THE UNIVERSITY OF MINNESOTA

GRADUATE SCHOOL

Report

of

Committee on Examination

This is to certify that we the undersigned, as a committee of the Graduate School, have given Raymond Horace Landon final oral examination for the degree of

Master of Science

We recommend that the degree of

Master of Science

be conferred upon the candidate.

William S. Cooper
Chairman

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F. K. Bullock

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Royal N. Chapman

Date May 31 1922

10-20 5M

THE UNIVERSITY OF MINNESOTA

GRADUATE SCHOOL

Report

of

Committee on Thesis

The undersigned, acting as a Committee of the Graduate School, have read the accompanying thesis submitted by Raymond Horace Landon for the degree of Master of Science. They approve it as a thesis meeting the requirements of the Graduate School of the University of Minnesota, and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science.

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Date May 31 1922

10-20 5M

Vegetational Development On The Rock Cliffs Of The Minneapolis Region

A thesis presented to the Faculty of the Graduate School of the University of Minnesota in partial fulfilment of the requirements for the Degree of Master of Science

by

Raymond H. Landon

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Vegetational Development On The Rock Cliffs Of The Minneapolis Region.

I. INTRODUCTION.

Since the only important surface exposures of the country rock in the Minneapolis region are along the gorges of the Mississippi and Minnesota Rivers my observations were confined to these places. The exact field of study extended along the Mississippi River from the Washington Avenue Bridge to the mouth of the Minnesota River and up the latter stream a distance of two miles. Both sides of the gorges were studied as well as the adjoining ravines.

The purpose of the study was to trace the development of plant life upon the two important rock exposures of the region, the St. Peter sandstone and the Platteville limestone with especial regard for the effect of all modifying factors.

The observations upon which my work is based were made during the fall of 1921 and the early spring months of 1922.

I wish to express my thanks to Mr. R. N. Williams of the New York Botanic Gardens and Dr. Bruce Fink of Miami University for their kindness in determining the mosses and lichens collected during my studies.

To Dr. W. S. Cooper, under whose direction this work has been carried on, I wish to express my appreciation for his interest and helpful suggestions.

II. NATURE AND ORIGIN OF HABITAT.

A. The rock formations. - The exposed rocks of the Minneapolis region are Ordovician in age and are all of sedimentary origin. They are exposed in steep escarpments along the valleys of the

rivers for a height of a few feet to over one hundred feet at the High Dam, depending upon the magnitude of the talus slope.

The lowest exposed formation, comprising about two thirds of the exposed rocks in vertical section, is the St. Peter sandstone. It is an easily weathered, thick-bedded, jointed, and cross laminated rock with very few crevices.

The sandstone is capped by a layer of Platteville limestone which varies in composition in that it can be separated into four quite distinct strata. The lowermost, about four feet in thickness, is a transition between the St. Peter and Platteville formations. The next stratum, thirteen feet in thickness, is composed of irregular compact laminae separated by partings of a claylike nature. Then comes a five foot bed of partly shaly limestone which weathers very easily. The top stratum, eight feet in thickness, is a quite homogeneous limestone which breaks with a conchoidal fracture, and falls away in blocks. Crevices are common in the limestone formation.

The Platteville limestone is covered by the Decorah shale with a maximum thickness of about seven feet. This heterogeneous shale weathers to clay after short exposure. It is of no importance as regards vegetational development with the exception of the weathered material which collects in the crevices and upon the ledges of the underlying exposed rock faces to aid in soil formation. Material from the mantle of glacial till which covers the Decorah shale is also of importance in that it contributes to the soil that is being formed.

As far as the chemical composition of the two chief rock formations is concerned it has little effect in determining vegetational development in that the sandstone is more or less calcareous

as a result of the water precolating down from the limestone containing lime salts in solution. The differences in the development of vegetation are therefore due to other causes which will be considered later.

B. History of the gorges. - After the Wisconsin ice sheet finally disappeared the post-glacial Minnesota River, the River Warren, then the dominant stream of the region, flowed in a shallow gorge over the limestone, following the present course of the Minnesota and of the Mississippi below Fort Snelling, to a point in the southern part of the present city of St. Paul where it entered the much deeper valley below St. Paul. A fall began here, which worked its way back to Fort Snelling and up the Minnesota Valley to a point about two miles above Mendota, where the limestone disappears. The cliffs which bound the resulting gorge form a part of the field of study. When the fall in the River Warren reached Mendota it encountered a narrow, buried, pre-glacial valley extending in a northwesterly direction up the present course of the Mississippi to a point about a mile above Fort Snelling. The portion of the buried valley crossed by the River Warren was quickly cleared of drift and the fall continued up the present Minnesota Valley. The Mississippi also cleared its portion of the old valley to a point where it entered over the rocky wall on the northern side, thus initiating the Falls of St. Anthony. This fall has worked back to its present position, resulting in the formation of the gorge to the same point.

