana,*
Ro. *Rosa blanda,*
S. *Salix* sp.
Sp. *Symphoricarpos pauciflorus.*

The length of its duration depends upon the rapidity of the development of the shrub associes if denuding agents cease. If the pines are removed by cutting, unaccompanied by burning, there develops and prevails for a



A. Photograph of quadrat shown in figure 6.

B. Herbaceous stage in a cut-over consisting principally of weeds, *Amaranthus, Erigeron, Achillea* and *Solidago* appearing in the background; *Aster, Actea* and grasses appearing in the foreground and to the right. Bemidji, Minnesota.

short time, comparatively speaking, an herbaceous stage consisting chiefly of *Aster, Aralia, Cornus canadensis* and *Pteris,* all of which intensify their stands by means of offshoots.

In areas badly denuded by fire, herbs must invade by seeds. Wherever red pine has occupied sandy areas, repeated burning selects the herb domi-

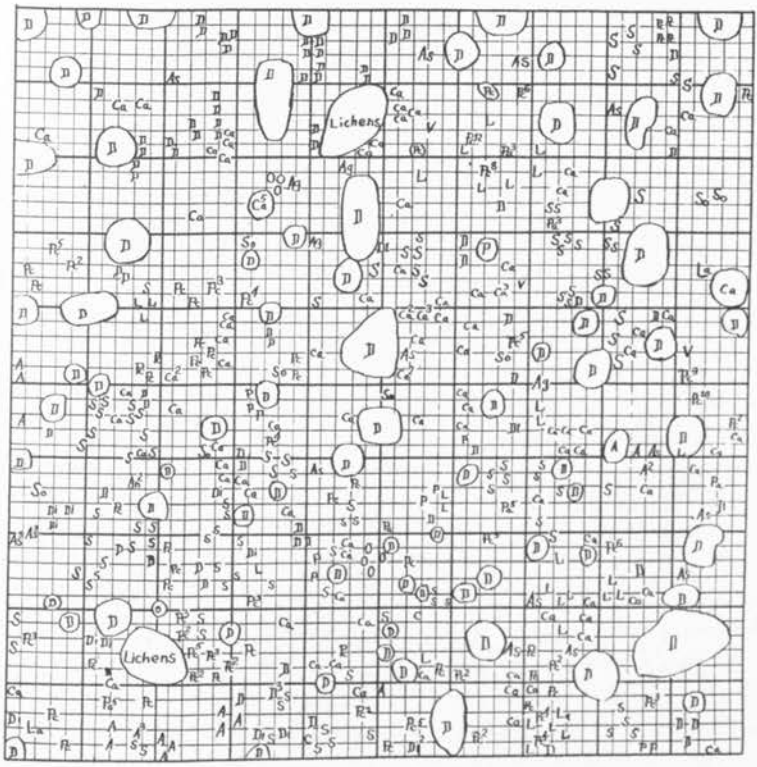


FIG. 6. One-meter quadrat of prairie near Benedict, Minnesota. Made by H. F. Bergman. Exponents denote number of individuals in a group.

LEGEND:

A. *Andropogon furcatus,*
Ag. *Agastache anethiodora,*
An. *Antennaria canadensis,*
As. *Aster laevis,*
C. *Campanula rotundifolia,*
Ca. *Carex pennsylvanica,*
D. *Danthonia spicata,*
Di. *Diervilla lonicera,*
L. *Lechea stricta,*
La. *Lacinaria scariosa,*
O. *Oryzopsis micrantha,*
P. *Panicum pubescens,*
Pc. *Polytrichum commune,*
S. *Solidago nemoralis,*
So. *Solidago canadensis.*

nants by exterminating those incapable of surviving and competing with those better adapted to such hazards. After one or several fires, the most prominent pioneer is *Agrostis hiemalis* whose dry plants with seeds attached

are tumbled about by the wind. The second year and for a few years following, such plants as *Chamaenerium angustifolium, Achillea lanulosa, Anaphalis margaritacea, Leptilon canadense, Onagra biennis, Solidago canadensis* and *S. nemoralis* are the most conspicuous dominants. The seeds of the biennials and perennials immigrate with *Agrostis,* but their plants appear the first year in the rosette stage underneath the thin veil of the annual grass which affords them their chief protection. In the driest places where only a small amount of litter has been deposited during the existence of the climax dominants, *Antennaria* persists after simple denudations and may even extend its areas if the denuding agents fail to recur. Repeated burnings, which are always to be associated with recurring annual droughts or dry soils, eventually lead to the invasion of prairie species such as *Danthonia spicata, Agropyron richardsonii, Andropogon furcatus, A. scoparius* and *Stipa spartea. Antennaria* persists through all the stages leading up to prairie, becoming a subdominant in this associes (Figs. 4, 6). In many areas of the state, the dominants retained in the herb associes and the relicts of the shrubs indicate that fires have occurred repeatedly, but more often in the western and southern regions.

Where the habitat is normally more mesophytic, *Falcata comosa, Fragaria virginiana, Lathyrus ochroleucus, Rubus americanus, Vicia americana* and *Maianthemum canadense* are prominent. Such plants as *Chimaphila, Gaultheria, Pyrola* and *Trientalis* occur, but never as dominants. They are able to persist in the open only for a short time, or for longer periods under the shade of larger shrubs and herbs. *Trientalis,* plants of which when suddenly exposed are often parched by the sun and wind, is unable to remain in competition with the other sturdier plants and hence rarely appears in the herb associes. *Maianthemum* can withstand rather prolonged exposure to evaporation and sun, for it will often remain a number of years on ground that has been occasionally burned over.

The behavior of the herbaceous associes may be summarized as follows: If cutting is the sole denuding agent, the initial stage, for the first few years at least, consists of herbs or their propagules which are present on the floor of the forest. If burning occurs repeatedly, nearly all the original herbs are replaced by perennial prairie species (Pl. V, *A*). When cultivated clearings are made and then abandoned, a weed stage appears which consists of *Amaranthus retroflexus, Ambrosia artemisiifolia, Brassica nigra, Chenopodium album, Erigeron canadensis, Lepidium apetalum, Rumex acetosella, Poa pratensis, Agropyron tenerum, A. repens, Elymus canadensis, Chamaenerium angustifolium, Achillea lanulosa, Anaphalis margaritacea, Leptilon canadense, Onagra biennis, Solidago canadensis* and *S. nemoralis* (Pls. V, *B,* VI, *A*). A grass stage may succeed a weed stage of this sort on a sandy soil sooner than it could on clay or loam soils.

The herbs prevent considerable erosion, runoff, exposure and loss of

A. Edge of a clearing showing a thinned stand of aspen in the background, weeds and grasses in the central zone, and hazel in the foreground. Bemidji, Minnesota.

B. *Corylus, Prunus* and *Rosa* in foreground; rapidly growing seedlings and young trees of *Populus* in the background. Walker, Minnesota.

duff which accumulated under the climax trees. Fires, before or after the initial herbaceous growth, consume large amounts of dry organic matter, making the soil much more subject to erosion and no doubt indirectly reduce the humus incorporated in the soil. From field determinations, it has been found that more than 50 per cent of the total organic matter is lost when a sandy soil is made bare by fires. The water-content is decreased from about 8 per cent to 4 or 5. A surface soil which has an average holard of less than 3 per cent produces only a scant growth of herbs, but when prairie has developed, the organic portion increases to about 9 per cent and the water-content of the surface 4 inches averages about 7 per cent. The decrease of light and exposure from the reaction of the herbs on sand is slight; when they are sparse and small, they cast little shade, and even when they are larger and more abundant never reduce the light more than 10 per cent.

The Shrub Associes: RELATION BETWEEN DOMINANTS AND DENUDATION: It has already been mentioned that the agencies initiating subseres nearly always leave on the ground propagules, seeds, or plants of the damaged stages. A number of the species participating in the herb associes are secondary species and subdominants which have lingered in dwarfed forms under the climax trees and survived denudation. At first only a few species migrate from neighboring territories, but if the herbs are not followed by shrubs, or if denuding forces recur periodically, most of the herbs are replaced by invaders which are foreign to the flora of the pine forest. Such a replacement of herbs would effect a total displacement of the shrubs of the climax forest. The nature of the stages of the subsere depends to a large extent upon the initial water-content of the habitat, which is conditioned principally by the degree of denudation and the mineral nature of the soil. The species destined to appear in the shrub and tree stages are determined by the following conditions: the nature of the soil, degree of denudation, the nature and structure of the vegetation preceding the denudation, and the methods of migration and ecesis of the invaders.

The herbaceous plants precede the shrub stage largely because they grow and propagate more rapidly. Shrubs follow promptly if fires do not interfere. They fall into two different communities, the *Arctostaphylos-Vaccinium* stage and the larger *Corylus-Rubus* stage (Pl. VI, *B*), the former representing all the smaller shrubs and the latter the taller. The smaller shrub stage consists of *A. uva-ursi, V. pennsylvanicum, V. canadense* and *Symphoricarpos pauciflorus* (Fig. 5). *Rosa blanda* may be present but never conspicuous except when in bloom. *Arctostaphylos,* by lying close upon the surface of dry soils, often having its principal horizontal stems wholly or partly embedded, collects through its small adventitious roots the needed moisture from the first and second inches. Wherever it appears, the surface soil is distinctly colored by organic material. It also owes its establishment

principally to parents which lived on the floor of the forest and survived denudation. Its chief method of propagation is by means of trailing stems (Fig. 7).

Vaccinium, likewise propagating chiefly by means of rootstocks of parent plants which are more or less suppressed in shade, promptly increases

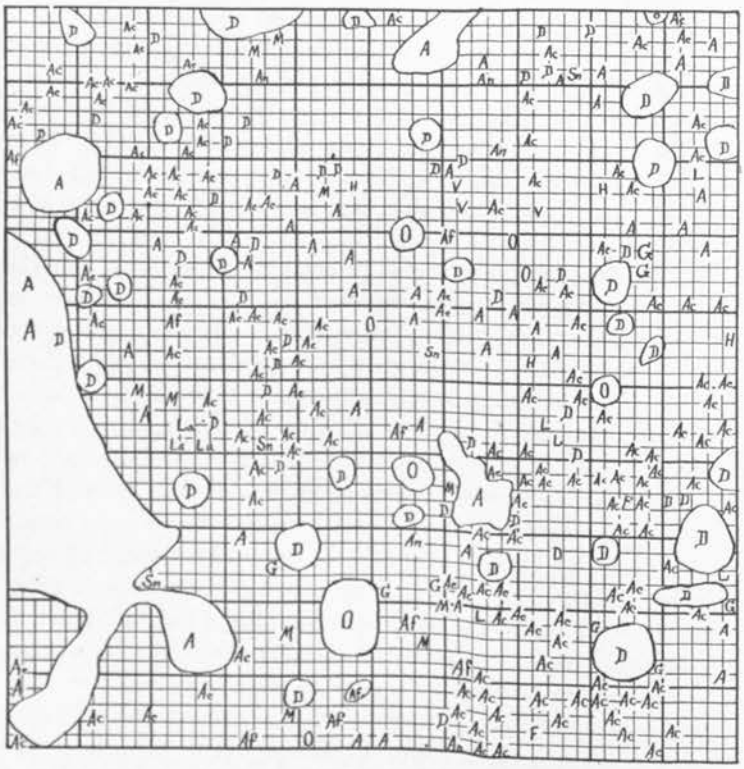


FIG. 7. One-meter quadrat showing mat of *Arctostaphylos* and its companion plants occurring in a clearing. Benedict, Minnesota.

LEGEND:

A. *Arctostaphylos uva-ursi*,
Ac. *Aster cordifolius*,
Af. *Andropogon furcatus*,
An. *Anemone quinquefolia*,
D. *Danthonia spicata*,
F. *Fragaria virginiana*,
G. *Gaultheria procumbens*,
H. *Helianthus* sp.,
L. *Lathyrus venosus*,
La. *Lacinaria scariosa*,
M. *Maianthemum canadense*,
O. *Oryzopsis micrantha*,
S. *Solidago canadensis*,
Sn. *Solidago nemoralis*,
V. *Vaccinium pennsylvanicum*.

its numbers after the subclimax or climax trees are removed. A whole colony of apparently separate plants may be the branch members of a single individual. In tracing the extensions of single rootstocks by digging in the

ground, it has been found that they often exceed several yards in length, representing a migratory growth of several years. Such a method of propagation and migration makes it possible for *Arctostaphylos* and *Vaccinium* to occupy the dry sand areas where ecesis from seeds is difficult. As they send up shoots they form mats (Fig. 7) which collect the falling leaves and thus accumulate organic material. The writer's belief that they owe their

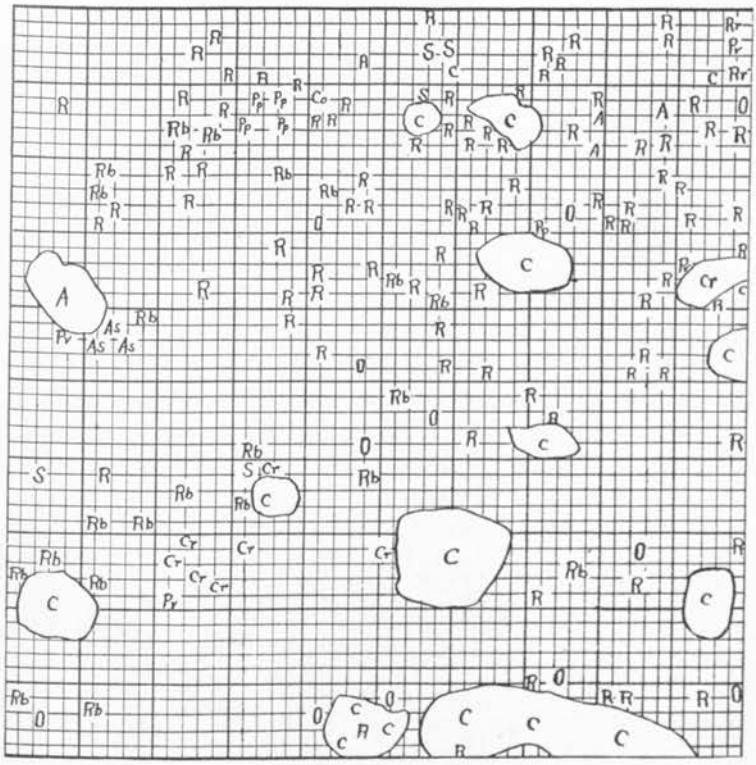


FIG. 8. Ten-meter quadrat of *Rhus-Ceanothus* associes. Hubert, Minnesota.

LEGEND:

A.	*Arctostaphylos uva-ursi,*	R.	*Rhus hirta,*
As.	*Amelanchier spicata,*	Rb.	*Rosa blanda,*
C.	*Ceanothus ovatus,*	Pp.	*Prunus pumila,*
Co.	*Corylus americana,*	Pv.	*Prunus virginiana,*
Cr.	*Corylus rostrata,*	S.	*Salix* sp.,
Rr.	*Rhus rydbergii,*	Sa.	*Salix discolor.*

establishment chiefly to rootstocks is supported principally by the fact that during the summers of 1915 and 1916 he could not find seedlings anywhere by diligently observing areas partly occupied by seed-bearing plants.

The dominants of the taller shrubs are *Corylus americana, C. rostrata, Rubus strigosus, Diervilla lonicera, Rosa blanda, Rhus hirta* and *Ceanothus*

ovatus (Fig. 8). *Prunus virginiana, P. pennsylvanica, Amelanchier canadensis* and *A. spicata* are usually present but generally sparse. *Ceanothus* may form consocies in the driest soils with better success than any of the others mentioned above. *Alnus crispa* (Fig. 9) in certain vicinities is quite abundant, but it is not regularly distributed as widely as the other species of this stage. Species of *Salix* are present, but in sand barrens they assume little or no importance.

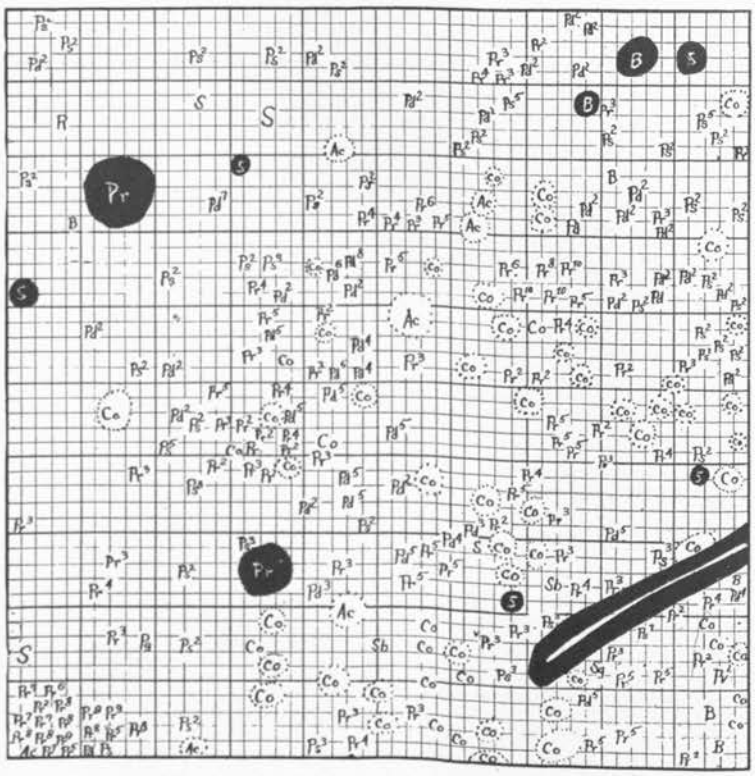


FIG. 9. Ten-meter quadrat of shrubs in a red pine forest which has been partly cleared. Benedict, Minnesota. Made by H. F. Bergman.

LEGEND:

Ac. *Alnus crispa,*
B. *Betula papyrifera,*
Co. *Corylus americana,*
Pd. *Pinus banksiana,*
Pr. *Pinus resinosa,*
Ps. *Pinus strobus,*
Pv. *Prunus virginiana,*
R. *Rubus allegheniensis,*
S. *Salix* sp.
Sg. *Salix glaucophylla.*

Exponents represent the approximate height in feet of the shrubs and tree seedlings. Long figures represent fallen decayed logs of red pine.

Diervilla, Corylus, Rubus and *Rosa,* being present in the climax in suppressed forms, multiply in the open more vigorously and grow more rankly.

A. Photograph taken near Hubert, Minnesota, of a shrub stage consisting of *Rhus, Rosa, Corylus, Ceanothus* and *Diervilla.* Jack pine seedlings are seen in the distant portion underneath a parent tree.

B. Pinus banksiana consocies growing on a sand dune near Benedict, Minnesota. Sedges and heath plants this side of the road.

Diervilla, sometimes the first member of this associes to assume prominence, reaches its maximum development early in the formation of the shrub stage, often the first year after denudation. It multiplies by basal shoots and forms thickets which attain their best development on rather dry soils.

Corylus usually produces a considerable quantity of nuts each year, but only very rarely does one find its seedlings. In the summer of 1913 an abundance of nuts was produced, but by the time the fruits had ripened the red squirrels had taken most of them. Large numbers were devoured while the seeds were still soft, and by the last of August scarcely a sound fruit could be found on the bushes. In the shade of dense woods it appears sparsely and bears no fruit. Here and there is found a solitary slender sprout having only three or four leaves, but after denudation in the presence of more light, it grows sturdier and by propagating through underground or basal shoots forms a cluster, hence its clustered appearances in open fields. It grows best in clay or loam soils, but it may thrive fairly well on sandy soil (Pl. VII, *A*).

Rubus during the same summer produced a copious amount of fruit. Nearly every year it yields a fair crop, but its seedlings are seldom found. Crows, partridges, grouse and other birds and, perhaps, bears are responsible for its seed distribution. By its well known method of propagation, its numbers may be doubled every year, but its rate of advance into newer fields is slow. Multiplying in a geometric ratio, it develops an exclusive dominance in favorable areas. Sandknolls are the most suitable places for its best growth; in the poorest soils or barrens its plants remain small.

Rosa each year bears quantities of achenes which are thought to be distributed by winter birds, but its seedlings are rare. It is usually present in the subsere of sand barrens though seldom as a pure dominant in any large area. It is fairly abundant in the shrub associes on other soils. Its subterranean migration is accomplished by means of rhizomes which grow beneath the surface 3 to 8 inches and from which sprouts arise at intervals of 12 or more inches. This manner of propagation accounts for its open stands and nonclustered growths.

Prunus and *Amelanchier* bear fruits annually, the former being the more productive. In the summer of 1914 and 1916, *Amelanchier* yielded the largest crops since 1911. Seeds of both species have been found in the entrails of crows and partridges, but it is not known how much such birds are responsible for their distribution. Water currents and wave actions of lakes may transport the fruits whenever riparian plants drop them into the water. Seedlings of *Amelanchier* have been found a number of times in groupings which indicated that the seeds were deposited in the excrement of animals thought by the writer to be bears. Little is known concerning the ecesis of *Amelanchier* and *Prunus*. If the degree of dominance is the final measure of migratory and ecesic ability, one may justly conclude that

theirs is relatively poor. Their life-forms apparently lack no structures which normally make plants good competitors. They are among the tallest of this associes and when in clusters cast considerable shade. They are not injured by frosts and seem to be free from disease and parasitic insects.

Ceanothus plays no part, at least a minor one, in the associes, if edaphic factors favor the other shrubs. Where frequent burnings occur, the associes is modified and this plant becomes a conspicuous dominant, as on the sand barrens near Hubert. Here in many places it appears clustered amid prairie grass, a development due chiefly to fires, since it can withstand grass fires better than the other shrubs. It also endures exposure better, apparently, than *Corylus* and *Rubus*.

The dominants of the shrub associes, varying in height, life-form, vigor and ecesic ability, often compete severely with each other, the more vigorous and prolific taller ones being naturally the most successful. When the shrubs are not followed promptly by trees, *Corylus*, on account of its forming dense thickets and being higher than the other shrubs, can shade out most of its companions, namely, *Rosa, Rubus* and *Diervilla*. On fertile soils it may exclude 95 per cent of the light, but in xeroid habitats it seldom reduces the light value to more than 30 per cent.

The water-content of the first decimeter in the *Corylus-Rubus* associes is always higher than that of the herb stage. The main roots of *Corylus* lie beneath the duff, chiefly in the second decimeter. The duff is maintained and produced in part by the shrubs which, by collecting fallen leaves, retain the annual accumulation of the dead foliage. The shade of the shrubs maintains a higher water-content, during the days immediately following a rain, than does bare soil or any of the herbaceous associes. Field determinations show that the average holard of the shrubs is about 14 per cent, that is, about twice that of the herbaceous stage.

The Temporary Tree Associes: *Pinus banksiana* is the usual dominant of the subclimax found growing on sand or gravel outwash plains and dunes, where the water table is several feet below the surface (Pl. VII, *B*). On such soils previously occupied by red pine it is the first tree invader to become conspicuous (Pl. VIII, *A, B*). This consocies may appear immediately after denudation, after a prairie development, or after the *Arctostaphylos-Vaccinium* stage or in a thin stand of the higher shrubs, namely, *Corylus, Rubus, Rosa, Rhus* and *Ceanothus*. In more mesophytic habitats it is associated with *Betula papyrifera, Populus grandidentata* and *Quercus coccinea*. *Q. macrocarpa* and *Populus tremuloides* are also sometimes present but never abundant, nor do they attain a normal adult size in such dry soils.

The *Pinus-Betula* Associes: The winged seeds of jack pine are not carried very long distances by wind. Its trees may shed their cones or retain them indefinitely on their branches. Squirrels may harvest their cones and

A. Jack pine seedlings in a recently burned area. Hubert, Minnesota.

B. Jack pine seedlings in a cut-over, Shevlin, Minnesota. Red pine stump in lower left corner. Seedlings near by found to be 5 years old and bearing cones. Those on the right bearing several cones were ten years old.

disseminate considerable quantities of their seeds, though wind is the chief agent of distribution. It was formerly believed that the cones open only when heated by fire, but Beal (1888: 74–78) showed as early as 1888 that solar heat opens them. The same writer, testing the viability of their seeds, found that those of new cones germinated 95 per cent, but only 85 per cent of those in cones 4 to 6 years old sprouted.

Mature trees of jack pine are prolific, so that areas in their vicinity are abundantly sown with seeds (Pl. VIII, *A, B*). Vigorous trees growing in the open frequently bear 1 or 2 cones at the age of 3 years, or as many as 10 or 12 at the age of 6, and at the age of 10 they may bear an appreciable amount of seeds. A few parent trees may in a period of 30 years indirectly colonize large surrounding areas by reproducing in short generations seed bearers in the outer zones of the initially invaded territory which broadcast, in their turn, offspring of the second generation into more remote areas. Such a method of invasion not only increases the size of the colony but its density in the border regions. Jack pine is thus able to invade and densely populate relatively large barrens in a comparatively short time, because it bears at an early age abundant seeds which have a high viability, a suitable migratory device and sufficient endosperm to make ecesis relatively easy.