The ravine of Minnehaha Creek, which exhibits some rock exposure, was formed in part by a former channel of the Mississippi, and in part by the creek itself.

The action of erosive forces, especially along certain of

the fissures and fault lines in the rock formations, has resulted in the development of occasional ravines along the gorges of the Mississippi and Minnesota rivers. Ravines are more numerous and of greater size in the older portions of the river gorges; the upper portions being almost straight, unbroken cliffs. This is especially true of the Mississippi. The ravines, which are in all stages of development, offer excellent contrasts as regards the factors furthering or retarding plant development.

III. VEGETATIONAL DEVELOPMENT.

The various stages of vegetational development are as a rule not sharply defined on the rocks of our region. The pronounced steepness of the exposed rock, its friable nature, and the effect of slumping from the upper parts of the exposures are responsible for the repeated destruction and reestablishment of pioneer stages. Until the talus slope becomes important or shading results from the growth of trees the habitats remain very much the same. The effect of steepness on the development of vegetation was noticed by Cooper (5) in his work on Isle Royale. Crustose lichens and sub-climax forest trees side by side are not uncommon. This has also been noted by Miss Braun (2). Succession is generally slow for the reasons just given, and many stages are discernible within a limited area.

A. Development on the St. Peter sandstone.- The St. Peter sandstone is the lowermost of the exposed rocks of the region available for study. It contains more water than the overlying limestone, thus making initial plant establishment less difficult. The rock is softened by the leaching out of the binding material, especially where wet, and crumbles to sand very easily. Crevices are not numerous and are of little aid in affording places for the lodgment

of plant disseminules.

The rock has horizontal bedding planes of finer material running thru it at intervals of six inches to three feet which have a decided influence upon the development of vegetation.

The collection of water above these layers favors the development of plants and in one especially favorable place, there being some shade, eleven corresponding parallel zones of plant life were to be seen. On the exposed rock faces even the additional water above the bedding planes is not sufficient to counter-balance desiccating factors. A series of samples with reference to the bedding planes were collected and the water content determined. The results show quite clearly the effect of the finer grained layers upon the water content of the sandstone.

Location of Sample.	Water content in percent of dry weight.			
Above fine-grained bedding plane	4.3	7.7	7.9	9.0
Below " " " "	2.6	3.4	0.6	1.1

The samples were collected October 28, 1921.

The various successional stages will now be considered with consideration of their reactive effect upon the habitat.

Upon freshly exposed sandstone, where the rock is moist and especially where protected from the sun and wind, unicellular blue-green or green algae quickly establish themselves. The gelatinous sheaths of the algae hold the friable sandstone together and and retard weathering. This has also been noted by Clements (4) and Shimek (12).

A moist, shaded space about one foot square was freshly exposed on October 20, 1921, and when visited again, November 7, showed unmistakable evidence of the establishment of a low form of

plant life which was undoubtedly algal.

Following the algal stage come the crustose lichens which may be the pioneers when the algal stage is omitted. On the sandstone this stage is represented by a limited number of species, the region being deficient in lichens according to Fink (9), as the result of the dry climate. He states that in the Minneapolis region there is no single lichen characteristic of the river bluffs. The crustose lichens are important pioneers upon igneous rocks but upon our sedimentary exposures they are of minor importance. However they are important in that they furnish a place for lodgment of the disseminules of higher plants. Lichen hyphae are able to penetrate the rock for short distances, Bachman (1), and by the secretion of acids among which carbonic acid is probably the most important, slowly assist in the disintegration of the rock. This has also been noted by Fink (8). They also add their mite to the accumulating humus.

Crustose lichens, with one exception, are better represented upon the limestone than upon the sandstone even tho the moisture conditions are more favorable nearer the river level. Their poor development is due to the rapid weathering of the latter.

The most numerous lichens of the crustose variety upon the sandstone are: Amphiloma lanuginosum (Hoffm.) Nyl., Placodium cinnabarinum (Ach.) Anzi., Placodium citrinum (Hoffm.) Leight., Lecanora varia (Ach.) Nyl., and Lecanora subfusca var. coilocarpa Ach. Amphiloma is probably the most abundant crustose lichen of the sandstone. It grows luxuriantly in shaded places and at times smothers low growing mosses. Miss Braun (3) has observed this lichen growing extensively upon the shaded rocks of the Cincinnati region.