The precise conditions for the optimum germination of jack pine have never been fully determined, but judging from the success it enjoys in sand and gravel areas, its seeds are capable of sprouting in dry soils almost every year. Trees of various ages have been found on elevated hummocks of bogs, occurrences which are rare. Probably the seeds germinated there during drier years when the water-level was subnormally low. Jack pine seeds apparently germinate soon after being sown in the field, for Beal (1888: 74–78) found that they sprout in 4 or 5 days after being planted in warm moist sand.

In xeroid habitats, the rate at which jack pine seedlings grow depends upon the amount of light. In the open, the average vertical growth during the first season is about 8 centimeters, a rate which is increased as the tree grows older, the maximum being attained about the tenth year. In shade where the light values range from 6 to 20 per cent, the first season's growth of the seedlings averages about 3.5 centimeters (Fig. 10). After that, the average annual growth diminishes until they perish, the average age attained in this diminished light being about 6 years. Apparently, the first year's growth of the shaded seedlings depends largely upon the food stored in the endosperm. Light is, therefore, the paramount factor for the full ecesis of jack pine on dry soils.

The edaphic conditions of such soils as coarse sand, gravel, or rock thinly veneered with humus do not permit a luxurious growth of herbs and shrubs. Hence, on such areas jack pine finds an easy entrance, because it is never in much competition with herbs, shrubs, or other shade-producing

species which require a holard greater than 2 or 3 per cent, a minimum which appears to exclude *Populus tremuloides*. *P. grandidentata* appears scatteringly with jack pine or may form small groves in the more favorable places. *Betula alba* var. *papyrifera* is often a codominant, for it can ecize in similar conditions with fair success and when burned, sprouts arising from its stumps form small groups of trees where individuals were badly injured. *Quercus coccinea*, surviving burns and other injuries in the same manner, is often a subordinate of this subclimax. In shaded soil, *Q. coc-*

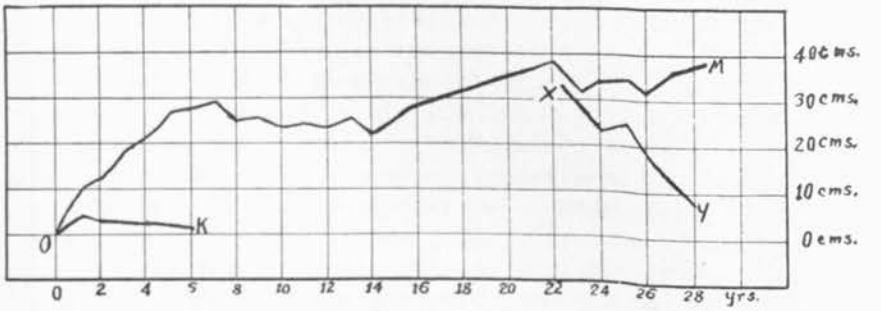


FIG. 10. Curves showing mean annual vertical growth for jack pine at the ages indicated horizontally. OK, growth of seedlings in shade. OM, growth of seedlings and trees in the open. XY, yearly rate of growth of trees in the shade of red pine.

cinea never forms a large tree because its main stems and branches die at the tips after a few years growth and consequently its trees are low, bushy and irregularly formed. In such habitats *Betula* and *Quercus* will not produce enough shade to prevent the ecesis of jack pine.

The jack pine associes usually appears with or after an abbreviated herb or shrub stage, though individual trees may mature on bare sand or gravel, as on the banks of young ravines or lake shores, which areas it will also populate just as fast as soil conditions become more uniform. In heterogeneous areas, it frequently happens that the subsere develops more rapidly in spots that produce a diversified vegetation in which appear clumps of vigorous *Ceanothus* or *Corylus* bushes; among these, jack pine may ultimately grow tall enough to subdue them by its shade. It not only can invade a thin stand of herbs, a poorly sodded prairie, a struggling meadow of bluegrass or bald barrens, but can also displace consocies of *Rhus, Rubus, Corylus* and *Ceanothus*, if its seedlings arise before the shrubs form thickets.

If, under favorable circumstances, jack pine forms a thick stand (Fig. 11), a severe competition ensues. All the smaller trees and most of the lateral branches of the larger individuals die because of the shade which gradually relegates the photosynthetic area to the tops of those surviving. The tops seldom branch, and hence the main food-making area of a single tree is small. If the tops are in any way injured, the trees die from star-

vation that season or soon afterwards. Often trees standing close to each other are mechanically injured by rubbing against each other during a storm. Such friction, if it breaks the bark of even the internodes below the terminal bud, either dwarfs or kills the growing apex. A tree having had its terminal bud killed endeavors to resume upward growth through several

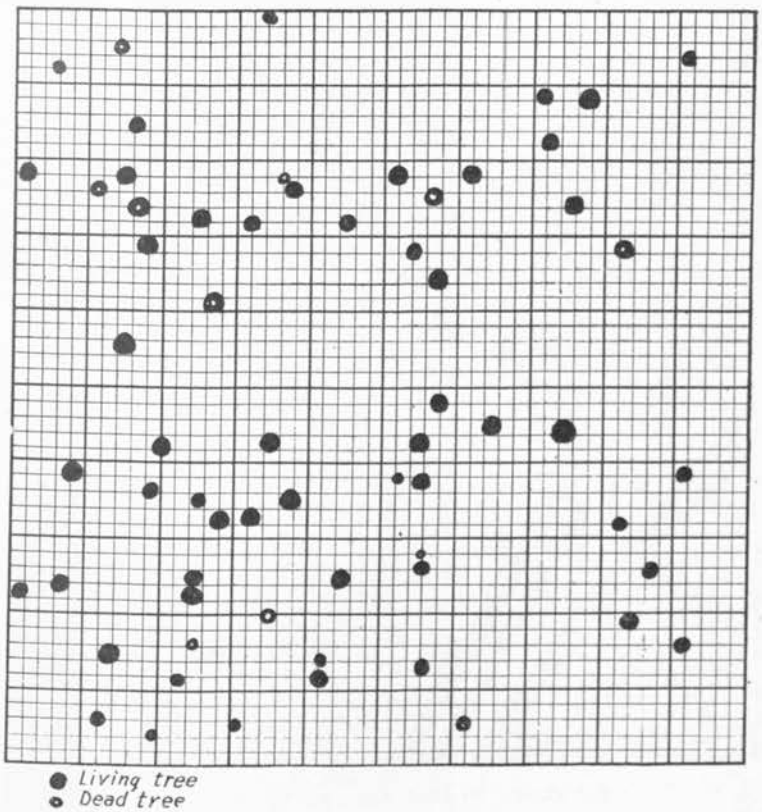


FIG. 11. A ten-meter quadrat of jack pine trees ranging in age from 15 to 20 years. Of the 64 trees included, 12 have already died, a loss of 18.69 per cent.

competitive adventitious branches, one of which by outgrowing the others becomes the main leader, but meanwhile the tree has lost a year's growth and can never attain sufficient height again to be a successful competitor with the uninjured. By the time crowded jack pine trees have attained the age of 25 years, the competition has been lessened, and each surviving tree has acquired in the struggle an allotment of space sufficient for its adult needs until the invading representatives of *Pinus resinosa* (Fig. 12) begin displacing them.

The reaction upon the habitat by the plants of this associes, as disclosed

by light values, water-content of the soil and the percentage of organic materials, is as follows. The thickest stands of jack pine in mature stages cast a shade, the light value of which at the forest floor is seldom less than 8 per cent and never higher than 30, the average being about 16 per cent, an amount insufficient to support the invasion of *Populus* and *Betula*. The

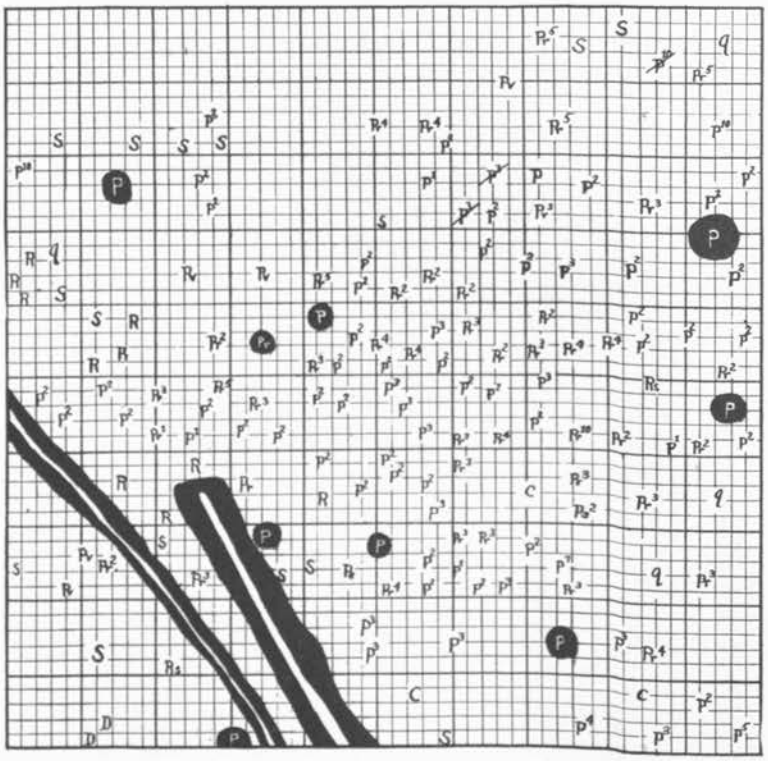


FIG. 12. Ten-meter quadrat of jack pine showing the invasion of red and white pine. Benedict, Minnesota. Exponents indicate approximate age of the seedlings. Logs indicated are of red pine. Oblique line drawn through letter indicates that the tree or seedling is dead.

LEGEND:

C. *Corylus americana,*
D. *Diervilla lonicera,*
P. *Pinus banksiana,*
Pr. *Pinus resinosa,*
Ps. *Pinus strobus,*
Pv. *Prunus virginiana,*
q. *Quercus coccinea,*
R. *Rosa blanda,*
Rs. *Rubus strigosus,*
S. *Salix* sp.

fate of the jack pine seedling in this shade is graphically represented in figure 10. The reaction on the water-content is illustrated in the curves of figures 13 and 14.

The curve (Fig. 13) representing the first decimeter's holard in a bare

sand area shows how abruptly the water-content rises after a small rain and how rapidly it drops to the minimum after a few days of fair weather, reaching the lowest percentage of all the curves. In the prairie the rise and fall of the curve is almost as abrupt, but the maximum and minimum holards are greater than those of the bare soil. The reaction of the *Pinus-Betula*

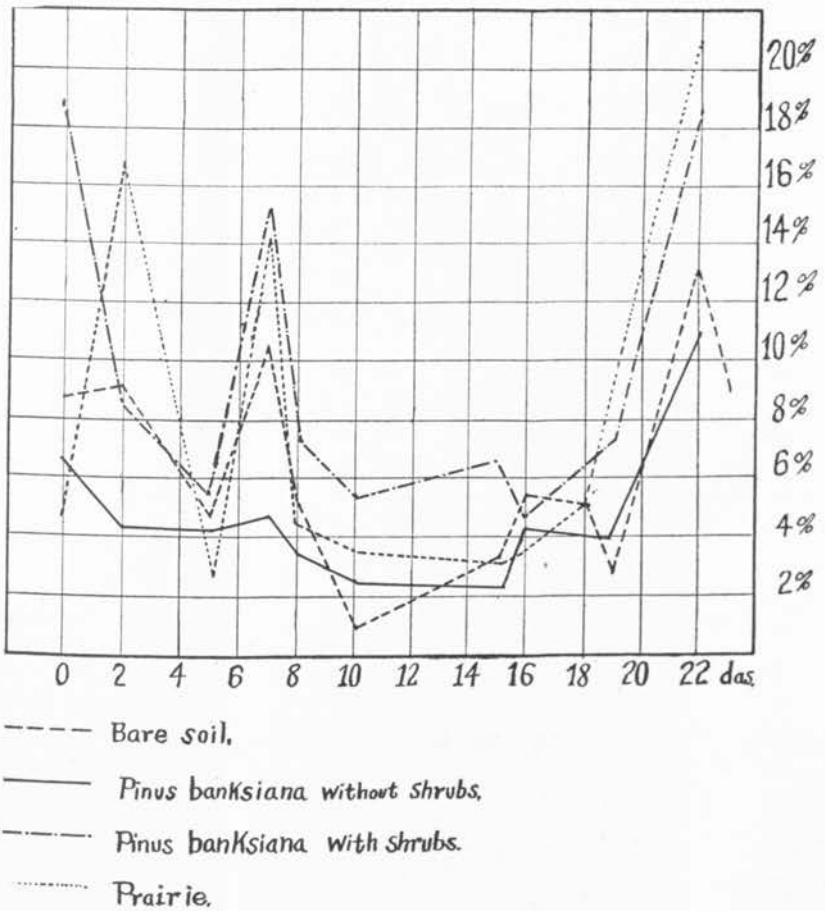


FIG. 13. Curves showing range of soil moisture to a depth of one decimeter in bare soil, in prairie and in a forest of jack pine near Hubert, Minnesota, for the summer of 1916 between July 18 and August 13.

associes is represented by two curves, one showing the added reaction of the shrubs and herbs, the other the reaction of the trees alone. The floor vegetation increases the holard and, although the range in variations is rather wide, extreme low percentages are seldom reached where these small plants grow. In their absence the forest floor is bare or covered with only a small amount of duff, hence the water-content is less though rather uniform, at least not subject to as radical changes as that of prairie or bare areas.

The water-content of the second decimeter (Fig. 14) of the bare soil is higher than that of the prairie or jack pine, which may be accounted for by the fact that the first decimeter of loose soil, acting in dry periods as a mulch, permits the rain-water to penetrate easily and rapidly. Furthermore, only a small amount of water is extracted by the few scattered weeds and dwarf plants. The lowest curve of figure 14 is that of the prairie. Its grasses have surface roots which, no doubt, absorb considerable water before it penetrates into the second decimeter. The holard of the second

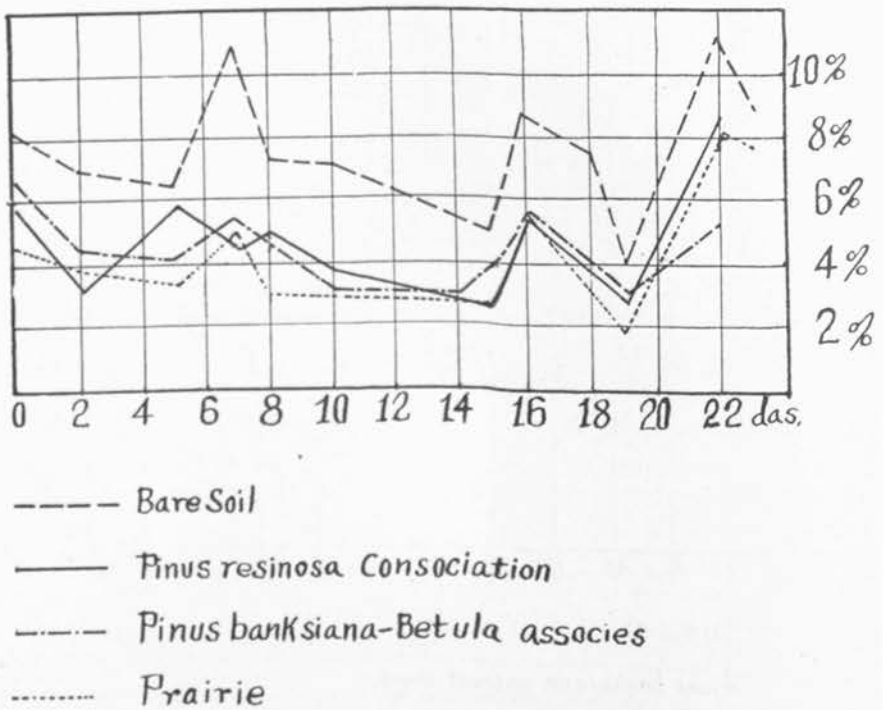


FIG. 14. Curves showing range of water-content of the second decimeter in bare soil, in prairie and in the jack pine consocies at Hubert, Minnesota, for the summer of 1916 between July 18 and August 13.

decimeter in jack pine is represented by a single line because it was found that, although the small shrubs and herbs do increase appreciably the soil moisture for the first decimenter, they have only a slight effect on the holard of the second decimeter.

The dominants of this associes draw the bulk of the water directly from the second decimeter, but the seedlings of the incoming trees receive their moisture from the surface decimeter. From a study of the above curves, it may be inferred that seeds of red pine can germinate more easily and its seedlings grow with less hazard under jack pine than in the open, especially

in case of sand barrens. Conzet (1913) concludes that, whenever the rainfall amounts to four inches or more during the months of May, June and July seedlings of red pine may become fully established. In figure 15 are curves which show the total amount of rainfall in inches for these three months at five representative weather stations for the years from 1906 to 1916 (inclusive). In only one year, 1910, was this portion of the year's rainfall less than four inches. This tends to substantiate the claim that red pine can grow wherever jack pine produces a forest, since the period of germination is a most critical one but favorable most years because of sufficient rainfall. The jack pine forest may even be regarded as a natural nurse crop for the red pine.

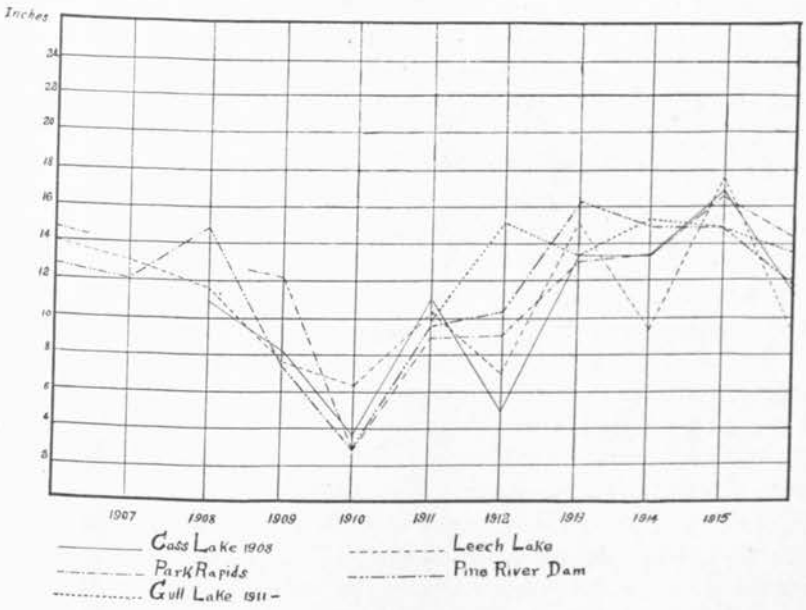


FIG. 15. Curves showing amount of rainfall during May, June and July for 11 years.

The organic content of the first decimeter of the soil covered by jack pine, red pine and hazel is about twice that of the prairie or the bare fields. No matter whether jack pine develops after prairie or shrubs, the forest floor has an organic content of about 6.5 per cent. That of the second decimeter is affected very little by the development of the subsere.

The Climax: *Pinus resinosa,* which forms the consociation following the *Pinus-Betula* associes, is widely distributed in the coniferous area of the state, ranging somewhat less widely, perhaps, than *P. banksiana,* yet wherever the latter is found abundantly, stumps or young trees of the former are usually present. As has been pointed out before, the stand of the rather uniformly disintegrated stumps show that red pine trees existed as a forest and not as individual trees at different periods or ages.

Red pine is not a very prolific seed-bearer. Its trees usually begin to bear seeds at the age of 25 years. When parent trees are scarce, invasion is naturally slow. The tardy appearance of its seedlings is due to the slower rate of its growth. Its greater age of maturity delays the increase in numbers of seed-bearers. If planted on the ground at the same time with seeds of aspens, birch and jack pine, its seedlings and young trees would be overshadowed by the quicker growing weed-like trees.

As is well known, the seeds of red pine are adapted for wind carriage, although, to some extent, they are disseminated by squirrels and other rodents. Conzet (1913: 81) estimates that 25 mature trees, allotted evenly to an acre of ground, will establish annually 5,000 seedlings, even if only 5 per cent of the seeds germinate. In such groves, as those studied near Benedict (Pl. I, *A*), it is estimated that less than 1,000 mature climax trees occupy an acre, hence, it would seem, fewer trees than 25 per acre, if reasonably well spaced, could produce in a few decades enough seeds to replant the climax.

The ecesis of *P. resinosa* has been studied by Conzet (1913) and Hoffman (1914). The former found that the seedlings could begin and continue growth in the shade of *Populus* or *Pinus banksiana* (Pls. IX, *A, B,* and X, *A*) or in the open, though he suggested that they succeed best when protected from the sun by a nurse crop. For some time it has been asserted that *P. resinosa* succeeds either *Populus-Betula* stages (Green, 1898: 69) or *P. banksiana,* an inference drawn from general observations which the following studies in competition and comparative growth rates of seedlings and young trees rather definitely confirm.

In order to ascertain the average annual rate of growth at the different ages of trees growing in different light intensities, but on the same soil, without chopping down the trees and counting the annual rings, the following method of age determination was used. The tip of a pine tree, when examined closely, exhibits quite clearly the bud-scale scars of the last 10 years of its growth. Beginning with the present year's growth and measing backward, it is easy to determine the amount of growth for as many years as corresponding scars are visible. The more exact method of counting rings in tree stumps cut off close to the ground is too destructive to apply to trees of white and red pine. Only the fewest possible number of them were cut down to check upon the above method. In dealing with seedlings or trees younger than 16 years old, estimates based upon these scars are sufficiently accurate, but for older trees they are less valuable.

The results of such countings are plotted in the curves of figure 10, OM showing the behavior of jack pine trees in the open, the short curve OK their growth rate in the shade of their parents, and curve XY representing the decline of annual growth-rate of trees above the age of 25 years, when 50 per cent of the light is removed by trees of *P. resinosa.* The

A. Seedlings of *Pinus resinosa* on the floor of a forest consisting of *P. banksiana*, *Betula alba* var. *papyrifera* and *Populus grandidentata*. Hubert, Minnesota.

B. Older seedlings of *P. resinosa* (15 to 20 yrs. old) in a *P. banksiana* consocies. Shevlin, Minnesota.

A. Seedlings of *P. resinosa* about to emerge through a cover crop of *Betula* and *Populus*. Craig, Minnesota.

B. Fire hazards increased by brush made from cutting off the climax trees and subdominants. St. Louis County, Minnesota.

upper curve in figure 16 indicates the growth-rate of *P. resinosa* in the open; the lower curve represents that in the shade of jack pine. These results show that, although seedlings and trees of red pine grow faster in the open, yet they develop fast enough in shade to guarantee successful ecesis.

Jack pine and birch are incapable of reproducing in their own shade which is not sufficient, however, to prevent the ecesis of red pine; hence, if enough parent trees of the latter are present in a given area, the subsere will inevitably reach the climax stage. Where parents trees are few the

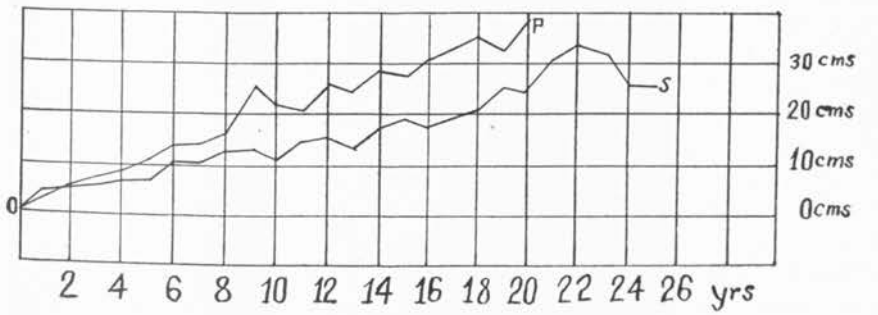


FIG. 16. Curves showing mean annual growth for red pine at the ages indicated horizontally. OP, growth of seedlings and trees in the open. OS, growth of seedlings and trees in the shade of jack pine and white birch.

progress is slower, since it requires 25 to 30 or more years for a tree in the outer edge of the initially invaded zone to start reproducing seed, and from there to make new steps of advancement into unoccupied areas. If, however, the seeds are scattered uniformly with the jack pine and birch, or shortly afterwards, a complete restoration of the consociation would be accomplished in about 75 years. The time required is indefinitely longer when destructive denuding agents act freely, so long that the recurrence of fires may keep the sere in a jack pine associes perpetually. Within the state, smaller fires have been frequent, a few have been extremely severe. The vegetation on sand or gravel plains is most subject to fires, and, because they keep the subsere in a jack pine subclimax, the casual observer might mistakenly believe that red pine can never again become a dominant in such areas. However, from a study of the vegetation about Hubert, Benedict, Shevlin and Bemidji, where the former climax has been removed by fire prior to the late period of lumbering, the writer is convinced that the red pine consociation is redeveloping in spite of small local fires.

When the mature trees of red pine form a thick stand, the light value ranges from 5 to 10 per cent; rarely is it reduced to 1 per cent. This shade is much greater than that cast by mature jack pine. In well-developed red pine consociations the shade is always dense enough to stunt most of the shrubs appearing conspicuously in the jack pine forest. In 1 per cent or

even 5 per cent of light, the ground is sparsely covered with dwarf plants mentioned in the earlier discussion of this subsere, but in such shade a few seedlings of white and red pine may be found. *Betula, Populus* and *P. banksiana* are not found growing from seedlings in the shade of a well-matured red pine consociation. Stunted seedlings of *Picea canadensis* and *Abies balsamea* appear occasionally in damper places, but are so rare and so dwarfed that they never become dominants. There is little evidence to show that they have ever in the past been dominants on the soils of the state now or formerly occupied by red pine.

A study of the reaction data of 1916 would seem to show that the shrubs of this consociation have little effect upon the holard. Water from small showers falling during the late summer months often does not reach the forest floor. The curve of the water-content for the second decimeter is about the same as the corresponding one in jack pine (Fig. 13). From the holard and light readings, it appears that light plays the most important part in the competition between a given set of dominants in the various stages in the development of this subsere. Water-content is important in the early steps of the sere; a low holard delays the succession by inhibiting germination and the initial growth of the seedlings, but after the initial stage the elimination of competitors is due, apparently, to increased shade which kills out and prevents reproduction of plants which cannot develop shade tolerance.

The following reasons may, then, be assigned to explain the stability of the *Pinus resinosa* consociation in dry soils: (1) Its seedlings can persist and mature in deeper shade than seedlings of other trees of the subsere. (2) Its trees live longer than those of any other species participating in this succession. (3) The height attained is greater than that of jack pine, birch, or aspen, and consequently, it subjects all of its competitors to a shade which eliminates them. The development of the red pine consociation marks the maturity of this subsere under the present conditions of climate and soil, since no other trees in the state except white pine can ecize in its shade.

Summary of Exceptions: The following exceptions to this general development may occur, some of which are abbreviations, others are prolongations of the subsere. In small areas of the climax a disturbance, such as those from windfalls or from the death of a few trees killed by lightning or any other local agent, does not initiate the early stages of a subsere. Very often, in such cases, the red pine seedlings are so abundant that they spring up soon enough to prevent the ecesis of aspen, birch and jack pine. If the area is larger, seedlings of the last three are apt to appear sparsely among the young trees of the red pine. On drier soils periodic denudation by fire always introduces jack pine. Annual fires tend to develop prairie. If burning is prevented, the prairie is invaded by jack pine directly or jointly with sumac.

THE *PINUS STROBUS* CONSOCIATION

(2) *Subseres on Wet Clay and Loam Soils*

In contrast to the xeroid sands and gravels, denudation on clay and wet loams may sometimes afford rather hydrophytic conditions. The climax of this subsere is the *Pinus strobus* consociation, which is described on page 480. The usual causes initiating this succession are fires, lumbering, wind, flooding and cultivation. Fires are less frequent on wet soils, but in dry seasons they may cause considerable destruction of white pine, as is well known. The degree of denudation is never as great as that in sand, for much more organic material accumulates on wet soil, so that the fire in one sweep can never destroy the vegetable deposits to the same degree as on dry sands. Since the fires are also less frequent as well as less intensive, the complete removal of the organic deposits is rare. However, fires that are used to remove the brush after cuttings are more destructive to the organic soil where there is an abundance of brush from the slashings of dominants and undershrubs (Pl. X, *B*). Where a brush-pile has been consumed, charcoal remains constitute the chief organic deposits left. Cultivation in most of the wetter areas of northern Minnesota has not been pursued as long as in the drier or more mesophytic soils of the state, but enough fields, once cultivated, have been abandoned to furnish suitable places for studying the subseres started by this thorough type of denudation.

The Herb Associes: In the climax forest, fern societies are often found, those appearing on wet soils consisting of *Onoclea sensibilis, Osmunda claytoniana* and *O. cinnamomea.* Where conditions are more xerophytic, *Pteris aquilina* appears singly or in societies. *Aster macrophyllus* and *Aralia nudicaulis* are often the main subdominants for rather larger areas. In many places small societies of *Cornus canadensis, Fragaria americana* and *Rubus triflorus* occur. *Asarum canadense, Clintonia borealis, Mianthemum canadense, Pyrola americana, Petasites palmatus* and *Trientalis americana* usually appear in clans where the water-content is high. *Clintonia, Asarum, Maianthemum* and *Trientalis* often occupy mounds of organic soil. Clans of *Linnaea borealis* and *Mitella nuda* are found in similar localities and are frequently established on moss-covered logs. The following plants are sparsely scattered through the subdominants of the climax: *Actaea rubra, Aralia racemosa, Caulophyllum thalictroides, Coptis trifolia, Galium triflorum, Habenaria bracteata, Monotropa uniflora, Panax quinquefolium, Trillium erectum* and *T. grandiflorum.*

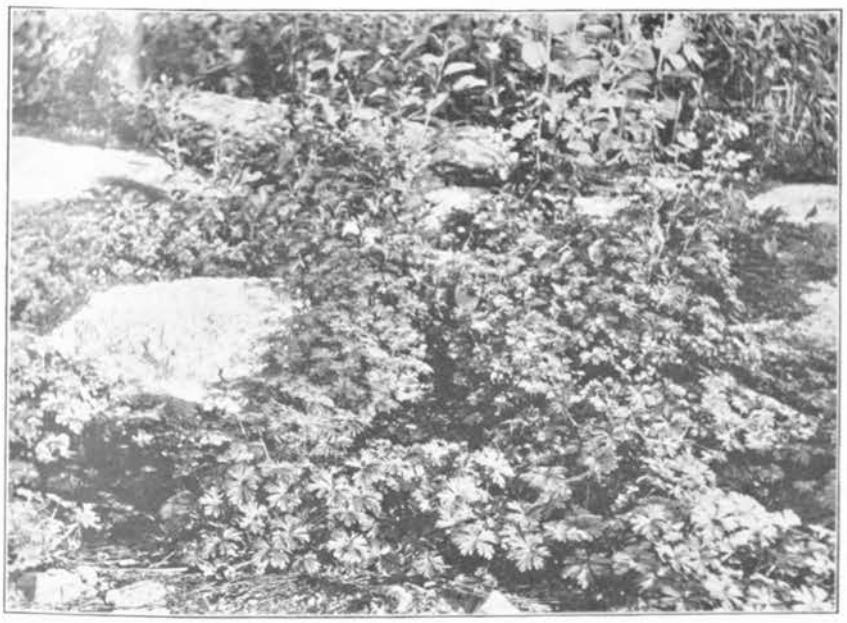
When fires have left a considerable amount of charcoal in wet lands, the first plant to appear is *Marchantia,* which often occupies areas amounting to one or more square miles. In small deeply burned areas where the surface of the soil is drier, the first invader of charred areas is *Geranium bicknelli* (Pl. XI, *A*), which forms characteristic families. In the wetter areas or on heavy clays, colonies are formed by *Mentha canadensis* and *M.*

piperita, the latter becoming more predominant and extensive. *Impatiens* socies often embrace colonies of *Mentha*. *Corydalis sempervirens*, a secondary species of clearings, is associated also with *Impatiens biflora*. Consocies are formed by *Aster paniculatus, A. azureus, Senecio palustris* and *Solidago canadensis* in areas that have been cleared and partly cultivated. The secondary species of these consocies are *Aster novae-angliae* and *Ranunculus abortivus*. *Calamagrostis canadensis* and *C. hyperborea* come in almost simultaneously with the other species. *Agrostis hiemalis* is often dominant in wet soils for a short period, as it is on drier soils. Species of *Carex* also invade wet regions rather early. If burnings occur, these grasses persist, developing a wet meadow, the *Calamagrostis* associes, which consist largely of the two above mentioned species.

Some of the pioneers in clearings are: *Chenopodium album, Echinochloa crus-galli, Corydalis sempervirens, Trifolium hybridum, Lathyrus palustris, L. venosus, Vicia americana, Brassica nigra, Setaria glauca, Poa pratensis, Prunella vulgaris, Plantago major, Solidago canadensis* and *Erigeron canadensis*. *Prunella* and *Plantago* usually appear in families. A grass stage consisting of *Calamagrostis* and associated plants either develops partly or completely after the weeds and, as usual, fires hasten its development into a meadow.

When the whole forest is removed by cutting alone, the herb associes during the first few years consists for the most part of an *Aster* associes or a mictium of *Fragaria, Rubus, Impatiens, Solidago* and *Lathyrus*, with socies here and there of *Onoclea, Osmunda* and *Pteris*. The herbs and shrubs, usually dwarfed or absent in the densest shade of the climax, become vigorous in any lighter places where some accident has removed a tree or two, or perhaps several branches of neighboring trees. It is by such chances that they are retained in amounts sufficient to reproduce and repopulate the bared areas promptly.

In fully developed herb associes of moist soils, the height of the asters and golden rods is often 4 or 5 feet, though normally they are seldom more than 2 or 3 feet high. The amount of light excluded is rarely more than 50 per cent. The reaction on water-content is various, depending on the amount present at the beginning. Wet loams with organic matter have a holard which varies from 15 to 35 per cent. The holard of clays ranges from 20 to 60 per cent during the growing season. Where such water-contents exist, organic debris accumulates rapidly from the annual crop of the herbs which, by retaining the water, often increases the holard of the first decimeter to 80 or 90 per cent. The second decimeter is never raised more than 10 or 15 per cent by the deposition on the surface of such amounts of organic material. When a well-sodded grass stage is developed, the amount of organic material and humus often gives the first decimeter of soil a holard of 100 to 300 per cent.



A. Family of *Geranium bicknelli* growing where a brush pile had been burned. International Falls, Minnesota.

B. The taller subdominant shrubs of the white pine associes which have increased in size and numbers in an open space. Craig, Minnesota.

A. Photograph of *Salix discolor* consocies with seedlings of *Abies* and *Picea canadensis* in the open. Meadowlands, Minnesota.

B. Photograph of the *Alnus-Salix* associes. Large tree of *Larix* in the right border of the picture. Meadowlands, Minnesota.

The Shrub Associes: The most important tall shrubs of the climax on clay or wet loams are: *Acer spicatum, Alnus incana, Amelanchier oblongifolia, A. spicata, Corylus americana, C. rostrata, Prunus virginiana* and *Rhamnus alnifolia* (Pl. XI, *B*). The lower shrubs are: *Cornus stolonifera, Diervilla lonicera, Ribes prostratum, Rosa blanda* and *Rubus strigosus.*

On wet soils the shrub stage of the subsere follows the herbaceous rather promptly and consists of *Alnus incana, Cornus stolonifera, Acer spicatum, Corylus rostrata, C. americana, Spirea tomentosa* and *Salix discolor* (Pl. XII, *A, B*). In the wetter soils *Alnus* and *Salix* completely replace *Corylus,* which rarely forms consocies in very damp habitats. *Rubus* is nearly always present but never as a pure dominant, except on higher and better drained knolls. *Cornus,* rather uniformly distributed through this associes, forms the largest clusters in the wettest places near streams or beside small sinks that are filled with water most of the summer. *Diervilla* is eliminated where the holard is high, and is sparse in places where the average water-content of the second decimeter is above 20 per cent. *Acer spicatum,* though appearing on rather mesophytic areas, forms the most luxuriant socies in such soil habitats as clay and wet loam soils (Pl. XI, *B*).

Of all these dominants, *Salix* has the most mobile seeds, which are produced in great abundance and disseminated readily by wind, often in such quantities that they whiten the bare soil. In the wetter areas its seeds find their best opportunities for germinating. The seeds of *Alnus,* perhaps next in rank in migratory ability, are sown by the wind, although not so generally and so readily as those of *Salix.* Apparently its ecesic ability is greater in marshes than that of *Salix,* since it more often forms dense stands with hardly a willow shoot present. It also endures shade better than *Salix,* persisting in the floor of forest vegetation in hardier forms and thus springs more quickly into prominence after the timber has been removed or killed. *Acer* produces seeds much less abundantly than *Alnus* or *Salix* and its seeds are much less mobile. It seems that large amounts of soil water and shade decrease the root aeration and vitality of *Corylus* and *Rubus* so that they are incapable of growing and propagating well in the very moist soils; the latter, under such conditions is often slender and drooping.

Experimental determination of the germinative requirements of the seeds of these dominants has never been made, but since their adult plants and seedlings appear on moist soils, it has been assumed that these conditions are optimum. From field observations it appears that all of them require an open area for ecesis. In the mutual struggle for these dominants, *Alnus, Acer* and *Salix* (Fig. 17) replace most of the other species as a result of their greater height, since the light intensity beneath them is often as low as five per cent.

Socies of *Impatiens, Dryopteris cristata, Rubus triflorus* and *Calamagrostis* occur in the lighter portions of the shade or between willow and alder

bushes. Families of *Caltha palustris* occur in depressions, ditches and along the banks of streams. A great variety of secondary species appear in this associes; some are relicts of the herbaceous associes, others are characteristic plants of the succeeding associes. The most common secondary species are the following: *Aralia nudicaulis, Aster macrophyllus, Campanula aparinoides, Carex diandra, Circaea alpina, Clintonia borealis, Coptis trifolia, Cornus canadensis, Equisetum fluviatile, Galium triflorum, Maianthemum canadense, Trientalis americana, Trillium cernuum* and *T. grandiflorum.*

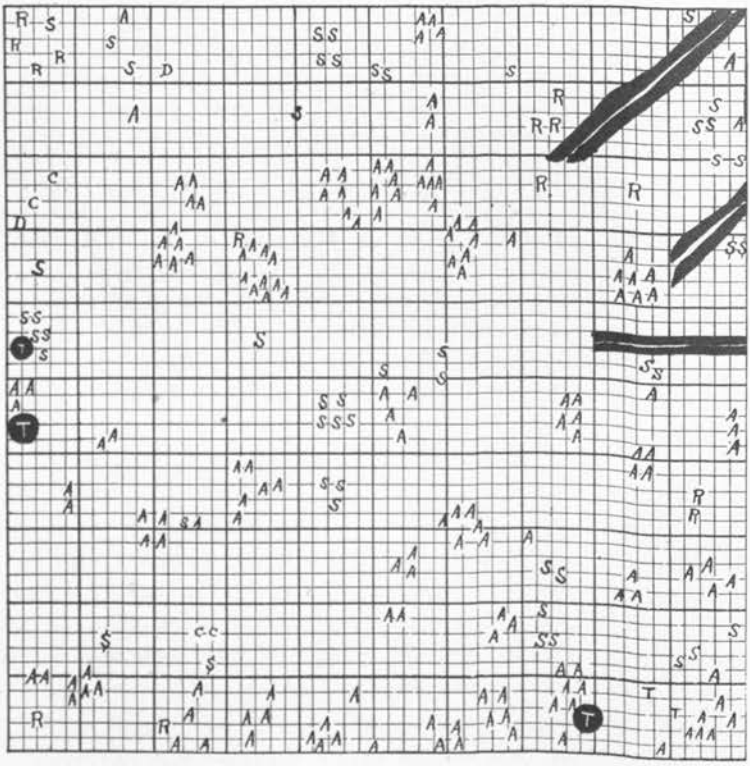


FIG. 17. Ten-meter quadrat of the *Alnus-Salix* associes shown by photograph in plate XII, *B*.

LEGEND: Oblong figures indicate decayed logs of white pine.

A. *Alnus incana,*
C. *Ribes triste,*
R. *Rubus strigosus,*
S. *Salix discolor,*
T. *Larix laricina.*

During the development of this associes 3 or 4 inches of organic debris are added which increases the water-content greatly, making the habitat appear more hydrophytic. However, the available water seems to be increased and the ratio between the organic portion and the holard is not much greater, if any, than that of mesophytic soils.

A. *Thuja, Picea* and *Abies* bordering the shore of Dora Lake, Itasca County, Minnesota. Trees of *Betula* and *Fraxinus* dying.

B. Photograph of mature *Larix* consocies. Meadowlands, Minnesota.

A. Thuja swamp near Meadowlands, Minnesota. See figure 18 for contents.

B. Asarum as it appears in deep shade. Meadowlands, Minnesota.

A. Vegetation growing in *Thuja* swamp quadrated in figure 18, consisting of *Clintonia, Aralia, Rubus, Trientalis, Petasites* and *Ledum.*

B. Herbaceous vegetation under *Larix-Populus* associes consisting chiefly of *Fragaria, Rubus* and *Maianthemum.*

A. Photograph of quadrat taken near that of plate XV, *B.* Small tree of *Abies* included. Herb dominants are *Cornus, Rubus* and *Fragaria.*

B. Larix-Populus associes on wet clay soil near Meadowlands, Minnesota.

The light values range from 5 to 15 per cent, but in older stands dead shoots and individuals killed by competition increase considerably the light penetration, often to 25 or 30 per cent. This is sufficient to permit the entrance of *Larix, Picea, Thuja, Pinus strobus* and *Abies,* if a sufficient number of mature trees survive the denudation to reseed the area occupied by these shrubs. The slowly developing conifers, even when sown before the shrubs develop, are not conspicuous in the subsere for many subsequent years. Their appearance is delayed indefinitely when seed-bearing trees are scarce and the shade deep.

The Subclimax: The dominants of the subclimax associes are *Abies balsamea, Thuja occidentalis, Picea canadensis, Picea mariana* and *Larix laricina* (Pl. XIII, *A*), the last two occupying soils having a higher water-content than those chosen by the other conifers of the subclimax. *Larix,* however, when sown abundantly, forms pure stands on wet clay soils, as along the St. Louis River and the White Face River in St. Louis County (Pl. XIII, *B*), where the soil varies in composition from heavy wet clays to very moist alluvial plains. It also will occupy bogs either as a codominant of *Picea mariana* or in a pure stand. *P. canadensis* has never been found occupying extensive areas in the state. It forms small thickets, often fringed with trees of *Abies,* or its isolated trees may occur throughout the stands of *Larix* occurring on wet upland soils.

P. mariana, which is either a codominant of *Larix* in bogs, or a pure dominant in its own consocies, is sparse or wanting in morainic soils. It appears regularly on accumulated muck in undrained bogs. Thickets of *Thuja* occurring in this associes usually occupy the dampest parts (Pl. XIV, *A*), as along a sluggish stream or in sinks where organic soil has been deposited and retains much water. *Abies,* often intimately grouped with *Thuja* and *Picea canadensis,* seldom forms extensive pure stands. Communities of these conifers sometimes contain *Populus balsamifera, Fraxinus nigra, Betula papyrifera* and *Acer rubrum* (Fig. 18), all occupants of rather wet localities. In the mixed forest, *Populus* is eliminated first, because it cannot reproduce in the shade and is more susceptible to injury and disease in its maturity than conifers of the same general age. *Fraxinus* and *Acer* persist longer because their seedlings live longer in shade and their mature trees resist disease and injuries better. Apparently, *Fraxinus* outlives *Acer* in such habitats.

Societies of *Asarum canadense* (Pl. XIV, *B*), *Clintonia borealis* (Pl. XV, *A*), *Aralia nudicaulis, Cornus canadensis, Petasites palmata, Trientalis americana, Rubus americanus* (Pl. XV, *B*), *Fragaria virginiana, Maianthemum canadense* and *Aster cordifolius* appear under upland communities of *Larix, Thuja, Abies* and *Betula.* Under the *Larix* consocies, *Asarum canadense, Rubus americana, Cornus canadensis, Fragaria virginiana* and *Anemone quinquefolia* form societies (Pls. XV, *B,* XVI, *A*). *Trientalis* is

rather abundant, forming a characteristic spring society during its flowering period. *Caltha palustris, Petasites palmata, Senecio palustris* and *Nabulus albus* are the most prominent large secondary herbs.

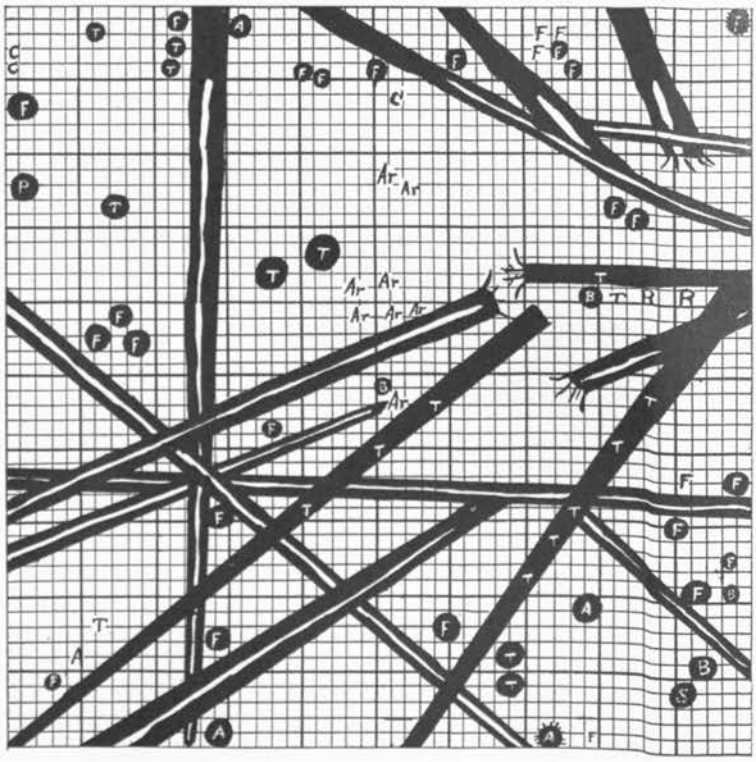
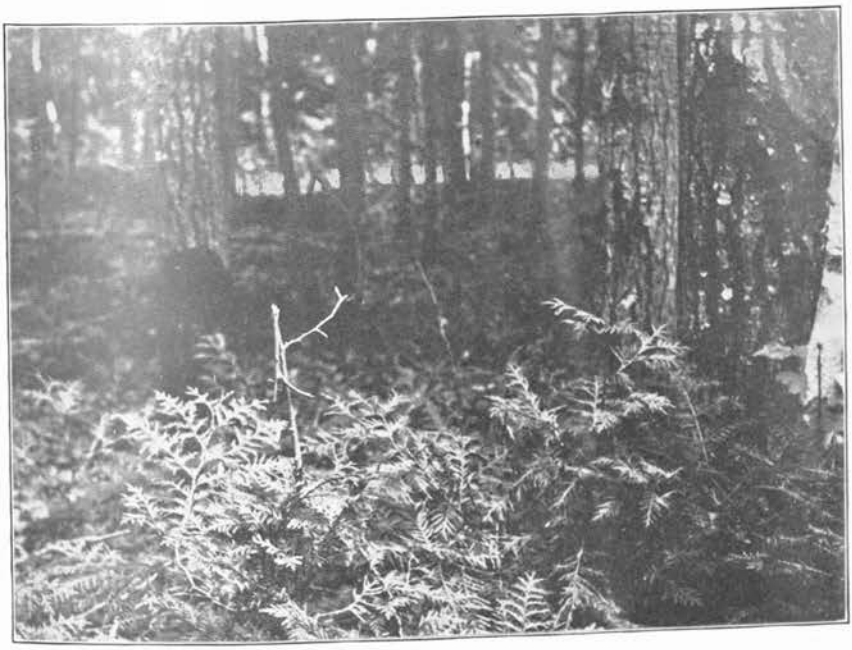


FIG. 18. Quadrat of *Thuja* swamp photographed in plate XIV *A*.
LEGEND:

A. *Abies balsamea,*
Ar. *Acer rubrum,*
C. *Cornus stolonifera,*
B. *Betula papyrifera,*
F. *Fraxinus nigra,*
P. *Picea canadensis,*
R. *Rubus triste,*
S. *Salix discolor,*
T. *Thuja occidentalis.*

Figures with white centers indicate fallen dead trees; solid figures indicate fallen but living trees.