The foliose lichen stage is best represented on the sandstone by Physcia pulverulenta (Schreb.) Ny. and Parmelia saxatilis (L.) Ach. Both of these lichens are fairly common on the moister shaded rocks. The foliose lichens frequently grow over the crustose forms, thus eliminating them.

An interesting case of the foliose lichen, Physcia speciosa (Wulf.) Nyl. growing upon and apparently parasitizing a moss was noted. McWhorter (15) believes that it is possible for lichens to sustain an organic relationship with mosses.

The fruticose stage is conspicuous in places because of the well developed patches of a Cladonia, unidentified because sterile when specimens were collected, which forms a thallus up to half an inch in thickness. It is the most mesophytic of the lichens and is found only in the most shaded and sheltered places. This lichen grows rapidly and was observed smothering out mosses very effectively. The thallus because of its uneven external surface affords an excellent place for the lodgment of seeds and spores. Occasional specimens of Cladonia fimbriata (L.) Hoffm. and Ramalina sp. were found in moist crevices. Other fruticose lichens also occur but are so infrequent that they are of no importance ecologically. Some idea as to the scarcity of the lichens on the sandstone may be obtained from the statement of Fink (8) that but five percent of the lichens of the region occur on that rock.

The moss stage is fairly well represented in places with an interesting variety of mosses correlated with various habitat conditions. Shade and moisture together with the degree of hardness of the sandstone determine what species occupy certain areas. The moist crumbling sandstone rarely supports well developed moss

colonies while the dry shaded rocks are frequently covered with a dense mat. The moss seems able to retain what water it needs if shaded somewhat and is not dependent upon the water of the substratum to the extent that the higher plants are. In a dry shaded place a sample taken from beneath a well developed moss mat showed a water loss of only 0.6 percent thus leading to the conclusion that shading is more important than water content in determining moss development on the sandstone. The moss mat enables herbs to obtain a foothold. Even trees can establish themselves here until the roots have had an opportunity to reach a suitable crevice. In one place bur oak seedlings were found growing well with their roots confined entirely to the moss mat. The mosses add more humus to the accumulating soil than any of the other plants so far considered.

On the exposed, unshaded sandstone the xerophytic moss Grimmia megapolitana Hedw. forms dense tufts. On the slightly less exposed dry rocks Catharinea angustata Brid. is found tho it never attains any considerable development as regards area covered. Polytrichum juniperinum Willd. is fairly common and can be seen at times struggling to maintain itself against the more mesophytic mosses after the habitat has become less xerophytic. On the shaded rocks the following mosses grow very profusely at times and form dense mats which can easily be lifted from the rocks: Bryum sp., Mnium cuspidatum Hedw., Dicranella heteromalla (L.) Schimp., Heterophyllum haldanianum Kindb., Brachythecium acuminatum Hedw., and Brachythecium cyrtophyllum Kindb. On the wet rocks where there is abundant moisture, and especially seepage water, Amblystegium fluviatile (Sw.) B. & S. and Dicranum flagellare Hedw. are the dominant mosses. It is of interest to note that Grout classes the former as a floating aquatic.

On the wet rocks liverworts are frequently the first plants. This has also been noted by Clements (4) and by Miss Taylor (13). Conocephalus conicus Dum. is very common on the wet rocks and Preissia quadrata (Scop.) Nees. is the more abundant on the slightly drier areas. Preissia however is more frequent upon the wet limestone. The liverworts seem to maintain themselves despite fairly keen competition with the mosses.

The fern stage is represented by the common polypody fern, Polypodium vulgare L., which grows profusely in the moist places above the bedding planes especially where shaded. This fern competes successfully with the mosses and eliminates them by shading, the moss mat being frequently supplanted by the matted fern roots. The fern stage is of little importance except where the steepness of the rock face is not pronounced.