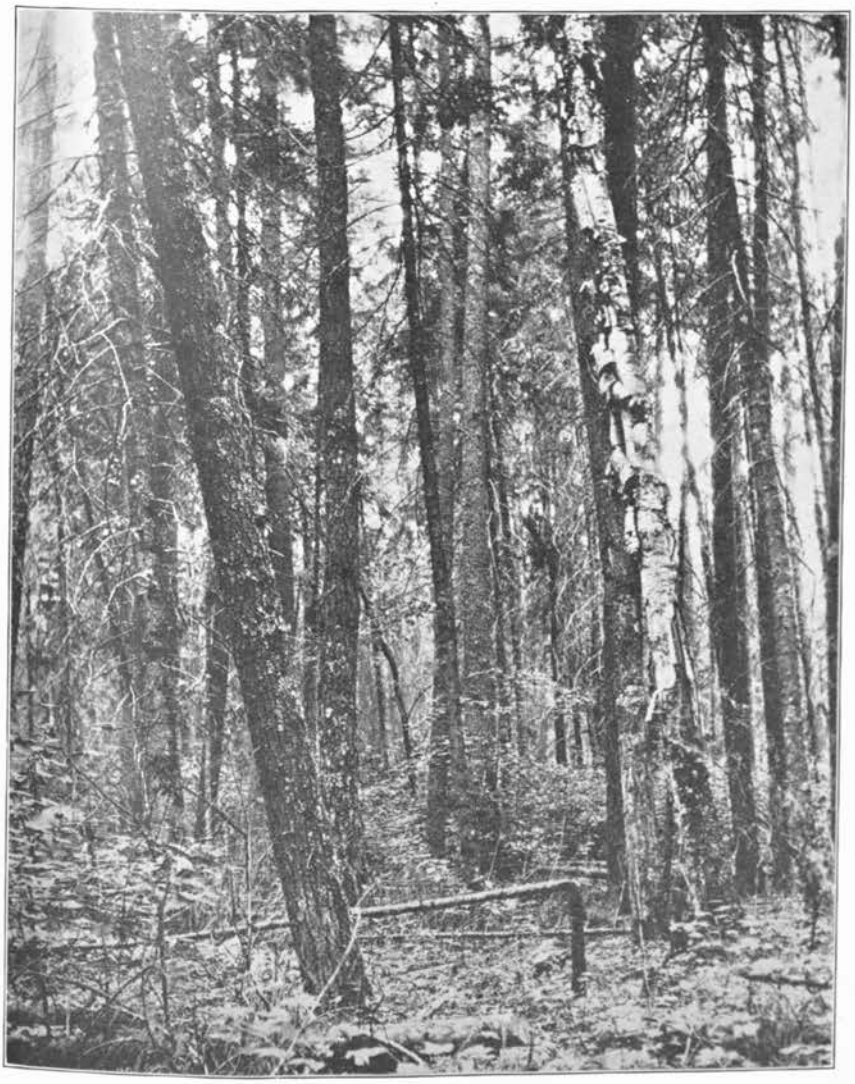
Larix bears seeds at an earlier age than the other dominants, and they are not so readily destroyed by squirrels. It is not unusual to see a few squirrels devour the bulk of the seed crop of *Abies* and *Picea* even before the cones are matured. Seeds of *Larix* can germinate on rather drier soils, for occasional mature trees are sometimes found on sand outwash plains and in the same habitat a considerable number of seedlings make a start, though they rarely attain the age of 15 years.



A. Young trees of *Thuja* in the shade of the *Larix-Populus* associes.

B. Photograph of edge of pine tract near Craig, Minnesota.

Mature consocies of *Thuja* in which occur occasional trees of *Pinus strobus*. Craig, Minnesota.



Photograph of quadrat in figure 20, camera facing the basal line. Dead birch and balsam trees visible in the center and to the right.

A. Quadrat in figure 20 photographed from right, showing dead balsam trees in the center.

B. Young pine association between Gull and Hubert lakes.

In shallow muck deposited on clay or alluvial soils, *Abies* and *Picea* are much less capable of layering (Cooper, 1911), a method of propagation best favored in *Sphagnum* bogs or in lichen beds where the lower branches are more easily covered by the organic deposits. In hydrophytic soils, not strictly organic, *Larix* is the principal tree pioneer and forms almost pure stands. In the less hydrophytic habitats, *Populus tremuloides* or *Betula alba* var. *papyrifera* become codominants (Pl. XVI, *B*). In their shade seedlings of *Thuja* may persist indefinitely (Pl. XVII, *A*).

In a subclimax forest, not promptly replaced by pine, the competition between the dominants on mineral soils is more severe than in bogs, because more plants ecize there and the trees stand closer together (Pl. XVII, *B*). In those hydrophytic habitats having *Larix* as a codominant of *Betula* and *Populus*, the latter is eliminated first, but trees of *Betula* remain longer, grow taller and are the last deciduous trees to disappear from the coniferous forest. *Abies* and *Picea*, since they are nondeciduous, and live longer, also cast a greater shade than *Larix*, can replace it. In suitable habitats, *Pinus strobus* may replace tamarack before balsam and spruce can become established. When white pine does not invade, the mature associes consists of *Abies*, *Betula* and *Picea*, listed in the order of their numerical importance. *Fraxinus*, *Thuja*, *Populus balsamifera* and *Acer rubrum* are present in this stage, all four occupying wet places, although occasional trees of each may be found scattered among the birches, balsams, spruces and aspens (Pls. XIII, *A*, XIV, *A*).

When the subclimax consists principally of *Abies*, *Betula* and *Picea*, the invasion of pine is slow, even when there are enough mature seed-bearing trees in the vicinity. However, it is not unusual to find in such an associes occasional pine trees, probable relicts of a former climax (Pl. XVIII), standing with their tops elevated 10 to 20 feet above the trees of the subclimax. Since *Abies* is incapable of reproducing in its own shade, and since whole thickets of it, young trees as well as the mature, die for reasons unknown, pine seedlings finally have opportunities for starting, some eventually maturing. Smaller spaces, caused by the death of birch or spruce, having a light value of 5 or 10 per cent, afford other opportunities for the local ecesis of white pine seedlings.

The curves in figure 19 show that white pine trees on mesophytic soils grow in height almost as rapidly in light values of 10 to 30 per cent as in the open. The optimum conditions for the germination of white pine seeds are not known, but field observations tend to show that they are tolerant of a higher holard than seeds of red pine. In the various light conditions, white pine seedlings grow faster than those of balsam and spruce.

As the white pine consociation develops in number, age and height, birch, balsam and spruce vanish, as may be witnessed in a rather mature stand of white pine (Pls. XIX, XX, *A*) located on the banks of the Big Fork River.

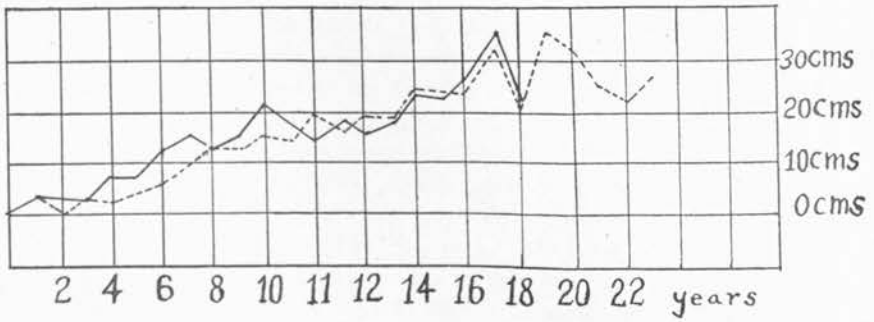


FIG. 19. Curves showing annual growth rate of white pine. Solid line indicates rate in open. Dotted line, the rate in shade.

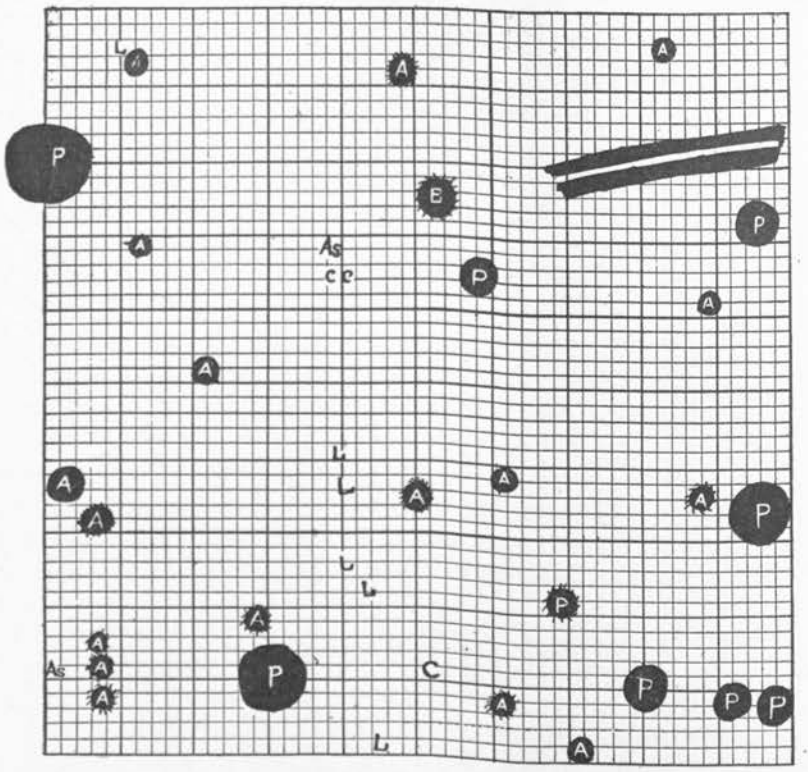


FIG. 20. Ten-meter quadrat in the Big Fork white pine tract. Made by H. F. Bergman.

LEGEND:

A. *Abies balsamea,*
As. *Acer spicatum,*
B. *Betula papyrifera,*
C. *Corylus rostrata,*
L. *Lonicera oblongifolia,*
P. *Pinus strobus.*

Rayed projections extending from figures designate dead individuals.

Here, the tops of most of the birch trees are already dead; some trunks still standing have only a few living sprouts. Bark fragments, found at the foot of the pine trees, show that relatively larger number of birch trees once grew here. Dead trees of *Abies* and *Picea* may be found either standing or lying on the ground. There are no visible remains of *Fraxinus* or of *Populus*. The quadrat (Fig. 20) taken in the Big Fork tract shows in detail the structure of this stage of the pine consociation. The tract studied near Craig (Pl. I, *B*) is surrounded by a zone of spruce and balsam (Pl. XVII, *B*), and it is reasonable to suppose that the seedlings of pine will ultimately replace the spruce and balsam as they undoubtedly have in the Big Fork tract.

In the pine consociation, where large amounts of humus have accumulated, the water-content of the soils is high, reaching at times in the organic portion 300 to 500 per cent, and yet, except in very wet seasons or after a drenching rain, this organic material is not mucky when so overcharged. The light values of the pine consociation are low, varying from 5 to 8 per cent, an amount too little to support the seedlings of any of the dominants. In the deepest shade, even seedlings of white pine are absent, but where the value is above 5 per cent, a few seedlings may be present.

The climax, when reached, is maintained because of the usual stabilizing factors, namely, the greater age, the larger life-form and the greater reproductive and ecesic powers of the pine trees.

(3) *Subseres on Drained Clays and Loams*

The Climax: On the mesophytic soils, composed of silt, well-drained clay, or loam, the climax is a more or less mixed stand of red and white pine (Pl. XX, *B*). The herbs and shrubs found underneath the climax trees are of the more mesophytic types. *Corylus, Rosa, Rubus, Diervilla* and *Acer spicatum* are the usual shrubs. *Cornus, Alnus* and *Salix,* representing the more hydrophytic types, and *Ceanothus,* the chief shrub indicator of dry soils, are wanting on these soils. On the other hand, minor shrubs, such as *Vaccinium, Arctostaphylos* and *Chiogenes,* found on sand barrens and representing more xerophytic types, are seldom present in the mixed pine forest. The following include the majority of herbs of this association. Those appearing in societies are: *Anemone quinquefolia, Aster laevis, A. cordifolius, A. macrophyllus, Falcata comosa, Fragaria virginiana, Geranium maculatum, Maianthemum canadense* and *Pteris aquilina.* Those appearing as important secondary species in the herbaceous mictium are: *Actea rubra, Aralia nudicaulis, A. racemosa, Carex pennsylvanica, Caulophyllum thalictroides, Lathyrus venosus, L. ochroleucus, Nabalus albus, Streptopus roseus, Smilacina racemosa, S. stellata* and *Vicia americana.*

The Herb Associes: The herbaceous stage will consist of many of the above species, provided denudation does not remove all their propagules.

Chamaenerium, Erigeron canadensis, Solidago canadensis and the asters are the usual dominants appearing after fires. *Lathyrus, Vicia* and *Pteris* are also conspicuous dominants in slightly burned areas. *Rubus triflorus* and *Fragaria* form socies here as in the subsere just described but grow more vigorously.

After cultivation, the usual weeds and grasses appearing are: *Achillea millefolium, Agropyron tenerum, A. repens, Brassica nigra, Chenopodium album, Corydalis sempervirens, Elymus canadensis, Bromus inermis, Hordeum jubatum, Lepidium apetalum, Poa pratensis, Melilotus alba, M. officinalis, Rumex crispus, Setaria viridis, Stipa spartea, Trifolium album* and *T. hybridum.* The grass stage developing after the weeds, either through grazing or on account of fires, consists largely of blue grass, white clover and quack grass.

The herbs on mesophytic soils exhibit rank growth (Pl. XXI, *A*), the decay of which adds a considerable amount of organic debris every year. The average holard of the first decimeter of a soil lacking organic deposits ranges from 8 to 15 per cent in the better grades of soils. In a few years, thick annually deposited crops of herbs raise this to an average of 25 to 45 per cent, and the second decimeter from 15 to 30 per cent, thus trebling the holard of the first decimeter and doubling that of the second.

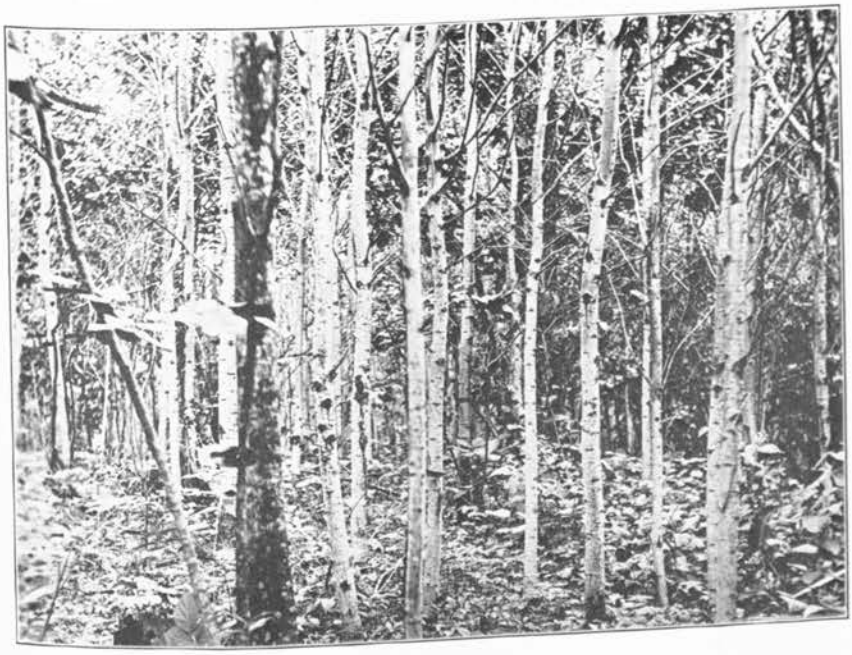
In the rankest growth of herbs, the largest reduction of light at the surface of the soil is seldom more than 50 per cent. Since the shrubs and young trees make their greatest upward growth in early spring before the herbs have attained their greatest height, they are able to rise above the densest shade of the herbs, provided they made a start before a permanent sod has been formed.

The Shrub Associes: The shrubs in the mesophytic habitats consist principally of *Corylus* and *Rubus.* Of the smaller shrubs, *Diervilla* and *Rosa* are nearly always present, even abundant in places. *Prunus virginiana, P. pennsylvanica, Amelanchier canadensis, A. spicata, Sambucus racemosa* and *S. canadensis* appear also on these soils.

The reproduction of hazel and raspberry is best in this soil habitat; the former is usually more vigorous and dominates the largest areas, while the latter forms thickets in sandy knolls or in vicinities lacking hazel. The ecesis of these shrubs has been discussed in the treatment of the first subsere which appears in a habitat that tests more rigorously the ability of plants to establish themselves. A discussion of their development here is of interest because of their effect on this particular type of soil habitat.

With the development of a shrub stage, the holard of the first decimeter of soil is increased above what it was when occupied by herbs, but the increase is not as great as that made by the litter formed by the herbs. The invasion of the shrubs affects the holard of the second decimeter of the soil very little, if a previous herb stage has deposited much organic material.

A. Weed and grass stage on an abandoned field, Bemidji, Minnesota.



B. *Populus* consocies on loam. Meadowlands, Minnesota.

However, where a *Corylus* or *Rubus* consocies appears slightly before or jointly with the herbs, their reaction increases the holard of the first decimeter to more than twice that of the bare soil. The shrubs, by preventing rapid evaporation and runoff and the consequent fluctuations of the surface moisture, favor the ecesis of white and red pine seedlings, some of which often appear in this stage. In sandy soil, as has been shown previously, the second decimeter is little affected by the accumulation of organic material, because the water percolates so rapidly through the coarse sand that no great amount can be stored for a long period, and when the surplus has passed downward the major amount is retained in the organic portion of the first decimeter. But on clay or loam, gravity does not withdraw the water so rapidly; hence, the holard of the second decimeter is increased definitely by an increase in the surface decimeter, particularly if the loam has a clay subsoil.

The light reduction by the shrubs in well-developed associes, varying according to their growth and age, often leaves values of about 10 per cent or less, which is sufficient to prevent ecesis of *Populus, Betula* and *Pinus banksiana*. However, as has been previously shown (Pl. VI, *B*), birch and popple often are established before the shrubs form a dense covering, and, by growing rapidly in height, they rise above the tops of the shrubs and form the typical *Populus-Betula* associes. In the dry loams the subclimax may consist of *Betula* and *Pinus banksiana.*

The *Populus-Betula* Associes: The *Populus-Betula* associes, typical of mesophytic conditions, usually follows shrubs on land areas where the holard of the first decimeter averages more than 10 per cent. Thus it occupies ravines, lake edges, swamp margins or favorable slopes of valleys in sandy loams, well-drained clay or black loams. The *Populus* consocies is represented in the photograph reproduced in plate XXI, *B*.

The seeds of these dominants are scattered annually by wind; those of *Betula* are less mobile but are sown during the winter and germinate in the spring as soon as conditions are favorable; those of *Populus* are produced in the spring and are scattered early in June. The migratory device of popple seeds make them very mobile, but their period of viability is apparently short; consequently, it seems, *Populus* is less successful on xeroid soils than *Betula* for no other known reason.

P. grandidentata and *P. tremuloides* propagate rapidly by shoots which spring from long horizontal roots, 1 to 5 inches beneath the surface. A 7 or 8-year-old tree often may have produced 10 or more separate shoots which appear as individual trees grown from seeds. A number of these may be killed, at least the above-ground portions, by rabbits or fire, yet sprouts will arise again from the underground system. Trees of either species, even at the age of 15 or 20 years, when killed by fires will produce sprouts in the same manner and reproduce the stage directly, but naturally,

several or repeated burnings will finally kill the underground propagules by starvation. The pioneer plants in a bare area are established from seeds (Pl. XXII, *A*, and Fig. 21), but the rapid multiplication which intensifies the stand results from root propagation. *P. grandidentata* seems more capable of ecizing on drier soils, and consequently it is found scattered with jack pines (Pl. IX, *A*) when *P. tremuloides* is entirely absent. Sprouts of *Betula* arising from stumps do not stand far enough from the parents to migrate much, hence the clustered appearance of birch trees in areas which have been fired.

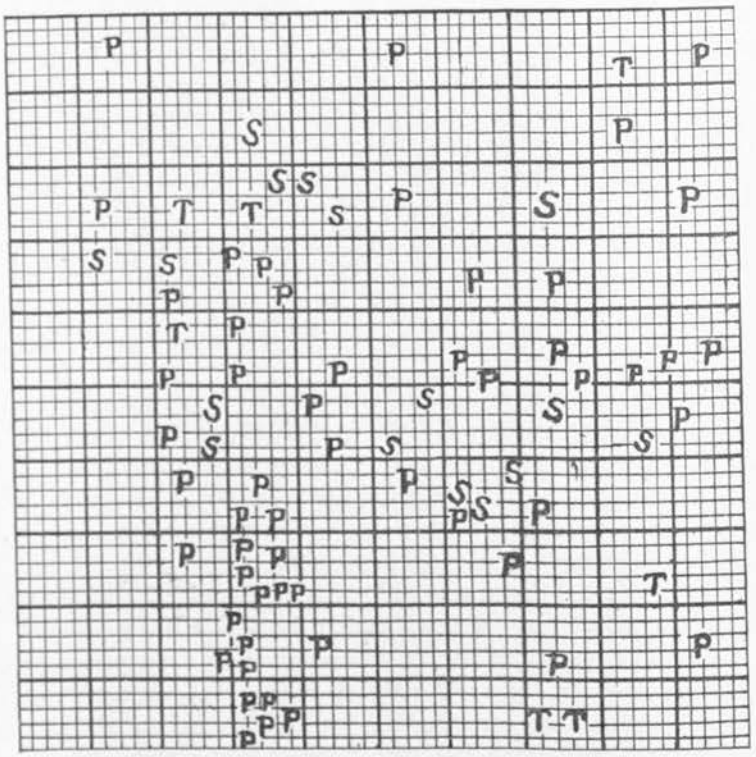
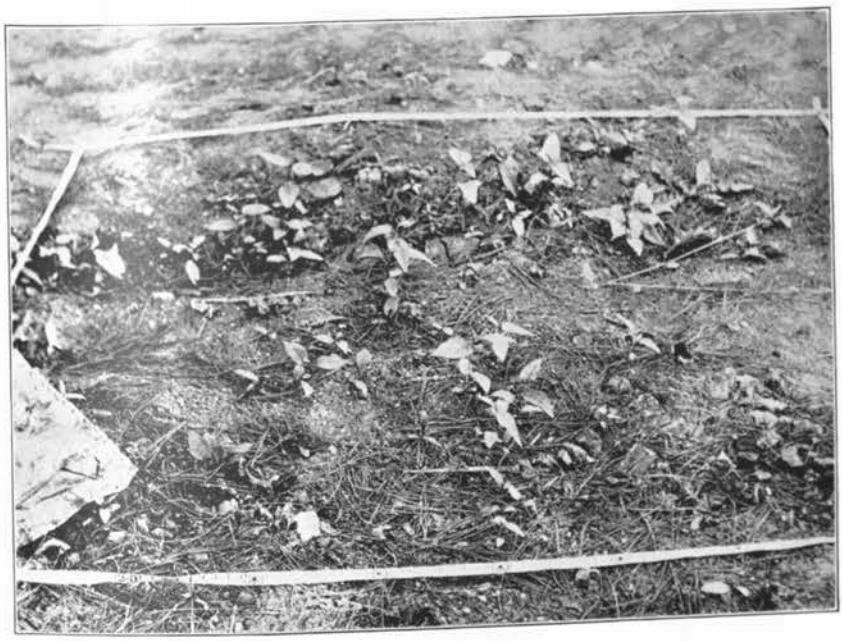


FIG. 21. Quadrat of young seedlings of *Populus* and *Salix*. International Falls, Minnesota.

LEGEND:
P. *Populus tremuloides*,
S. *Salix bebbii*,
T. *Taraxacum officinale*.

When the climax dominants are cut off, pioneer aspen and birch seedlings start soon afterward. By growing from 8 to 20 inches yearly they soon outgrow the shrubs and herbs. Often in 6 or 7 years their tops are



A. Seedlings of *Populus* and *Salix* growing on bare soil. International Falls, Minnesota.

B. Seedling of white pine, hazel bushes and aspen tree. Craig, Minnesota.

A. Young trees of *Pinus strobus* in a *Betula-Populus* associes. Hubert, Minnesota.

B. Trees of *P. strobus* growing above *Betula* and *Populus*. Red Lake, Minnesota.

A. Trees of *Thuja occidentalis* and *Picea canadensis* in a *Populus-Betula* associes. Near International Falls, Minnesota.

B. Rocks bared by fire, being covered with crustose lichens. Grass and *Antennaria* growing in the rock fissures. Rainy Lake, Minnesota.

well above their shrub competitors. At ages between 14 and 25 years, these 2 dominants have definitely begun to suppress the shrubs by the reduction of light values. On soils made bare by cultivation, aspen finds its best germinating grounds. The flying seeds are caught in crevices or by slight ridges or any other uneven surface. This accounts for the pattern of distribution in figure 21, as is shown in plate XXII, *A*, a photograph of the quadrat taken from the right. On abandoned farmlands, where they have followed the the weed stage directly, their first seedlings grew up with the annuals and were hidden for the first 2 years to the casual observer. So far as has been observed, these subclimax trees never arise directly on severly burned areas without being accompanied or preceded by herbs and shrubs. On cultivated fields they may arise with the weeds, and the subsere, in such an event, will lack the usual shrub stage. They seldom, if ever, follow immediately a well-sodded prairie, and their seedlings find it hard to grow in a dense stand of *Rhus* or any other definitely established shrub associes which casts much shade.

Birch, by living longer than aspen, persists in the early stages of the mixed pine forest, but neither live as long nor grow as high as the pine trees. In studying this associes, it has been impossible to find enough seedlings of birch and aspen growing in shade to ascertain their behavior under different degrees of light. Both are eliminated in shade which pine will tolerate (Pls. XXII, *B*, XXIII, *A, B*, IX, *A*). It is a recognized rule of reforestation (Pearson, 1914) that these two subclimax dominants may be used as a nurse crop for pines and other similar shade tolerant conifers.

In regions where the holard is high, seedlings of *Picea canadensis, Thuja occidentalis* and *Abies balsamea* (Pls. XXIV, *A*, XVII, *A*) may enter or linger beneath the shade of aspen and birch until they have favorable opportunities to mature. But in communities where red pine becomes the chief dominant, few individuals of these species are found. The pines compete for the most part with aspen and birch in the better soil habitats of the state. Trees of birch attain various ages before being overcome in the struggle. However, it is nearly always impossible to determine accurately their age in mature trees since they are often decayed or hollow at the center. From estimates made, birch dies at ages ranging from 100 to 200 years; aspen at ages from 50 to 120 years.

When this subclimax is succeeded by a pine association, the increase in water-content on sandy loam is shown comparatively by the curves of figures 22 and 23. The holard under the subclimax dominants is higher than that of the shrubs. This is true whether the shrubs precede the development of the aspen-birch associes or not. In both decimeters, there is an increase of soil moisture, but a greater percentage occurs in the surface decimeter, because of the increased amount of duff.

The light value of the aspen-birch associes ranges from 6 to 8 per cent,

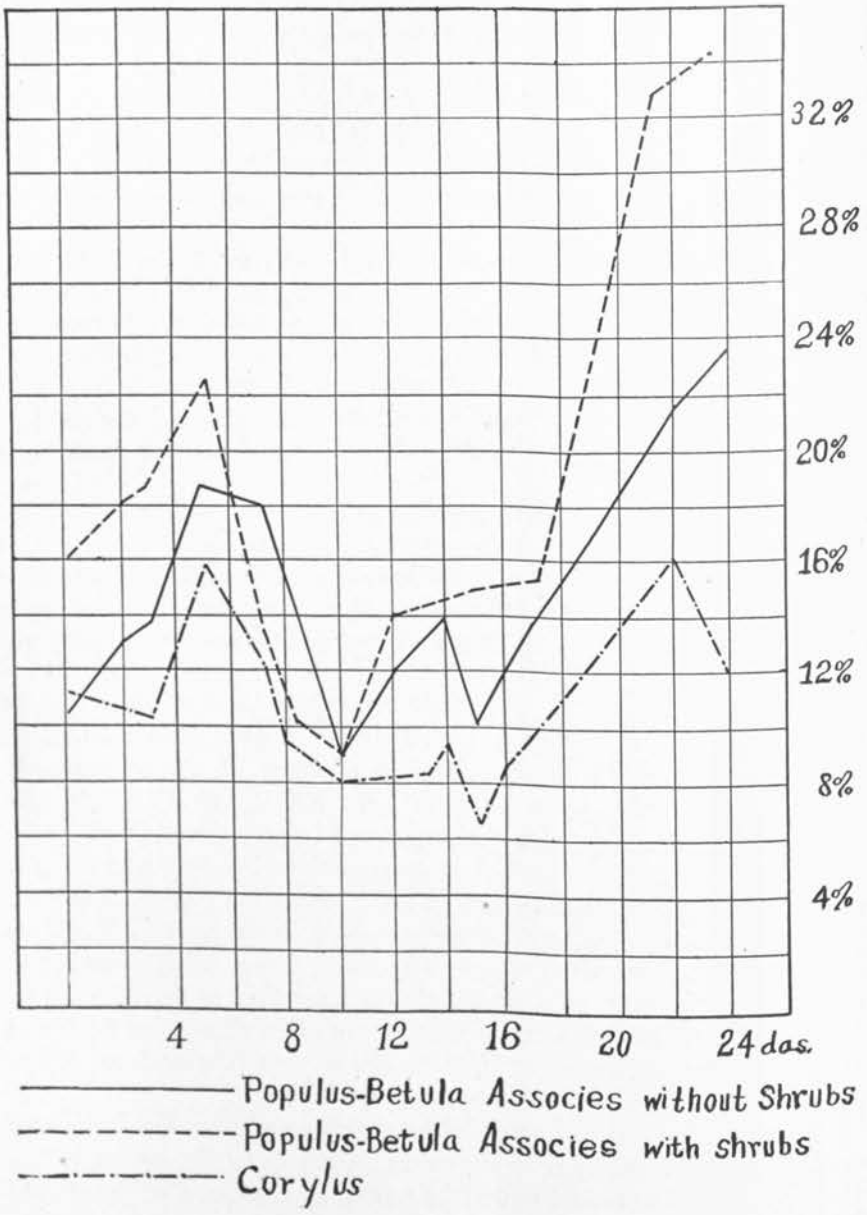


FIG. 22. Curves showing the range of soil moisture to a depth of one decimeter in the *Corylus-Rubus* and *Populus-Betula* associes on sandy loam for the summer of 1916 between July 18 and August 12.

a reduction greater than that of the jack pine consocies; this is not enough to prevent invasion by the white and red pines, but checks the rapidity of the red pine invasion. The establishment of pines after aspen and birch has long been accepted as a natural process of reforestation (Green, 1898), the red pine occupying the drier soils, the white pine the wetter places, and a mix-

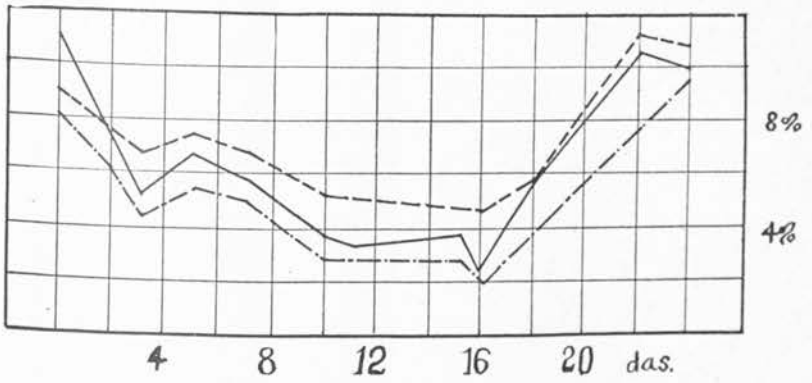


FIG. 23. Curves showing the range of the holard of the second decimeter in the *Corylus-Rubus* and the *Populus-Betula* associes on sandy loam for the summer of 1916 between July 18 and August 12. Legend same as figure 22. Near Hubert, Minnesota.

ture of the two the more moderately watered soils. The reaction of the association upon the habitat factors is not radically different from that of the consociations of either species on somewhat mesophytic soils. The water-content and light values of the association are really the means of the extremes represented by the red pine consociation, on the one hand, and the white pine consociation on the other.

(4) *Subseres on the Rock Areas Covered with Organic Soil*

The climax formation on the rock out-crops is in the main similar to that on morainic till, that is, it is composed of similar species that under similar conditions form consociations, and it is replaced after denudation by practically the same sort of subseres as those growing on better and more permanently formed soils. Fire, passing over such areas several times, followed by washing rains, start the succession again at almost primary conditions, because the run-off carries away the ashes, charcoal and fine rock debris, leaving the bare surface of the rocks exposed in the more elevated places. The unbound material washed away from the hill-tops and rock knolls gathers in the crevices and depressions and promotes secondary succession in the usual way, but the bared rocks are reoccupied by lichens and small mosses (Pl. XXIV, *B*).

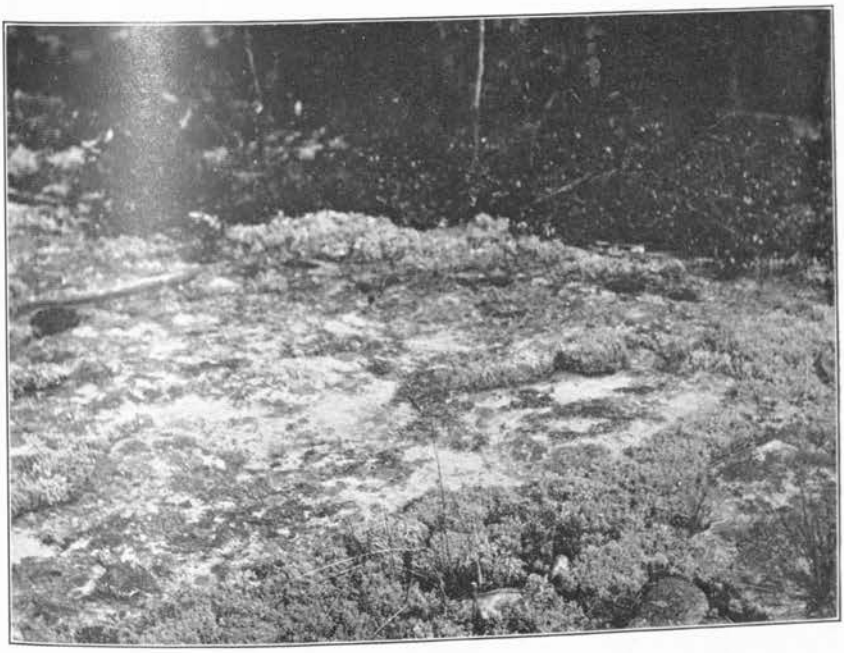
The character of the initial and climax stages of the subsere depends upon two circumstances, namely, (1) the degree of denudation and (2) the

nature of the soil formed. The first condition is dependent upon the agents of destruction, their severity and the number of times they operate. The second condition depends on the length of time that former successional forces have been allowed to act and to incorporate mineral materials into the sub-soil lying on top of the table rock. Where the soil is thin and the water-capacity accordingly small, red pine becomes the climax dominant. Where the deposition of inorganic and organic soil is deeper and has a consequent higher water-content, as in valleys, ditches or on hillsides favored by seepage and silting, a white pine consociation appears. The degree of denudation by fire is more extreme in the red pine rock tracts because it occupies soils of less stability. Jack pine is the usual subclimax dominant following its destruction, but on the damp hillsides or in ravines aspen and birch are the usual subclimax dominants.

a. Subseres on Burn-overs, Organic Material Burned: HERB ASSOCIES. Rock areas which have had the initial xerarch conditions restored through denuding agents can be revegetated only by a primary succession commencing with crustose lichens (Pl. XXIV, *B*), the initial stage of a prisere already described in a previous article (Bergman and Stallard, 1916). Less destructive fires and rain-washes leave charcoal, ashes, semi-burnt vegetation and disintegrated rock, forming a thin loose soil, which will promote the growth of foliose lichens, mosses and small herbs (Pl. XXV, *A*). Slightly thicker residual deposits, as in rock crevices and ledges, yield the usual herb growth, and the associes will consist principally of the following dominants: *Agrostis hiemalis, Anaphalis margaritacea, Dryopteris thelypteris, Chamaenerium angustifolium, Erigeron canadensis, Muhlenbergia mexicana, Polypodium vulgare* and *Solidago canadensis.*

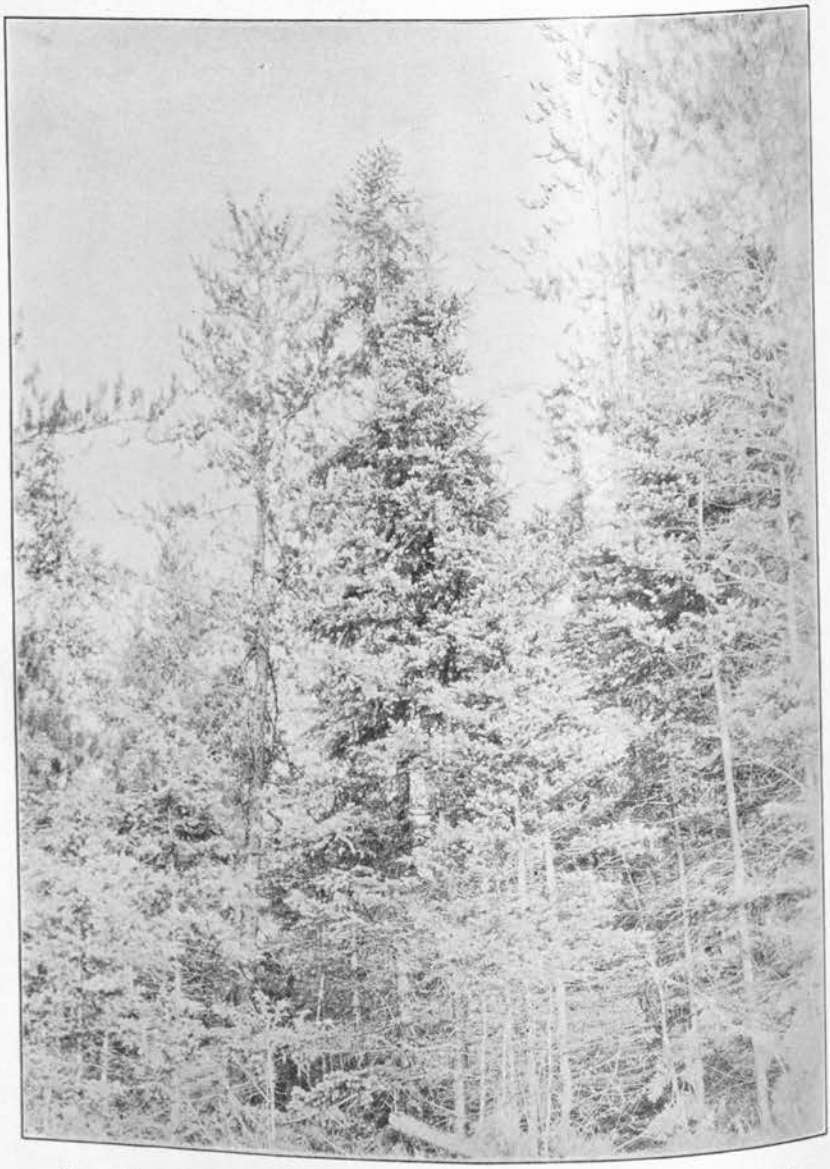
On large rock areas thinly coated with vegetable deposits, continual or annual burnings cannot establish a general grass stage because the soil is destroyed. However, grasses of even the prairie, as well as those more common to this region, may grow locally wherever considerable amounts of mineral soil have been formed and left in depressions, trenches and crevices between the larger rocks.

THE SHRUB ASSOCIES. The shrub stage here differs from the corresponding stage of the outwash plains principally by *Juniperus communis* replacing *Ceanothus. Corylus* (Pl. XXV, *B*) and *Rubus* are the chief shrub dominants. *Diervilla* and *Rosa* are conspicuous only in the early development of the shrub stage, as they are in the subsere on sand barrens. A uniform stand of shrubs is often impossible due to the variable conditions of the areal surface, as the more vigorous plants appear only in the soil of the crevices where the developmental rate of the sere is comparatively rapid. In the drier spots *Vaccinium pennsylvanicum* and *V. canadense* and *Arctostaphylos* occur. *Prunus pennsylvanica, P. virginiana* and *Amelanchier spicata* appear here and there under about the same conditions and nearly



A. *Cladonia* appearing in the more favorable places, with crustose lichens on the less favorable. Lake of the Woods, Minnesota.

B. The *Corylus* consocies appearing on a thin soil covering rocks near Ely, Minnesota.



Picea-Pinus associes on northern slope bordering Boundary Lake, Minnesota.

A. Thin soil under jack pine and spruce (see plate XXVI).

B. Soil and forest floor of a more mature associes of jack pine and black spruce.

as frequently as they do in the sand and gravel barrens. *Symphoricarpos pauciflora* is also a secondary species of this associes. The shrubs here, as elsewhere, produce some litter but catch and retain wind driven leaves. In addition they bind the organic soil together and to the rocks by roots which extend into the cracks and crevices.

THE *PINUS-PICEA* ASSOCIES: Jack pine, often an exclusive dominant in severely burned regions, may be associated with *Betula alba* var. *papyrifera, Populus tremuloides* and *P. grandidentata* in areas less denuded, or sometimes in deep mossy soils with *Picea mariana* (Pl. XXVI). The association of jack pine with black spruce is a peculiar forest mixture which may be explained by the uneven conditions of soil in the rock areas, the former occupying the more xeroid spots, the latter the places where much organic soil has been gathered. The *Pinus-Picea* associes occurs on islands of Lake of the Woods, of Rainy Lake, Isle Royale of Lake Superior (Copper, 1913) and of many other smaller lakes in the northern part of the state near the Canadian boundary. This mixture is infrequent on the mainland this side of the border. It seems that *Picea* would ultimately eliminate *Pinus* in these regions, for it is more shade tolerant, casts a denser shade, lives longer, and in such soil can multiply to a limited extent by layering (Fuller, 1913), all of which gives it an advantage over its competitor.

THE *PINUS RESINOSA* CONSOCIATION. The subclimax of *Pinus banksiana* of this subsere is followed by *P. resinosa* in the drier areas. But in the more mesophytic habitats, occupied by the *Picea-Pinus* associes, *P. strobus* becomes more numerous. The character of the organic soil is represented in plate XXVII, *A* and *B*, *A* representing a thin veneer under jack pine, *B* a carpet under spruce. White pine is also found occupying the crevices where sufficient water is found. Its young seedlings may start on scant amounts of organic soil, but perish after a few years for want of water at critical dry periods. The climax forest formed over such areas produces a stand corresponding to the thinner sand barren tracts of Hubbard and Crow Wing counties. In St. Louis County, several miles west of Ely, there was found a young forest of *P. resinosa* apparently reproduced from a small group of trees left at the crest of a hill. White pine seedlings and young trees, descendants of the parent included with the red pine trees (Pl. XXVIII, *A*), occurred here in the places having the deepest soil.

b. Subseres on Rock Areas, Organic Soil not Burned. It is patent that a mere removal of the climax trees, growing on rocks covered with moss and organic deposits, without destroying the organic carpet will initiate a subsere that begins with an herb stage consisting chiefly of the dominants which grew on the forest floor. The shrubs, present on the forest floor, likewise will promptly develop a stage succeeding the herbs. They may form a thin stand which will have scattered through it jack pine seedlings or, in places with better soil, young trees of birch, aspen and spruce. These

trees may grow so rapidly that the shrubs become obscured except in places here and there where clusters have taken advantage of open spaces having good soil. The trees soon form a cover crop for the coexisting slower-growing red and white pine seedlings, or for any entering later in the development of the subsere. Such simple denudation as plain clearing is seldom the fate of a forest on rock out-crops, for the carpet of moss and pine leaves is like tinder during dry seasons, and only by exercising the greatest care can rangers prevent fires or subdue them before the soil has been seriously damaged or totally destroyed in the thinnest spots.

(5) *Subseres on Rocky Clay or Loam Soils*

The presence of rocks in a clay or loam soil does not materially modify the succession in such habitats, but clay or loam on rocky side-hills or sloping rock out-crops have diversified areas ranging from xeroid conditions to mesophytic soils. On land that continues to be well drained, xeroseres tend to terminate into mesophytic conditions by depositing and retaining organic material. When the soil is built up chiefly of lichens and mosses, mesophytic conditions are approached as the climax pine association is reached and maintained. In small depressions, or in the bottom of deep valleys, or in hillsides, or any other places favoring the deposition of clay or silt, approaches toward hydrophytic conditions are made by the addition of mineral soil and organic deposits in the natural drainage channels, which either block or misdirect the natural seepage, causing local elevation of the water-level or water-table. This, however, is a denuding process which ultimately is stabilized by secondary succession. There is no place in the state where organic soils suck up the water, as they grow in depth, and make general hydrophytic conditions, as if retrogression were occurring in the succession.

The damp areas in rocky soils of clay or loam promote the development of a subclimax of birch, balsam and spruce, identical with that of such soils in rockless areas. A large part of the mesophytic rock areas of St. Louis County in the vicinity of Ely and Vermillion Lake are now covered by the *Populus-Betula* associes which is being succeeded by a mixture of red and white pines.

(6) *Subseres in Bogs*

INITIAL CAUSES: The following causes may start subseres in a bog: (1) The bog may be flooded by man or by beavers damming up the natural drainage outlets. (2) Drainage ditches, often made to reclaim bog-land for farming, and railroad cuts, may drain a swamp sufficiently to kill many of the swamp species, including trees, herbs, shrubs and particularly *Sphagnum*. (3) The trees of a bog may be removed by cutting without subsequent burning or accompanied by fires of small consequences so far as the soil itself is concerned (Pl. XXVIII, *B*). (4) The bog may be naturally dried

A. Parent trees of *Pinus strobus* and *P. resinosa* on rock crest. St. Louis County, Minnesota.

B. Bog covered once with *Larix* and *Picea.* Deer River, Minnesota.

A. Edge of bog destroyed by fire. Glenwood Park, Minnesota.

B. Cluster of *Cyprepedium; Ledum* surrounding it. Benedict, Minnesota.

out by a lowering of the water-level of the parent pond during drought, and subsequently burned deeply by a fire originating in the upland vegetation, like the Great Baudette Fire of 1911 which destroyed the peat deposits completely in spots, leaving only an ashy layer on the clay or sand bottoms. Although the region devastated was extensive, the areas deeply burned were small, varying in size from three or four feet in diameter to areas of several acres. Wet peat does not burn rapidly, but if a fire is started during a dry season, it will continue after considerable rainfall or until it is submerged by a rise in the water-level.

During dry periods, a fire may destroy the edge or rim of a bog, burning the peat down to the marginal floor of the original parent pond. When the water-level rises after rains, a trench of water surrounds the bog, forming the atoll bog, first described and named by MacMillan, but whose origin was later found by Dr. H. F. Bergman and the writer to be due to fire (Stallard, 1916). (5) Bogs may be drained, cleared for cultivation and then abandoned, after which they are very apt to be set on fire, as has happened many times not only in northern Minnesota but also in the middle and southern part of the state. This series of denuding processes may remove the peat deposits altogether, thus erasing most of the visible traces of the bog and the edaphic factors promoting its development. This has happened more frequently in the southwestern and south central parts of the state where the land has been under cultivation for more than half a century.

The denuding forces affecting bogs may be separated into two general classes, namely, those increasing the amount of water in the soil and those decreasing it. However, as will be seen later, such opposite forces as flooding and fires, during droughts, may initiate similar seres. Drought seasons unaccompanied by fire do not kill bog vegetation, but drainage—a permanent lowering of the water-level—will kill the swamp trees and damage many of the herbs and shrubs. Seasonal floodings from rainfall and runoff, frequent in bog districts, do not kill off bog vegetation, but permanent raising of the water-level through permanent flooding or through flooding for several months destroys most of the trees and many of the subdominant herbs and shrubs. The plants undoubtedly die because the water covering the roots lacks sufficient available oxygen.