The herbaceous stage in the succession is represented by a mixture of prairie and woodland species, the dominating type being governed by the intensity of illumination, with every gradation in mixture being represented. It is found growing in crevices, upon the humus-covered rocks, and upon the mats of mosses and ferns. Where conditions are favorable the flora is very mesophytic and persists under the shade of the trees growing on the talus slope until the rock exposures are eliminated. Where there is little or no shade the plants are more xerophytic and the prairie species predominate. On the decayed sandstone surfaces in the more mesophytic ravines almost pure woodland vegetation is to be found. To attempt to list completely the herbaceous vegetation is unnecessary. The most abundant and typical crevice plants are as follows: Campanula rotundifolia L., Aquilegia canadensis L., Artemisia frigida Willd., Arabis hirsuta (L.) Scop., Heuchera americana L., Achillea mille-

folium L., Solidago latifolia L., Laportea canadensis (L.) Gaud. Among the grasses Panicum virgatum L. and Elymus canadensis L. are perhaps the most common. Taraxacum taraxacum Karst. was also noted as an occasional crevice plant tho apparently not in flourishing condition.

Crevice plants are of importance as a means of adding humus to the accumulating soil and in that they improve the conditions for the lodgment of shrub and tree seeds. On the sandstone in our region crevice plants are of relatively little importance. The herbaceous development on the sandstone is limited with most of the plants rooted in the crevices.

The shrub stage is poorly represented upon the sandstone. Ribes bushes are the most common and occur as crevice plants as a rule. However it is possible that practically any of the local shrubs may occasionally grow in the crevices or upon the ledges where sufficient soil has accumulated.

Trees are not at all common on the sandstone proper so that this stage must be considered as being poorly represented. The gradual transition between the sandstone and the talus slope with its trees, gives the sandstone the appearance of supporting a well developed tree vegetation when viewed from afar. The trees on the sandstone however are not numerous by any means and are as a rule limited to the following: red and white elm, basswood, red cedar, ironwood, and occasional stunted white pine. The dearth of suitable crevices and the unstable surface prevent the attainment of the tree development that is seen on the limestone.

B. Development on the Platteville limestone.- The Platteville limestone differs from the sandstone as regards vegetational development principally as a result of being more creviced and of

possessing a more stable surface. There are frequent horizontal fissures and ledges which afford anchorage for trees of fair size and at times bear considerable soil.

The crustose lichen stage is much better represented here than upon the sandstone as regards both number of individuals and species. Cowles (6) states that lichens ordinarily shun calcareous soils while according to Fink (8) seventeen percent of the lichens of our region occur on the limestone. Practically all of the lichens on the limestone are of the crustose variety and attain their superior development here as a result of the more stable surface and freedom from heavy shade. The following are the most common crustose lichens on the limestone: Verrucaria muralis Ach., Verrucaria nigrescens Pers., Placodium citrinum (Hoffm.) Leight., Placodium cinnabarinum (Ach.) Anzi., Lecanora subfusca Ach., Lecanora erysibe Nyl., Endocarpon pusillum Hedw., and Amphiloma lanuginosum (Hoffm.) Nyl.

The foliose lichens are rare and are represented by occasional Parmelias or Physcias. The more xerophytic conditions are the limiting factor for this stage.

The fruticose lichen stage is even poorer and occurs only on moist crevice or ledge soil, in shaded ravines as a rule, where Cladonias and Ramalinas can be found after diligent searching. Neither this nor the preceding foliose stage play any successional role.

The moss stage is developed much less than on the sandstone and exhibits no especial variations. The air is much drier, which according to Miss Taylor (13), is responsible for a limited moss flora.

The liverworts Conocephalus and Preissia cover the rocks where the water trickles over them and may be the pioneers in such places. As noted before, Preissia seems to be slightly more xerophytic than Conocephalus.

The fern stage is represented by Polypodium vulgare L. on the north-facing slopes and in the narrow ravines. Ferns are by no means as abundant on the limestone as upon the moister, more shaded sandstone.

The herbs on the limestone grow in crevices and upon soil accumulations on the ledges. Crevices here are much more important than in the sandstone and contain soil capable of supporting higher plants without any of the pioneer stages very frequently. Soil from the mantle of glacial till which covers the region together with the clay which results from the disintegrating overlying shaly layers collects in the crevices. The limestone itself weathers to form clay according to Merrill (10). The crevice plants of the sandstone all occur on the limestone and in greater number. Artemisia frigida Willd. and Campanula rotundifolia L. are the most characteristic crevice plants here. If shade and moisture permit, almost any of the herbaceous plants of the region may be found in the limestone crevices.

Shrubs are not of sufficient importance to be considered as constituting a successional stage. Trees are more numerous and the most important of the plants of the limestone. Of especial interest is the occurrence of the basswood in considerable numbers. This tree flourishes in calcareous soil, and therefore the river bluffs are much to its liking. The white birch and the ironwood are also common on the limestone. The ironwood seems to be quite xerophytic on the river bluffs. Cowles (6) states that this tree

is the most characteristic river bluff tree of the Chicago region.