When fire burns up the peat, and the water-level rises again, hydrophytic conditions simulating the beginning of a hydrosere, at least in small areas, are restored (Pl. XXIX, *A*). The trench made by the fire produces conditions similar to those effected in drainage ditches where the peat has been removed mechanically and the water-level allowed to recover its former height. A rise in water-level, after a succession of many rains, never makes it possible for winds and waves to destroy much vegetation in small bogs, or bogs surrounding small parent lakes. But in bogs bordering large

lakes, the wind- and wave-action may loosen parts of them and scatter the pieces about, landing them in other parts of the lake. This apparently occurred on the west shore of Leech Lake, but even there the portion of the bog supporting tamarack and spruce was not disturbed. A permanent rise

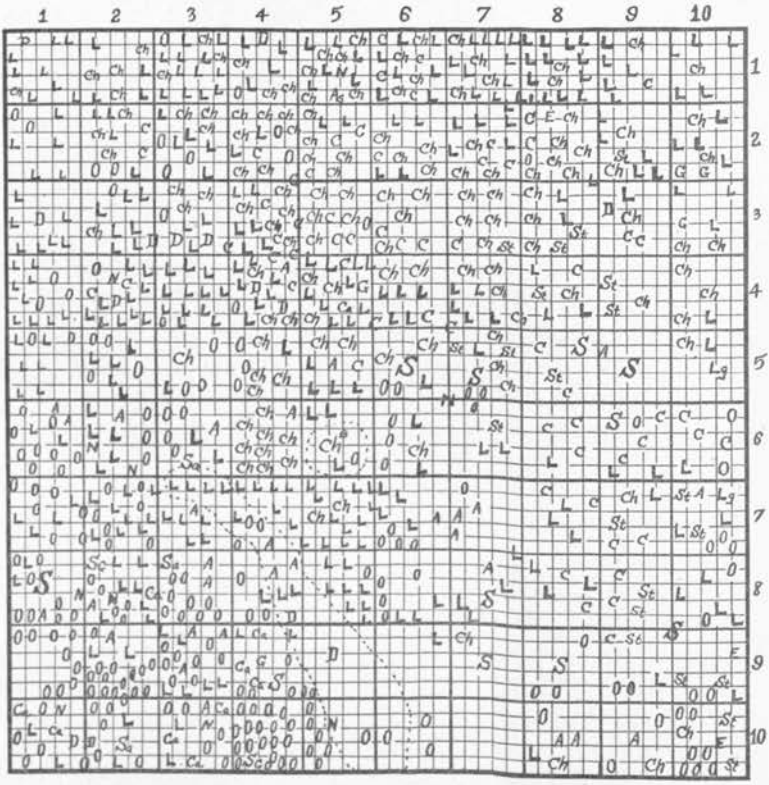


FIG. 24. Quadrat showing the ground layer of the *Larix-Picea* associes. See plate XXX *A*.

LEGEND:

A. *Andromeda glaucophylla,*
As. *Aster junceus,*
C. *Carex gynocrates,*
Ca. *Campanula aparinoides,*
Ch. *Chiogines hispidula,*
Ct. *Coptis trifolia,*
D. *Dryopteris thelypteris,*
E. *Epilobium densum,*
G. *Galium trifidum,*
L. *Linnaea borealis,*
Lg. *Ledum groenlandicum,*
N. *Naumburgia thyrsiflora,*
O. *Oxycoccus oxycoccus,*
P. *Pyrola secunda,*
S. *Sarracenia purpurea,*
St. *Smilicina trifolia,*
Sx. *Saxifraga pennsylvanica.*

in water-level not only kills the trees, but obliterates much of the *Sphagnum* and several other bog species. The dead vegetation decaying and finally

A. Bog carpet showing *Oxycoccus, Ledum, Menyanthes, Sarracenia, Chamaedaphne* and young individuals of *Picea mariana.*

B. Consocies of *Phragmites* on bank of Kabekona River, Benedict, Minnesota.

sinking to the bottom forms loose muck. The water-covered muck becomes vegetated by such species as *Typha, Phragmites* and *Zizania,* the same as occur in burned-out holes or mechanical excavations.

A permanent lowering of the water-level by drainage not only kills the bog plants, but may also hasten the entrance of the climax dominants or introduce such subseres as occur on the surrounding upland soils. Complete consumption of the bog by fire initiates on the mineral soils thus exposed regular upland subseres, if the drainage remains adequate.

The Subclimax in Bogs: The subclimax of a peat bog consists of *Larix laricina, Picea mariana, Thuja occidentalis* and *Abies balsamea,* the former two being the earliest to become ecized in the wetter places. *Abies* and *Thuja* apparently occur where the water-level is not high or subject to radical fluctuations throughout the seasons. *Thuja* is readily killed by an elevation of the water-level. *Abies* requires a more mesophytic soil for its ecesis than that afforded by a loose carpet of *Sphagnum.*

The following often form distinct shrub socies in a *Larix-Picea* community: *Andromeda glaucophylla, Chamaedaphne calyculata, Kalmia glauca, Ledum groenlandicum, Vaccinium canadense, V. pennsylvanicum, Oxycoccus macrocarpa* and *O. oxycoccus* (Figs. 24, 25; Pls. XXIX, *B,* XXX, *A*). *Ledum* is the most shade-tolerant of the bog shrubs, often lingering under the dense shade of *Thuja-Abies* associes. *Andromeda* is the most water-tolerant and is often found invading the water between the culms of the sedges in the *Carex* zone surrounding ponds and small lakes.

Scattered plants of the following are found among the shrubs of this subclimax when occupying bogs: *Betula pumila, Cornus stolonifera, Ribes prostrata, R. triste* and unidentified species of *Salix.* Occasional plants of *Taxus minor* occur in well wooded bogs.

A great variety of herbs is found with *Sphagnum.* Among those that form conspicuous socies are *Clintonia borealis, Linnaea borealis, Sarracenia purpurea* and *Smilicina trifolia.* Dense socies of *Dryopteris cristata* and *D. thelypteris* are common. *Cypripedium parviflorum* and *C. hirsutum* are the characteristic dominants in the spring and early summer aspect. *Osmunda cinnamomeum* and *O. claytoniana* form families in the outer edges of the bogs. Socies of *Eriophorum gracile* are present in shallow water. *Linnaea* and *Chiogenes* appear in families on logs and well-rotted peat surfaces.

Many small plants are found occupying the hummocks and the depressions of the sphagnum areas, the following being the usual secondary species observed in such places: *Coptis trifolia, Cornus canadensis, Drosera rotundifolia, Menyanthes trifoliata, Pyrola asarifolia, P. secunda, Naumburgia thyrsiflora* and *Trientalis americana.*

Secondary succession in bogs is complicated by a variety of conditions created by the various denuding forces, but it may be discussed under the following heads:

a. Subseres in Shallow Water,
b. Subseres beginning with the Grass Associes,
c. Subseres in Cut-overs,
d. Subseres in Drained Cultivated Bogs.

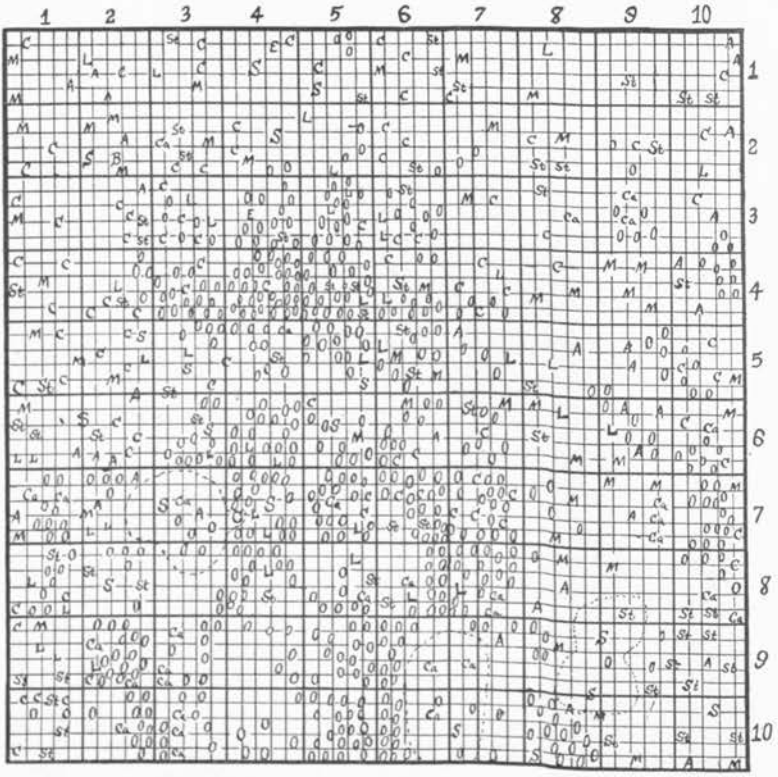


FIG. 25. Quadrat photographed in plate XXX, *A*.
LEGEND:

A. *Andromeda glaucophylla*,
B. *Betula pumila*,
C. *Chamaedaphne calyculata*,
Ca. *Carex* sp.,
E. *Eriophorum gracile*,
L. *Ledum groenlandicum*,
M. *Menyanthes trifoliata*,
O. *Oxycoccus macrocarpus*,
S. *Sarracenia purpurea*,
St. *Smilicina trifolia*.

a. Subseres in Shallow Water: THE *TYPHA-PHARGMITES* ASSOCIES: Subseres of the peat bog may begin with water plants whenever flooding or burn-outs occur. Following flooding, the typical associes consists of *Typha angustifolia* and *Phragmites phragmites* (Pl. XXX, *B*), the chief dominants. Socies are formed of *Alisma plantago*, *Acorus calamus* and *Sparganium eurycarpum*. *Scirpus occidentalis* and *S. validus* may be scattered among the thick stands of the dominants. In small pools occur fam-

A. Seedlings of *Typha* in the mucky bottom of a drainage ditch.

B. Seedlings of *Typha* growing in clay soil in the bottom of ditch.

A. Floating bog on Kabekona River. Note new sprouts of *Phragmites* appearing in the water-lily zone.

B. Clump of reeds washed upon shores of Rainy River.

ilies of *Sagittaria arifolia*. Scattered through the associes may be found representatives of *Carex, Menyanthes* and *Polygonum amphibium*.

Typha and *Phragmites* produce a large amount of seeds; those of the former having a high percentage of viability and apparently no destructive enemies. *Phragmites* in less than three feet of water matures and bears an abundance of seeds which are often consumed, for the most part by birds. *Alisma* and *Sagittaria* produce seeds less abundantly and do not provide them with special migratory devices. Seeds of *Scirpus*, which are rather copiously produced, are light enough to be scattered by wind. The seeds of *Polygonum* are comparatively larger and are not disseminated effectively. The fruits of *Sparganium*, which are large burr-like bodies, are not numerous and are poorly sown.

The seeds of *Typha* are scattered in the spring, when the heads containing them begin to disintegrate, but all of them are not dispersed until about the middle of June. The seeds are capable of germinating on the surface of mud, but the seedlings cannot become anchored to earth where there is much wave-action. The seeds may float on the surface of quiet pond water until they germinate, and then drop down to the bottom and become anchored. From experiments, it was learned that seedlings of *Typha* can ecize even where the seeds are covered with an inch of mud and 8 inchs of water. In all probability, the bulk of the seedlings arise during the time the water-level is low or on mud when uncovered by water (Pl. XXXI, *A, B*).

For *Phragmites* ecesis is more difficult. From experiments, the writer found that the only suitable place for it to ecize is on mud covered with just enough water to insure germination. Its ecesis is prohibited by wave-action or by fluctuating water-levels. A rise in water-level drowns the small seedlings or floats those insufficiently anchored away before they become planted. A depression in the water-level permits the sun to encrust the soil and this prevents their establishment. It was found that only feeble germination of its seeds could be obtained under water of any depth, but when seedlings become rooted and attain subsequently a height of 5 or 6 inches, a depth of 3 or 4 inches of quiet water does not disturb their normal growth.

All the important plants of this associes propagate by rootstocks (Pl. XXXII, *A*), but *Phragmites* and *Typha* are no doubt the most aggressive and consequently form denser stands as well as more extensive ones. The mat formed by *Phragmites* is more compact and firmer than that of *Typha*. In fact, a whole community of the former may be moved during a storm from one part of a lake to another, as has occurred in Leech Lake where several acres became unmoored during a storm, moved about a mile and became anchored in a new place. Smaller bunches of *Phragmites* (Pl. XXXII, *B*), torn from river banks, may be floated down a stream during a flood and be deposited at levels higher than it would ordinarily grow. Those kept watered will start a new community.

Typha, by not forming such compact mats, develops communities which floods, waves or wind may break up into small pieces, consisting of three or four stalks or shoots, which may start new communities if transported to new places. This type of propagation and migration seems to be of importance in places where ecesis by seeds is difficult.

Typha and *Phragmites* suppress and eventually replace most of the secondary species of this associes (Pl. XXXIII, *A*). A sufficient number of instances of the competition between the two have not been found to determine the outcome of the struggle, but from the work of Sherff (1912) it would seem that *Phragmites* remains in a habitat longer than *Typha* or any of the other plants of this stage because of its rootstocks, which can grow well at several different levels. It is also taller than the other plants and can shade out most of them by its rapid spring growth. Wet meadows often contain relicts of both species or surround small areas populated by either when local denuding agents destroy the grass or sedge plants (Pls. XXXIII, *A, B,* XXXV, *A, B*). In time the grass and sedges replace them, but in areas not regularly burnt or grazed, alders and willow may enter from the margins of the bog or pond and gradually replace the reeds or cattails before an associes of *Carex-Calamagrostis* can fully develop (Pl. XXXIII, *B*). In their infancies these shrubs may be coexistent with the reeds but not noticed among them. These two species, by depositing much soil-forming debris and binding it together thoroughly by means of rootstocks and roots, raise the surface of the swamp above the normal water-levels and thus afford an opportunity for the ecesis of sedges, grasses, alders and willows.

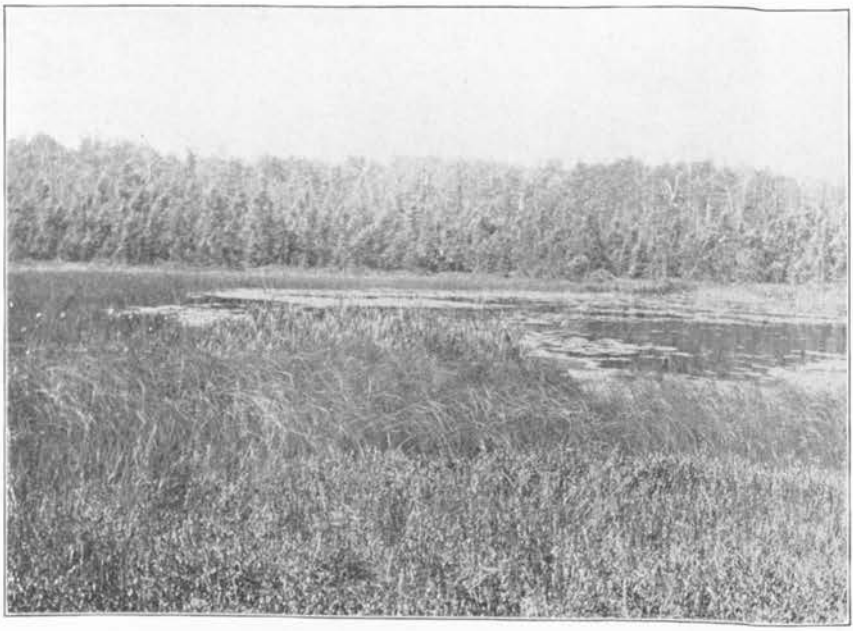
THE *CALAMAGROSTIS-CAREX* ASSOCIES: Whenever the subsere develops rapidly, *Calamagrostis canadensis* and *C. hyperborea* may reproduce a grass stage before the sedges can invade. But where the subsere grows slowly or is interrupted by occasional fires or mowings, *Carex aquatilis, C. filiformis, C. trichocarpa* and *C. bebbii* invade, forming a stage which in many respects resembles the *Carex* associes of the prisere (Pl. XXXIV, *A, B*). The photograph *B* of plate XXXIV shows rectilinearly the stages of a prisere, exhibiting the same shown in profile in *A*. The sedges constitute a stage in the primary succession preceding the heath-sphagnum mat (Pls. XXXIV, XXXV), and with their establishment the secondary succession terminates in a stage of the prisere.

The migration of these dominants depends primarily upon the wind, but secondarily upon basal offshoots by which they intensify their stands and by which they can migrate into neighboring zones in which ecesis by seeds would be impossible. The relative migratory efficiency of any of the species of sedges and grasses of the wet meadows has not been studied. All of them probably require organic or inorganic earth for germination and ecesis. The dominants, by stooling or developing new plants from longer rhizomes, can invade water zones, and by their reactions increase constantly

A. An associes of *Typha* and *Phragmites* near edge of a wet meadow. Benedict, Minnesota.

B. *Alnus* and *Carex* invading swamp previously occupied by *Typha.* Near Walker, Minnesota.

A. Zones surrounding quiet water shown in profile. From left to right the following may be identified: *Picea-Larix, Ledum-Chamaedaphne, Carex* and *Nymphaea-Castalia.*



B. Same zones shown rectilinearly. From the foreground backward, *Ledum-Chamaedaphne, Carex* and *Nymphaea-Castalia.*

A. Primary zones of small lake near Stanley, Minnesota. At right where canoes have landed frequently are a few plants of *Typha*.

B. Small patches of *Typha* and *Phragmites* growing in a place where the *Carex* and heath-sphagnum zones have been disturbed.

A. *Typha* in bogs burnt deeply. Near Baudette, Minnesota. Leaves of *Caltha palustris* may be identified between those of *Typha*.

B. Left side, *Ledum-Chamaedaphne* associes in *Sphagnum;* right side, a sedge meadow after fire. Hubert, Minnesota.

the density and area of the sod which becomes gradually higher from depositions, affording the newer shoots each year a more elevated foundation. The light values under grass are always high, ranging from 15 to 20 per cent, not enough reduction to prevent the invasion of the shrubs, especially if they use secondary methods of propagation.

THE *SALIX-ALNUS* ASSOCIES: The seeds of *Salix candida, S. petiolaris, S. discolor, Betula pumila, Alnus incana* and *Cornus stolonifera* germinate above the water-level, but their seedlings after several years of growth can live and grow with their roots and bases submerged in water for a greater part of the growing season. This is especially true of the seedlings of willows which often stand in two or three feet of water, as on lake borders. However, if their ages are determined, it will be found that they germinated in a dry year, when the water-level of the lake was lower. *S. candida* is usually the first of these dominants to invade wet meadows, although *Betula, Alnus, Cornus* and other species of *Salix* enter soon afterward. The shrub invasion into a grass area is slow, even when fires are prevented, and often for a long period the shrub associes is represented only by bushes which keep increasing in size until they occupy the intervening open spaces, thus forming finally a more or less uniform stand.

THE *LARIX-PICEA* ASSOCIES: Tamarack and swamp spruce sometimes invade the grasses simultaneously with the alders and willows, but usually such pioneers are scarce, the former appearing to be a forerunner of this associes. By their continuous invasion and ecesis, there is formed the regular swamp subclimax, the *Larix-Picea* associes. Invasions into large grass areas are slow, but in small burn-outs which form small pools and ponds, the local seral development is faster but much the same as that of more extensive areas just described. In small areas *Typha* (Pl. XXXVI, *A*) is the chief representative of the reed associes. *Caltha palustris* is the most conspicuous subdominant appearing with *Typha*. The solitary occurrence in this stage of *Typha* is explained by the following facts, namely, that its seeds are more abundantly produced, more widely scattered, more viable and more adapted to growth and germination in various depths of water than those of *Phragmites*. The cattails at Baudette probably entered the summer following the fire, and five years later, when they were first observed, species of the wet meadows had already made invasions, and in many places alders, willows and swamp birch had become established. Apparently, it requires from 5 to 10 years to prepare the smallest pools for the invasion of sedges, *Sphagnum* and the heaths. The spruce and tamarack are able to reinvade such districts in bogs sooner than places more profoundly disturbed by an increase in water. A more detailed account of the invasion of *Sphagnum* and the heaths, which are the usual antecedents for tamarack in the hydrosere, is given below under the discussion of the following subseres.

b. Subseres Beginning with the Grass Associes: Fire in peat bogs very often destroys the surface so uniformly as to leave no deep holes (Pl.

XXXVI, *B*). When this happens, the *Carex-Calamagrostis* associes is the initial stage, which may be promptly followed by the *Salix-Alnus* associes or directly by the primary associes of *Ledum, Chamaedaphne* and *Sphagnum.* Contrary to current belief, *Sphagnum* can not develop well in standing or quiet waters, or in grasses where the water-level fluctuates too widely; in the last situations an elevation of the water-level perches its plants upon the culms of the grasses near their tops and, when the water recedes, leaves them suspended in the air to parch in the sun. In those meadows or sedge zones which supply abundant water at regular levels, *Sphagnum* develops best. Here both it and the heaths can form hummocks, which are often regenerated after a fire from a group of small clumps of *Sphagnum* relicts (Pl. XXXVII, *A*). By enlarging and coalescing, the clumps reproduce the heath-sphagnum bog which in its mature state is densely formed, its layers being quilted together by the vertical stems and roots which are bound together in all directions by transverse roots and rootstocks, the warp and woof of the muskeag structure, which is green, spongy and cold. It is incapable of absorbing the sun's heat, and therefore it thaws late in the summer. It has entrapped in its dead layers much carbon dioxide, which is produced a few inches below the surface from the decomposition. The hummocks, which are considerably higher than the surface occupied by the sedges and grasses, are continually elevated by the constant accumulation of the moss which smothers out the sedges and grasses more or less completely (Pl. XXX, *A*).

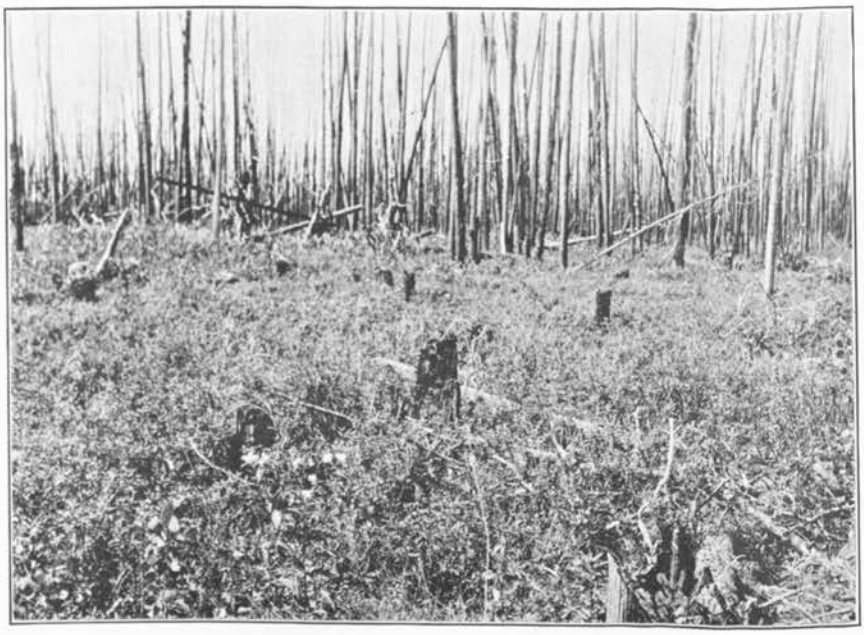
It is commonly but mistakenly supposed that *Sphagnum* acts like a wick and draws the water-level of the formation upward as its mat thickens. When clumps of it are placed in open glass tubes and watered regularly from the top, the plants will continue living and growing, but if watered only from the bottom, the top layers die and dry up. It is true that the mats hold water like sponges, but it is impossible for the plants to derive sufficient water from the subsoil by capillarity alone in unduly prolonged drouth periods. After the melting of the snow in the spring, the water-level is usually about as high as the hummock tops, a flooded condition, but in older bogs the water-level drops below the surface of the heath hummocks 6 to 18 inches nearly every summer or fall. The *Sphagnum* plants apparently need to be watered by the natural rainfall.

THE *LEDUM-CHAMAEDAPHNE-VACCINIUM* ASSOCIES: The following heaths appear simultaneously with *Sphagnum,* particularly in subseres: *Andromeda glaucophylla, Chamaedaphne calyculata, Ledum groenlandicum, Vaccinium canadense, V. pennsylvanicum* (Pl. XXXVII, *B*), *Oxycoccus macrocarpus* and *O. oxycoccus.* These are the regular shrub dominants found in the shade or open places of the *Larix-Picea* associes. The species of *Oxycoccus* are considered of secondary importance in the formation of the shrub associes, but they often occupy considerable surface. In open areas (Pl. XXXVII, *B*), *Chamaedaphne, Vaccinium* and *Ledum* are the main

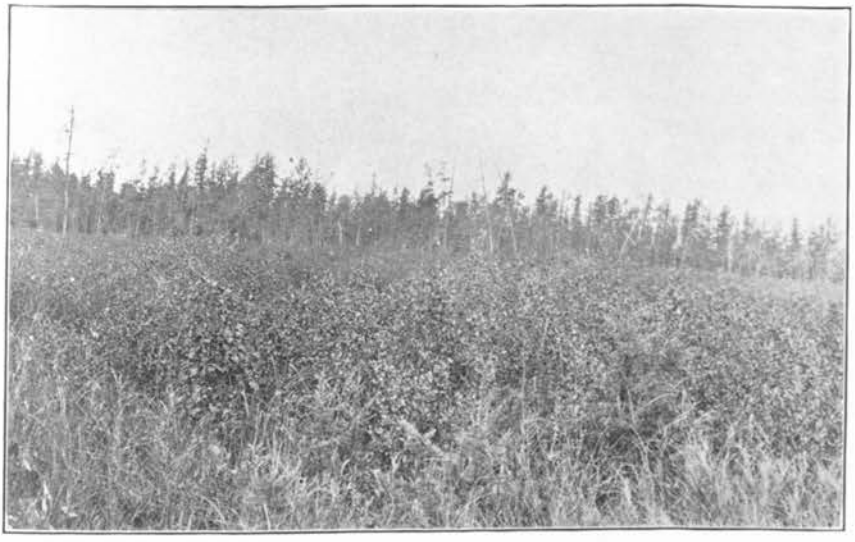
A. Wet meadow containing small hummock of heaths and *Sphagnum*. The Anderson Bog after the fire, described by Macmillan before it was burned. Hubert, Minnesota.

B. Vigorous bog-heaths in a cut-over. International Falls, Minnesota.

A. An associes of young *Larix* and *Picea.* Grand Rapids, Minnesota.



B. Cutting and fire in the *Larix-Picea* Associes. Seedlings from left to right in the foreground are of *Populus, Betula* and *Picea.* International Falls, Minnesota.



A. Consocies of *Betula pumila* on a bog. Shevlin, Minnesota.

B. An associes of *Larix* and *Picea* in which *Picea* is becoming an exclusive dominant through the death of the former. Meadowlands, Minnesota.

dominants, but in subseres, as in priseres, *Andromeda* is often the first to invade the grass or sedge zones that stand in water.

Nothing was determined experimentally or by field studies of the migratory efficiency of the seeds of any of these species. Of these dominants, only seedlings of *Ledum* have ever been noticed in the field by the writer, who, whenever he found them, noted that they grew on rather firm dead layers of *Sphagnum*, usually after recent fires. Hence, it seems that the shrubs here mentioned depend upon rootstocks for propagation and local migration. In most cases these rootstocks probably extend from relicts rather than from pioneers.

The following herbs appear in the hummocks and are probably also relicts of the grass or sedge stage: *Comarum palustre, Menyanthes trifoliata, Naumburgia thyrsiflora* and *Saxifraga pennsylvanica*. Socies of *Menyanthes* and *Smilicina trifolia* are developed in the mat while *Sarracenia purpurea* forms conspicuous families. Socies of *Dryopteris*, which begin and appear coexistent with the grasses, are also a part of the *Sphagnum*-heath associes.

THE *LARIX-PICEA* ASSOCIES: The heath hummocks which contain desiccated or even decomposed *Sphagnum* in their tops are fairly favorable for ecesis of *Picea* and *Larix*, which form on bogs an open forest for several decades. The pioneer plants of spruce and tamarack start from seeds, the most typical consocies of either forming after the *Ledum-Chamaedaphne* associes has been well developed. The shade of the subclimax kills out *Andromeda* and *Chamaedaphne*, but *Ledum* and *Vaccinium* survive the shade and occur more or less sparsely throughout the life of the subclimax trees. Even *Sphagnum* is prevented from making further extensive growth in dense shade. In the oldest stages of the subclimax, practically all the shrubs, herbs and mosses are subdued but retained in suppressed forms.

c. Subseres in Cut-overs: Since tamarack is used for fire-wood, railroad-ties and posts, and spruce for paper production, these trees have been extensively harvested in large areas. The two species, especially tamarack, do not yield much brush, and hence it frequently happens that the clearing-up fires do not damage the bog deeply, often only slightly more than that caused by a flood which might kill only the subclimax trees. Following such denudation, the succession may restore the subclimax sooner than is accomplished under any of the other conditions under consideration (Plate XXXVIII, *A, B*).

THE *BETULA-ALNUS* ASSOCIES: *Betula pumila, Alnus incana* and *Cornus stolonifera* are the dominants of a stage growing on denuded but not destroyed bogs (Pl. XXXIX, *A*). *Betula* is usually the first to appear, often forming pure stands, which are sometimes sparsely populated. *Alnus* and *Cornus* are invariably associated with *Betula* in larger areas. *Salix petiolaris, S. bebbii* and *S. discolor* are often conspicuous, especially when there is considerable grass present.

B. pumila at an early age bears a considerable amount of seeds which are more mobile than those of *Alnus*, though both are readily scattered by the wind. As judged by field observations, both have about the same ecesic ability in wet soils, but *Betula*, by bearing seeds earlier in life, can invade unoccupied areas faster. However, its life form is lower than that of *Alnus* and, when they are sown together, the latter finally overshadows it. Thick stands of either are seldom found where *Sphagnum* hummocks are loose and saturated with water, but where the peat is higher above the water-level, they form denser stands. In decayed peat material, devoid of living mosses, they make their thickest stands, though individuals of either may grow with their bases submerged in water throughout the spring and summer.

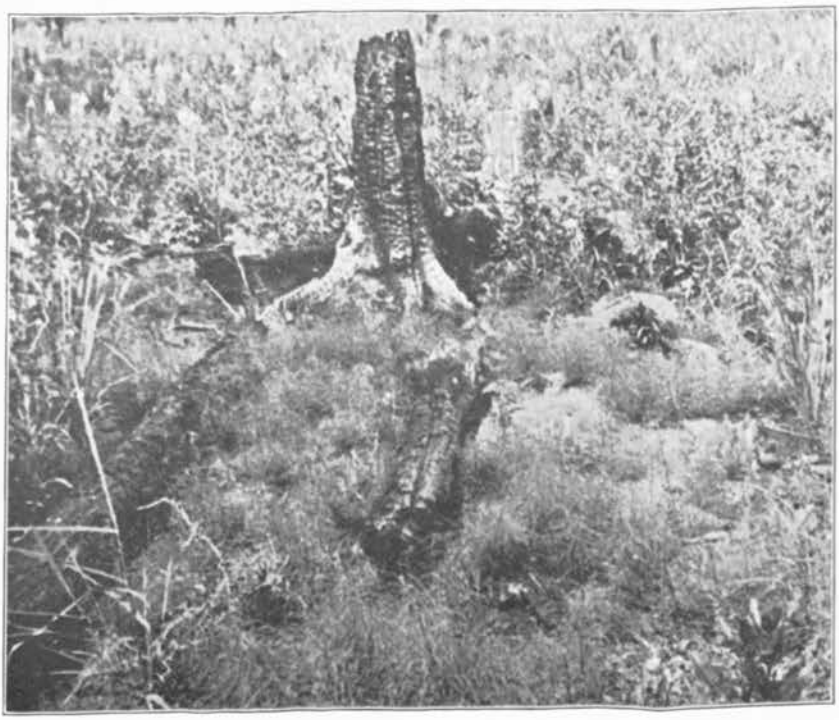
Light reduction in this community may vary from practically 0 to 95 per cent, a shade which seldom becomes uniform over great areas. *Larix, Thuja, Picea* and *Abies* have opportunities for ecesis in the open spaces in the early part of the shrub associes development or after the severest competition between the shrubs themselves has subsided, when here and there alder bushes die out, making available open spaces. If a thick stand of the swamp shrubs should develop before the seeds of the subclimax dominants are sown, the subsere is held locally in the shrub stage until the light values increase through the death of the mature shrubs.

The accumulation of leaves under the densest stand of alders and swamp birch often amounts to several inches, a deposit of organic matter which raises the surface soil above the water-level considerably, thus providing a better habitat for the subclimax dominants, especially after the shade and organic depositions have submerged and smothered out the *Sphagnum*.

In sparse stands of swamp birch and alders, tamarack and spruce begin to show their tops above the shrubs in about 15 years, but in the thicker stands, even should the seeds of the climax dominants germinate immediately after the spruce or tamarack harvest, a longer time is required for them to grow above the shrubs.

THE *LARIX-PICEA* ASSOCIES: *Larix*, since it grows faster than *Picea*, is first to show above the shrub-tops, which in the most favorable conditions requires 15 or more years. However, the time needed for it to form a consocies capable of shading out the shrubs is more than 40 years—a rough field estimate. In less favorable regions the time is indefinitely longer. At an age between sixty and a hundred years, the *Larix* consocies or individuals of it mature (Pl. XXXIX, *B*). As they die, *Picea*, if originally present in the vicinity, can invade and become the chief representative of the subclimax, because its seedlings can develop in the variable shade of the tamarack, the light values of which range from 10 to 50 per cent, quantities modified still further by the tamarack trees being deciduous and developing foliage somewhat late in the spring, before which time they cast little shade. In a mixed stand in which *Picea* occurs in equal numbers with *Larix*, the trees of the former in their natural growth will occupy the

A. Consocies of *Chamaecrium* on drained and burned bog. Baudette, Minnesota.



B. *Equisetum* on ash and charcoal remains in a bog. Baudette, Minnesota.

spaces occasioned by the death of the latter (Pls. XXXV, *A*, *B*, XXXIX, *B*). When the consocies of *Picea* is fully developed it reduces the light values to 8 or 4 per cent, a reduction sufficient to inhibit reproduction of tamarack seedlings, *Sphagnum* and many other of the accompanying plants of the heath stage. If tamarack and spruce appear in a mixed stand and the latter becomes an exclusive dominant, the invasion of *Abies, Picea canadensis* and *Thuja* is retarded until the swamp spruce reaches maturity.

As has been stated before, *Thuja* and *Abies* occupy the more mature portions of bogs, appearing ofttimes in the outer edges next to the mainland. Young trees of these dominants may start in the denser shade of spruce and tamarack, but either die or remain dwarfed until a removal of a few larger trees affords an opportunity for their growth. Apparently, seedlings of cedar, balsam and white spruce can start under swamp spruce and tamarack only after their soil, which is loose and mucky during wet seasons, reaches more advanced stages of decomposition and firmness. Their advent represents the maturity of the subclimax stage, because all of them live longer than tamarack and swamp spruce.

Swamps are often designated as tamarack, spruce, cedar or balsam swamps, but these may be regarded ecologically as phases or consocies of the subclimax. They may be regarded also as indicating the various ages of the subclimax. Most of the swamps of the state are immature, *i.e.*, they are at or below the spruce-tamarack stage. Younger bogs have just reached the *Sphagnum*-heath stage. In some cases this stage has been reached for the first time by a priseral development and, in other instances, perhaps the more frequent, it has been restored again and again subserally. The subseres of swamps, which have been burned just enough to have their trees killed, resemble essentially the succession under discussion. The main difference between them is the rapidity with which the former devlops as compared with the latter, since fire denudations tend to introduce foreign weeds and grass which hinder the invasion of trees.

d. Subseres in Drained and Cultivated Bogs: Theoretically, drainage and clearing may be sufficient to provide mesophytic conditions. However, the swamps which have been drained and cleared have not been abandoned and left undisturbed long enough to develop all the stages of a mesophytic subsere. From a study of those recently drained and cleared, it has been found that the early stages of the subsere resemble those on more mesophytic upland soils. The earliest invader is *Agrostis hiemalis*, which is followed usually by a consocies of *Chamaenerium angustifolium* (Pl. XL, *A*), or, in the places where brush has been burned, *Equisetum arvense* (Pl. XL, *B*) forms pure stands to be followed eventually by weeds and grasses, of which *Chenopodium album, Calamagrostis canadensis, Solidago canadensis* and *Erigeron canadensis* are the principal species. Seedings of *Populus* and *Betula alba* var. *papyrifera*, of an age of 5 or 6 years, have been found on drained and cleared bogs growing and increasing in numbers by vegetative

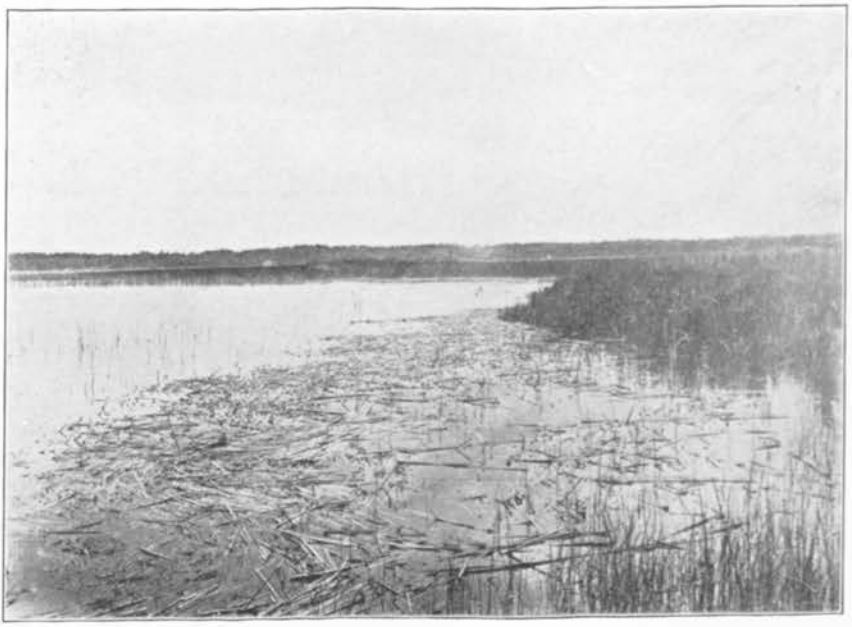
propagation as well as by seeds. Apparently, these had the same vigor as those on upland soils. Hence, it seems probable that a deciduous subclimax could be developed, which in its chief features would be like that growing on mineral soils. Drainage alone is sometimes complete enough to kill out the coniferous subclimax trees and initiate an upland sere which probably would develop into a *Populus-Betula* subclimax containing also a few individuals of *Abies* and *Picea canadensis*.

Cleared and drained bogs incur a great fire risk. Many in the middle and southern parts of the state, especially when bordering prairie, have been destroyed by fires. They are also poor frost hazards for the following reasons: Being wet lands, they give off during the brightest days much moisture which cools them at the surface. They are lowlands into which the cold air naturally drains on still, quiet, nights. Their soil, like sawdust or a mulch, is a poor thermal conductor; during the warmest days it absorbs little heat, a fact emphasized many times to the writer by his frequent discoveries of ice in the bogs in late summer. At night the non-conducting peat has little heat to radiate to the cold air blanketing it. On account of these factors, some insuperable to the agriculturist, the plants of a bog-land in northern Minnesota are subject to frosts during cold nights nearly every month of the growing seasons. Even killing frosts occur in July and August.

(7) *Subseres in Flood-plains*

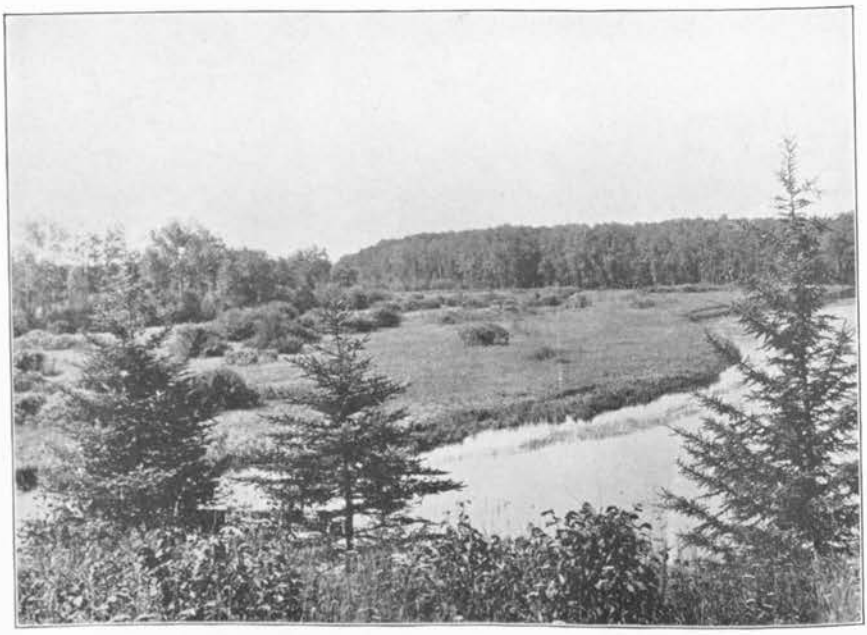
Along the banks of the upper Mississippi River and its tributaries, occur rather extensive flood-plains, a feature characterizing the streams of nearly all the rivers of the coniferous area in its middle and western portions. These plains have developed associes corresponding to the character and amount of flooding. Those flooded more or less continually produce the cattail-reed associes much like that of a lake in which the water-level fluctuates considerably. In the more sluggish streams that drain lakes, the fluctuations of the water-level are less extreme. Here the *Zizania aquatica* consocies or the *Scirpus* consocies (Pl. XLI, *B*) appears in the water next to the zone of *Carex*. In the small quiet lakes that maintain a more or less constant water-level, the rice-rush zone is often small or wanting, so that the *Nymphaea-Castalia* associes is adjacent to the *Carex* associes. But on large lakes, the rush zone sometimes extends a mile or so into the lake, and each year during storms can cast considerable quantities of debris ashore (Pl. XLI, *B*). In many shallow lakes rice may occupy all of the areas not covered by the rushes (Pls. XLII, *A*, XLIII, *A*). Higher flood-plains which are inundated occasionally or seasonally for a short time are covered by swamp grasses or sedges in which alder and willow bushes occur (Pl. XLII, *B*). On the upland border of such flood-plains may occur a zone of spruce and tamarack which tends to extend itself into the flooded area as fast as the high-water mark of the floods drops (Pl. XLIII, *A*).

A. Wild rice and sedge zones on Rice Lake. Itasca County, Minnesota.



B. Large zone of *Scirpus* in shallow water. Merrifield, Minnesota.

A. Rice and sedge zones on Popple River, Itasca County, Minnesota.



B. A narrow rice zone near large zone of grasses and sedges with clumps of willows and alders occurring on Big Fork River, Minnesota.

A. Small flood-plain showing zones of rice, cattails, sedges, tamarack and spruce. Deer River, Minnesota.

B. Wet meadow near Benedict, where fires have killed off trees and shrubs.

A. Photograph of quadrat in figure 26, viewed from right side.

B. Acer negundo, Ulmus, Ostrya and *Tilia* invading *Rhus* consocies. *Rosa blanda* in center. Gull Lake, Minnesota.

In the more mature river beds, there occurs the usual deciduous mictium subclimax of river flats, consisting of *Acer saccharinum, A. negundo, Betula lutea, Ulmus americana, Populus deltoides* and *P. tremuloides. Salix* and *Fraxinus* appear nearest to the banks, sometimes associated with *P. balsamifera. Quercus macrocarpa* and *Celtis occidentalis* are scattered along the higher portions of the flood-plain. Apparently, this mictium will be perpetuated as long as the river overflows periodically and denudes the area of seedlings incapable of withstanding flood conditions.

(8) *Subseres Beginning with Grass*

As has been mentioned before, grass stages are developed in subseres whenever the shrubs and subclimax trees are not allowed to follow the herb stage directly. Grazing, burning or mowing develops on mesophytic and wet soils respectively blue grass pastures or a sedge-grass meadow (Pl. XLIII, *B*). The latter, developed by burning, flooding or mowing, has already been discussed, together with the probable seral stages following it when denudations cease. A similar discussion will be subsequently made of bluegrass and the plants invading it.

Prairie on the driest soils may or may not be followed by jack pine without an intermediate stage. However, prairie on damper soils, or even bluegrass pasture, is invariably followed by the *Rhus* consocies, which on dry sandy outwash plains is never thick enough to prevent the entrance of the jack pine seedlings. The sumac consocies succeeding a bluegrass pasture or dense prairie is often shady enough to prevent the ecesis not only of jack pine but even that of aspen and birch.

The Rhus Consocies: The *Rhus* consocies may be formed by either of the two common species, *R. glabra* and *R. typhina.* The two may form in places near the southern boundaries of the coniferous area an associes. The former is more common in the areas studied. *R. rydbergii* is sometimes a subdominant in the sumac communities (Fig. 26 and Pl. XLIV, *A*).

So far as is known, seeds of *Rhus* are scattered by wind and birds. The seeds are only slightly adapted to either agent. The flesh is acrid, and, judging from the amounts left on the plants in the spring, very few birds visit the clusters. In late winter, the flesh of the fruits is dry and the epicarp is somewhat inflated, so that wind can drive the dislodged fruits, when lying on a snow crust, over long distances or until they are caught against some obstacle like a fence, shrub cluster or wind-break. When the clusters are disintegrating, the average weight of a fruit is about .014 gram and occupies about 30 cubic millimeters of space. This ratio between weight and volume makes it appear that wind dissemination is more effective and probable than animal. Birds do frequent the thickets in the winter, especially sparrows and snow birds. Bluejays, robins and woodpeckers peck at the clusters, but in most cases they seem to be hunting the larva or adult stages of insects.

Winter birds, by pecking at the clusters, aid the wind to disintegrate the bunches and scatter the fruits upon the snow. From the sporadic appearance of sumac in small remote areas, it has always been assumed that the seeds of the pioneer plants have been carried there by long distance means, but it is difficult to distinguish between pioneers and relicts. The germination of sumac has not been studied sufficiently to give trustworthy results. Its seedlings have rarely been found in the many places studied.

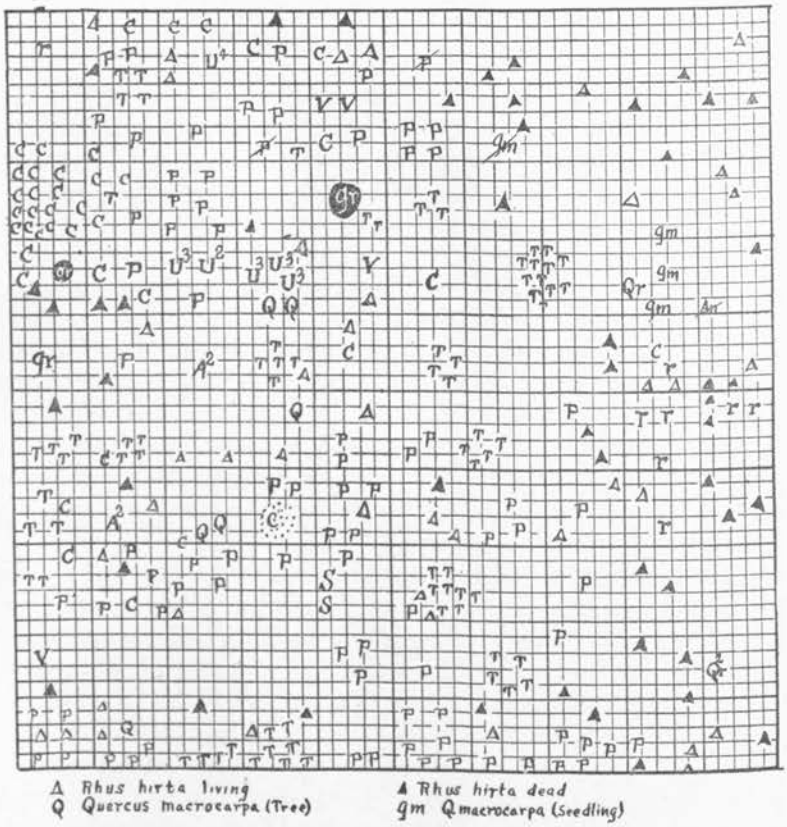


FIG. 26. Quadrat of a *Rhus* consocies being invaded by trees. Gull Lake, Minnesota.
LEGEND:

An *Acer negundo,*
A *Acer saccharum,*
C *Corylus americana,*
P *Prunus virginiana,*
Q. *Quercus macrocarpa* (trees),
qm *Quercus macrocarpa* (seedlings),
qr *Quercus rubra,*
r *Rosa blanda,*
ru *Rubus strigosus,*
S *Salix sp.* (seedlings),
U *Ulmus americana,*
V. *Ostrya virginiana,*
Δ See above.

It is a well-known fact that sumac makes its advances into the grass by means of its roots, which are seldom deeper than 2 inches beneath the surface of the soil. In loose soils, well-mulched with well-formed sod, the roots may be less than 1.5 inch beneath the surface, but in drier soils the depth is correspondingly greater. In the years of 1913, 1914 and 1915, the advance that sumac made upon the grass varied from 10 to 15 feet. During the summer of 1916, the total advance was less than 10 feet, a decrease due no doubt to a drouth in July. It is, of course, obvious that the annual advance is closely related to the amount or seasonal distribution of rainfall during the growing seasons. In years between 1912 and 1916, the average combined length of the main roots and their branches of a single plant often exceeded 30 linear meters and occupied about 10 square meters. Of the 10 or 12 important branches sent out in the development of such a root system, 3 or 4 main ones extend outward toward the open prairie. Those appearing farther out in the open naturally send up the more vigorous sprouts, which in turn feed more abundantly these more fortunate roots. The roots that happen to place their leafy shoots in shade or in otherwise unfavorable spots, being starved because their offspring fail in competition, cease growing and finally die; hence, the main growth of the root system is directed toward the open as a result of the individual competition for light on the part of the members of the consocies.

When the branches of the plants are burned, new sprouts take their places, and, owing to the underground system, the new shoots are very vigorous, some attaining a height of 3 feet the first season. It is evident then that *Rhus*, when once introduced, can remain in spite of annual fires, though it may not make new invasions. The importance of the root system is further emphasized when we realize that more than two-thirds of the total growth of sumac is underneath the ground.

In the coniferous area, sumac may appear unaccompanied by any other important shrubs, but in the southern and central parts of the state it is associated more or less intimately with *Symphoricarpos occidentalis*. In the vicinity of Hubert, on the sand outwash, it appears with *Ceanothus, Corylus* and *Rubus*, but in its best stands only a few shoots of *Rubus* occur. In mesophytic soils, *Corylus* may follow the advance of *Rhus* and terminate the shrub associes.

The sumac consocies reduces the light to 15 or 30 per cent, a reduction which thins out the grass. It raises the water-content very little, except when it is followed by *Corylus* or collects considerable amounts of loose vegetable matter during wind storms.

The Subclimaxes or Climax Following Rhus: In the northern part of the state, the successional stages following sumac are essentially like the well-known subseres of prairies or those beginning with prairie, only the former take place on a smaller scale. *Ulmus americana* and *Ostrya virginiana* are among the first invaders (Pl. XLIV, *B*), but in the vicinity of hardwood

communities, bur oak and basswood are the tree pioneers (Fig. 26). If the sumac consocies is too densely populated, white birch may be excluded together with aspen which rarely invades it. Apparently, red and scarlet oak are the more successful invaders of the oak genus.

From a study of the small patches of *Rhus*, it has been found that the following subclimax stages may appear after it:

a. Betula-Populus Associes.
b. Pinus-Betula Associes.
c. Ulmus-Tilia Associes.
d. Quercus Associes.

It also appears that sumac is followed directly by the hardwood climax, the smaller oaks and the basswood entering before or with the maples. The oak subclimax in the vicinity of pines is followed by both *P. strobus* and *P. resinosa*, a typical example of this occurring on the east and south shore of Gull Lake west of Hubert (Pl. XLV, *A*).

II. The Acer-Fagus Climax

Within the coniferous area of the state, *Acer*, which forms small groves varying from a few acres to areas embracing several square miles, is the chief representative of the *Acer-Fagus* climax. Along the west and south boundaries of the coniferous area, between the prairie climax and the pines, the hardwood forest occurs whenever it has had opportunities to develop, though the greater part of it probably belongs to the related community, the *Quercus-Hicoria* association. The soil of the hardwood forest has a comparatively high holard. Where the floor of the forest is covered with humus, 3 to 8 inches deep, the holard at the surface varies from 20 to 150 per cent, while that of the second decimeter ranges from 15 to 35 per cent.

The light reduction of such a forest, ranging from 1 to 5 per cent, excludes all trees except seedlings of *Acer, Tilia, Ulmus* and *Ostrya;* but those of the maples are the only ones that have much shade tolerance. Seedlings of white or red pine have seldom been found in the shade of the deciduous climax dominants, and conversely maple seedlings have rarely been found under the pines. *Tilia, Ulmus* and *Quercus* are intimately associated with maple, so much so that this association has been called the *Acer-Tilia* association, but basswood and elm are probably not climax dominants. *Q. macrocarpa* is to be regarded as a climax dominant of the oak-hickory association in this region (Clements, 1920, 1928; Weaver and Clements, 1929).

The herbs of the maple hardwood groves are sparse. In the lighter places, *Hydrophyllum virginianum, Geranium maculatum, Maianthemum canandensis* and *Phlox divaricata* appear in societies. The spring aspect is often due to colonies of *Sanguinaria canadensis, Anemone quinquefolia* and *Syndesmon thalictroides*. The aspect of midsummer is formed by such plants as *Rubus triflorus, Fragaria virginiana, Aralia nudicaulis, Aquilegia*

A. Oak grove being replaced by white and red pine. Hubert, Minnesota.

B. *Populus* consocies in Ottertail County, with grass at the edge.

canadensis, Urticastrum divaricatum and *Thalictrum dioecum.* In larger groves *Sanicula marylandica* and *Washingtonia longistylis* form characteristic societies.

Of the many herbs and ferns, found in the hardwood forest, the following list includes the most familiar species: *Actaea rubra, Aralia racemosa, Asarum canadense, Botrychium virginianum, Caulophyllum thalictroides, Smilacina stellata, S. racemosa, S. herbacea, Trillium cernuum, Uvularia grandiflora, Viola papilionacea, V. pubescens* and *V. sororia.*

The following shrubs are suppressed and scattered in the dense shade, but conspicuous and more abundant in the lighter spots: *Amelanchier canadensis, Cornus stolonifera, Corylus americana, Crataegus macrantha, Parthenocissus quinquefolia, Prunus americana, P. virginiana, Rhus rydbergii, Ribes cynosbati, R. gracile, Rosa blanda, Rubus strigosus, Viburnum opulus* and *Vitis vulpina.*

A list of secondary trees would include *Betula lutea, Celtis occidentalis, Quercus alba, Q. coccinea, Q. macrocarpa* and *Q. rubra.*

Q. alba and *Celtis* seem to be limited in their northward invasions by late frosts which destroy their flowers, or by early autumn frosts which kill the germs of their immature fruits. Individuals of hackberry appear as far north as the southern shores of Lake of the Woods. The most northern appearance of *Q. alba* in Minnesota noted by Bergman and Stallard (1916) is near the southern shores of Lake Superior where a few isolated trees were found, though it is said to occur commonly farther northward in Wisconsin. In these northern places, it seldom bears much fruit.

(1) SUBSERES IN THE MAPLE CLIMAX

Since the hardwood association is found on mesophytic soils, the most important subsere will be akin to those of the well-drained clay and sandy loam soils of the pine climax. The degree of denudation by fire in a deciduous forest is never quite so severe as in a pine forest. Fire rarely kills many of the adult trees, nor does cutting and burning combined kill all the stumps and seedlings of the climax dominants. Basswood and several other species, more particularly some of the oaks, regenerate from stumps.

The Herb Associes

The dominants determining the character of the herb associes here also depend much upon the degree of denudation. Where the forest is merely cut-off, the most prominent herbs of the forest floor, such as *Sanicula, Aster, Aralia, Washingtonia, Fragaria* and *Rubus triflorus* spring up, constituting the main dominants. Further denudation leads to the invasion of *Solidago canadensis* and *Erigeron canadensis.* Such grasses as *Andropogon, Stipa, Argrostis hiemalis, A. tenerum, A. repens* and *Poa pratensis* persist after the weed stage, in case the herbs are not promptly succeeded by the shrubs. In the vicinity of the prairie, annual or frequent burnings produce prairie from

the weed stages, and grazing will bring about a grass stage of quack grass and blue grass. The herbs developing the associes on abandoned fields are weeds which have persisted during cultivation, the main dominants being: *Ambrosia artemisiifolia, A. trifida, Brassica nigra, Bursa bursa-pastoris, Chenopodium album, Erigeron canadensis, E. ramosus, Lepidium apetalum* and *Solidago canadensis.*

The following grasses are almost sure to occur on cultivated fields: *Agropyron, Hordeum, Setaria, Stipa* and *Bromus. Melilotus, Trifolium album* and *T. hybridum,* often relicts of cultivated crops, are nearly always present in the herbaceous associes of cultivated fields. Either a blue grass or prairie stage may develop in abandoned fields if the invasion of shrubs and trees fail.

The Shrub Associes

After moderate denudation, the usual hazel-raspberry associes develops, differing in no essential features from the corresponding associes of the subseres leading to the pine climax. The prairie and the blue-grass stages are invariably invaded by snowberry and sumac, an invasion already described on page 535. In moist areas elder forms thickets of considerable importance, often along streams and bog edges.

The Populus-Betula Associes

The hazel-raspberry associes, which is regularly followed by aspen and birch in the pine climax, is succeeded by these in the western and southern part of the state where the maple consociation or oaks are the climax dominants. In large cultivated fields, the aspen (Pl. XLV, *B*) may follow. Where pastures are grazed, oak trees may stand directly surrounded by grass except at their bases. Where burning, mowing and grazing are withheld the *Rhus* or *Corylus-Rubus* associes appear.

The Climax

In small denuded areas of this consociation, the climax dominants restore the climax promptly from the seedlings and sprouts left on the land after the denudation. When a aspen-birch associes is established, the seedlings of maple, basswood and oak will finally crowd out the subclimax dominants, because they live longer and grow higher. The seeds of the latter trees can germinate and grow in considerable shade and mature in the more favorable places, though maple is the more shade-tolerant. The invasion of maple is preceded or accompanied by other species, usually secondary or subordinate, namely, white elm, ironwood, hackberry and certain oaks (Pl. XLVI).

(2) SUBSERES BEGINNING WITH PRAIRIE

On drier soils the subclimax may consist of *Quercus macrocarpa, Q. coccinea* and *Q. rubra,* each capable of enduring considerable burning without

Hard maple forest with white birch, ironwood, basswood and elms.
Gull Lake, Minnesota.

injury, or, if the parent trees have been severely fire damaged, capable of sprouting up from the stumps. *Q. alba* is unable to regenerate in the field by sprouts; hence it cannot endure in places frequently burned. This has been observed several times in Houston County by Bergman and Stallard who have surmised that it is limited westward in Minnesota by fires on the floor of the forest, since it grows principally in abundance on upland soils that are protected by fire barriers. Wherever fires are frequent, the entrance of maple and basswood is also inhibited. Small grass fires do not readily kill bur, red and scarlet oak, except when they are young, which prevents their establishment by seeds. Hence an area periodically burned, although maintaining the large trees of the oak associes, does not extend its boundaries until fires have been more successfully controlled. With better fire prevention, the maple and basswood invade and begin establishing the climax. The oaks or the deciduous mictium are usually, though not always, separated from the prairie grass by the shrub zone which consists of hazel, raspberry, wild plum and choke cherry near the timber, but of snowberry and sumac near the prairie.

Discussion

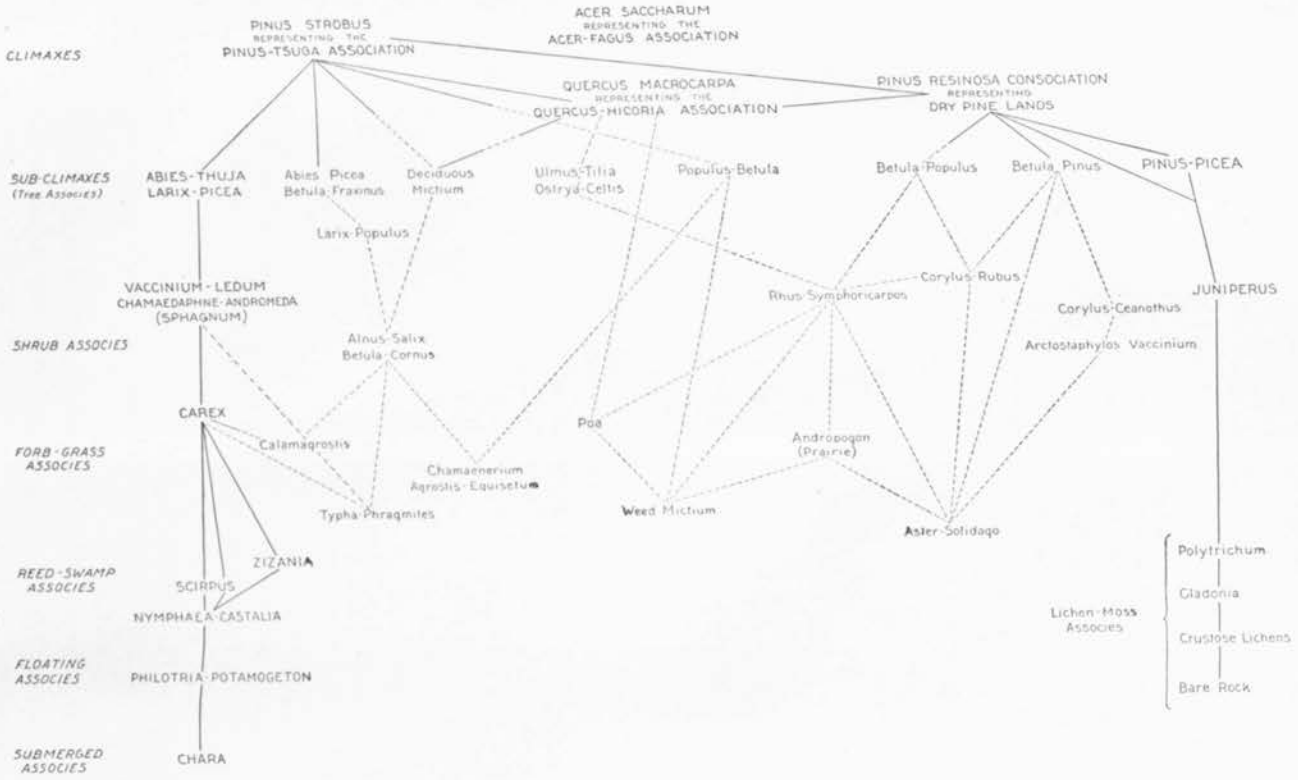
A summary of the successions and their relations to each other and the priseres, sketched in figure 27, differs in few respects (chiefly only in the bog seres) from the conclusions reached by Cooper (1913) in his extensive work on Isle Royale. Cooper regards balsam, white birch and white spruce as the climax dominants of Isle Royale, since he found so few pines there, repeated burnings having almost eliminated them; and since the islands are so far from the mainland that immigration to it by seeds is impossible. However, a few white pine relicts still exist on these islands which no doubt promote invasions into the subclimax at least locally, so that theoretically and logically it would seem that white pine is the climax dominant here as on the mainland, regardless of the time required for it to overcome the balsam, spruce and birch.

The subseres of burns and clearings in Minnesota upland are essentially like that which Whitford (1901) described for northern Michigan. He concludes that the pines form the coniferous climax and that maple-beech forms the deciduous association. Beech is, however, not present in the hardwood forest of northern Minnesota, and hemlock likewise is absent from the coniferous forests.

Jennings (1909), working in Pennsylvania, shows that clearing and continual burning on sand ridges produce almost the same sumac and oak associes as occur in Minnesota.

Howe (1910), in a study of the reforestation of sand-plains in western Vermont, finds that white pine ultimately regains control on abandoned fields by direct reseeding, by displacing white birch, or by replacing pitch pine; the latter does not occur in this region of Minnesota.

Lange (1901), in a study of the colonization of an island, noted that



NOTE - Fig 27. Solid lines represent course of the PRISERES ——
Dotted lines represent course of the SUBSERES ------

sumac, hazel, maple, dogwood and oak are very slow invaders, and decided that the main ecesis of the shrubs was from propagation, an opinion reached by the writer.

In discussing each subsere, the following processes upon which succession depends have been treated, namely, invasion, reaction and competition. Invasion results from successful migration and ecesis; successful migration depends upon the amount of seed produced, their mobility and the physical agents disseminating them. It also depends upon vegetative propagation of various forms, such as roots, rootstocks, runners, etc., which are slow but positive means of invasion where seed germination, growth and reproduction in a new habitat is difficult. The critical reaction of the most important invaders upon the soil and atmosphere of an occupied area is registered by the decrease in light and the increase of available water. Competition is produced through the influence that plants have upon each other through changes in the physical factors of the habitat, the most critical ones being water and light, for it is through these two factors that competitors wage their war. Invasions may be made upon the surface or underground or beneath water of ponds. Stability is produced when invasion is checked. Stabilization is attained in the two final stages, namely, the pine climax and the hardwood association.

Conclusions

The following are the probable reasons why pines form the mature stage in the coniferous forest:

(*a*) They are perhaps the most shade-tolerant of all the coniferous trees of the state. While red pine grows faster in the open than in the shade, its rate increases with age and height in the shade until it has no insuperable difficulty in eliminating jack pines where the two species compete. The best type of red pine does not appear on the xeroid soils, but such soils do produce a fair grade of timber. From counts made of seedlings of white pine, the rate of growth seems to be as rapid in the shade of hazel, aspen and birch as in the open. Its young seedlings, however, are more subject to disease and injury in dense shade than in the open, due to the increase of humidity, as Hofmann (1914) has shown, but a medium amount of shade is favorable to them. In the densest shade of balsam and white spruce, ecesis of white pine is slow; its seedlings are few, small and puny, but here also can scarcely be found seedlings of balsam and spruce. In medium shade or that of tamarack or swamp spruce on upland soil, its successful ecesis is comparatively rapid.

(*b*) The pine trees are higher, attain a greater age and develop stands which cast denser shade than any other trees of the state except dominants of the hardwood climax and dense clusters of spruce and balsam. The present pine stands are always protected by fire barriers, which would tend to prove that in disturbed areas they are the climax dominants of the coniferous area.

(*c*) The pine relicts, such as stumps, fallen logs and large trees with

forms characteristic of those grown in forests, which are now found in small nooks protected from fire, show that denuding agents have destroyed the pines that undoubtedly occupied a large portion of the upland of the state, and this evidence is supported by the accounts of lumbermen.

(*d*) In the mature stage of the two pine consociations, no other trees are being established. The forest floor of red pine stands has no successful seedlings of any of the subclimax dominants. White pine in competition with balsam, white birch and white spruce tends to eliminate them, as was noted in the white pine forests in Koochiching County on the Big Fork River, where no seedlings of the subclimax dominants could be found. In rather wet soils, where the mature stand is densest, not even successful seedlings of white pine are found.

Summary

1. The pine-hemlock climax is represented chiefly by red and white pine in the coniferous area of Minnesota.

2. The red pine consociation succeeds the following subclimaxes: the spruce-pine associes, the birch-pine associes and the aspen-birch associes.

3. The white pine consociation succeeds the following subclimax associes: aspen-birch, aspen-tamarack, oak and probably the tamarack-spruce.

4. Wherever a good stand of jack pine is attainable, red pine can invade and replace it. In most places seedlings of red pine are actually found coming up in the jack pine consocies.

5. The subclimax associes occur in soil habitats peculiar to them: (*a*) The spruce-pine associes, consisting of jack pine and swamp spruce, occurs on rock out-crops which have been covered with a deep deposit from lichens and mosses. (*b*) The pine-birch associes, consisting of jack pine and white birch, occupies xeroid sandy soils and rock out-crops where the deposition of lichens and mosses is less than that of the above associes. (*c*) The aspen-birch associes occurs on soils varying from rather dry sandy loam to wet clays and loams; even drained bogs may be occupied by it. (*d*) The aspen-tamarack associes inhabits wet clays and wet loams. (*e*) The balsam-spruce associes, consisting of balsam, white spruce and white birch, develops on wet soils which are veneered with organic depositions varying from a few inches to many, or in bogs. (*f*) The deciduous mictium is found on floodplains. (*g*) The tamarack-spruce associes is found principally in bogs. (*h*) The oak associes appears on sandy soils or on loams where prairie or grass stages have preceded it or encroached upon it. White oak seems to be limited northward by early autumn frosts, which kill the fruits, and by late spring frosts which kill the flowers. Its westward limitation is influenced by fires that easily kill the seedlings or larger trees, which are unable to propagate by sprouts. It is more readily killed by fire than are the other companion species of oaks occurring in Minnesota.

6. The subseres of the maple consociation are similar, if no identical, to those occurring in the pine formation.

7. The stage preceeding the subclimax consists of shrubs, the dominants of which vary according to various ecesic and edaphic conditions, as follows: (*a*) *Juniperus* occurs in the prisere developing on rock outcrops. (*b*) *Ceanothus* occurs chiefly on the sand barrens and outwash plains. (*c*) The hazel-raspberry associes occurs in the more mesophytic habitats. (*d*) The alder-willow associes occupies wet lowlands or bogs. (*e*) The birch-alder associes, consisting of swamp birch and swamp alder, arises under conditions similar to the preceding associes. (*f*) The sumac consocies occurs at the margins of hardwood timber adjoining dry or mesophytic grasslands and at pine forest margins.

8. The intensification of the shrub stands is, in most instances, accomplished by propagative methods rather than by seeds. Especially is this true of the following; sumac, raspberry, rose, hazel, willow, dogwood, and alder.

9. The more successfully a shrub can use subterrean methods for migration the better able it is to invade grass lands.

10. *The Effect of Fires:* Fire has been the most universal and frequent agent of destruction, destroying not only the upland vegetation but that of the bogs as well. Fire in a dry season, by causing burn-outs in a bog, which later becomes filled with water, initiates a succession similar to that started by flooding. Repeated burning on any soil, except on rock outcrops, will produce a grass stage, although in bogs deep burning starts a reed or rush associes. Fire may totally destroy a bog or the organic soil of rock outcrops, thus starting succession at almost primary conditions, hydroseral in the former case, xeroseral in the latter. The grass stage of the mesophytic and dry areas is invariably followed by sumac, except in dry outwash plains, when it may then be invaded directly by jack pine. Grass stages of wet lands, whether bog or mineral soils, are followed by willows and alders. The presence of the following plants in associes or consocies in bogs nearly always indicates disturbances of some sort: alder, swamp birch, blue joint-grass (*Calamagrostis*), cat-tail, reeds and willows. This conclusion is reached from the fact that few or none of these plants occur to any extent in zones surrounding undisturbed lakes.

Sphagnum hummocks left by fire regenerate the *Sphagnum*-heath mat largely by propagative methods. They do not raise the water-level by deposition and cannot live by deriving all their water from underlying layers. They too depend upon rain. The *Sphagnum* mat provides for the ecesis of tamarack and spruce, whose maximum shade is sufficient to curtail its growth or obliterate it altogether.

Applications

As may readily be seen from the plates and figures, the investigation proves that natural reforestation is occurring with a fair degree of rapidity wherever fires are inhibited. In rock areas severe burning has often bared the rocks to such an extent that it will require centuries for the forest climax

to return. Proper methods of forestry, followed in accordance with the nature of succession in the subseres, could, the writer believes, be readily used to increase the natural processes of invasion and reaction, thus hastening the subseres to the climax or subclimax, as may be desired, and with less expense than that incurred by transplanting.

Bogs may be converted into forests, meadows, or cultivated fields, at will, by withholding, applying or giving free rein to denuding agents. The forest of bogs may be of tamarack, spruce, balsam or cedar, depending upon the maturity of the soil. Cedar and spruce yield valuable timber, and bogs under proper treatment may be made to develop a forest suitable for commercial use about every century. From the characteristics of the natural grass, it would seem that cultivated grasses might be made to replace the wild species. It is doubtful that many cultivated plants can be grown on cleared bogs because of the frequency of frosts. Timothy apparently could be grown advantageously on cleared bogs. Hardy garden plants, as cabbage, lettuce, turnips, etc., can be successfully grown in bogs properly fertilized. Large crops of potatoes can occasionally be grown in bogs if killing frosts do not occur during the growing season.

A general function of vegetation is the maintenance of the soil and water. The government, by building dams at suitable places, has made an attempt to hold back and store up water in the head streams of the Mississippi River, a measure deemed necessary to keep the river supplied with water for navigation and power during seasons of insufficient rainfall. This control in the uncultivated portion of the state should be augmented by retaining forests around the reservoirs, which will prevent the natural run-off and erosion from filling the lakes with mud and sand. The forests are natural reservoirs which should be maintained, if for no other purpose.

Lake maintenance, as well as river-water maintenance, depends much upon preservation of the forest soils and lands. Particularly is this true where the soil is non-retentive and the runoff is rapid. The animal life of the lakes is best protected and cared for by retaining the natural vegetation surrounding the lakes and rivers emptying into them. Northern Minnesota is admirably located climatically for resort lands and public parks. Much of the soil will never be cultivatable because it is too rocky or consists only of organic debris upon rock outcrops. The state should make a soil survey and determine what lands should be made into public forests. It is more than a state problem in some of its aspects, because it involves the source of water for interstate and international sections. The national importance of reforestation in Minnesota has been admitted by the establishment of National Forests in certain portions of the coniferous region. But, comparatively speaking, up to this date (1917), the attempt on the part of both state and nation to deal constructively with the forests of Minnesota has been limited.

In making a soil survey, the subclimaxes may be used as soil indicators by methods already used extensively by ecologists and soil geographers. A

knowledge of seral stages and their reactions on the habitat makes it possible to predict, with a fair degree of certainty, the nature of the soil beneath them (Clements, 1920, 1928).

The construction of highways for rapid transportation, taking place in the state since this work was started, should aid forest patrols in preventing fires or subduing them after starting. But, by bringing greater numbers of visitors into the combustible regions, they also increase the likelihood of fires, a problem which can be met only by closer supervision of campfires and smoking habits.

A proper treatment of the waste lands of the state by the local and national government will provide handsome parks with beautiful fish-stocked lakes and ultimately supply quantities of desirable lumber.

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