Conifers are poorly represented on the upper portions of the cliffs by the juniper, red cedar, and white pine. These trees may be relicts of the coniferous forest that probably covered the region before being superseded by the present deciduous forest. Competition has resulted in the conifers being relegated to the least favorable habitats which include the upper xerophytic bluffs.

The red and white elms are common on the limestone bluffs. The red elm is the better suited of the two to endure the unfavorable conditions that are likely to be met with on the steep slopes and is therefore the more common in the less favorable places. It is interesting to note the development of the cottonwood on the bluffs. This tree grows in habitats that vary from fairly wet low grounds to the dry exposed bluffs. Cowles in his work in the Chicago region found the cottonwood to be an important tree of the sand dunes and able to withstand very adverse conditions. Given full sunlight, the cottonwood, which is unable to tolerate even light shade apparently, will establish itself almost anywhere. The burr oak is an occasional crevice plant. The seeds however are not suited for lodgment in crevices like those of the cottonwood therefore this xerophytic oak is not frequent along the bluffs where there is considerable rock exposure.

Tree roots assist in the degradation of the cliffs by the leverage exerted between the loose limestone blocks. Blocks of rock are split off and fall while the widening of the spaces between blocks aids the action of erosive forces.

C. Development on the talus. - The vegetational development on the talus slope is, for the most part, a continuation of the successional series of the two principal rock formations which merge

more or less at this point. The glacial till from the top mantle, the weathered shale, the weathered limestone and displaced limestone blocks, together with the white quartz sand from the decayed sandstone are the components of the talus slope. As regards bulk sand is the most important slope constituent. The humus content is higher than that of either of the two rock formations and the physical conditions are such that it presents more favorable opportunity for the development of the higher plants. Furthermore the degree of slope is reduced to a point where soil slipping is practically eliminated; this is also assisted materially by the binding action of the herb, shrub, and tree roots. The talus varies in height from practically nothing to a point where it completely covers the cliff face, entirely obliterating the rock exposures. From now on the future habitat changes are the result of organic rather than physical factors.

Since the contrasting exposures are affected differently by the various factors influencing plant development they will be considered separately. The east and north-facing slopes are the more mesophytic and the opposite west and south-facing slopes are the more xerophytic. The successional differences are sufficient to warrant this classification.

On the more mesophytic slopes there is considerable telescoping of stages, and one frequently finds that pioneers and subclimax vegetation are side by side.

The normal pioneer stages may be omitted entirely and trees may be the first plants to come in. Lichens are practically absent with the exception of rare Cladonias and Ramalinas which are not numerous enough to be important. Liverworts are common where there is abundant moisture; the principal species are Conocephalus conicus

Dum. and Preissia quadrata (Scop.) Nees., as on the wet cliffs. They are of no successional importance tho their thalli may add some humus to the soil.

Mosses are not as well developed as on the shaded cliffs because of the abundant herbaceous vegetation which eliminates them before they become firmly established. The most common mosses on the wet slopes are: Brachythecium acuminatum Hedw., Brachythecium cyrtophyllum Kindb., Bryum sp., Dicranella heteromalla L., and Heterophyllum haldanianum (Sw.) B. & S.

Polypodium vulgare L., the common polypody fern, is almost entirely absent, the competition evidently being too great.

The herbaceous vegetation is predominantly vernal and quite characteristic of the mesophytic forests. The following plants are among the most common: Asarum canadense L., Arisaema triphyllum (L.) Schott., Caulophyllum thalictroides (L.) Michx., Dicentra cucullaria (L.) Bernh., Laportea canadensis (L.) Gaud., Solidago latifolia L., Thalictrum dioicum L., and Trillium sp. Where the shade and moisture conditions permit, other woodland plants have no difficulty in becoming established. Even on the more mesophytic slopes prairie herbs are not uncommon in places. This is not extraordinary when the close proximity of prairie vegetation on the uplands is considered and the direction in which the prevailing winds are likely to carry the seeds kept in mind.

The shrub stage is unimportant and is represented by occasional Ribes bushes.

The mixed forest is interesting as regards the trees that compose it. The slope is more or less of a narrow transitional belt between the upland and the flood plain with tree representatives from both habitats present. The common upland trees are: the bass-

wood, red elm, ironwood, maple, and oaks, while the flood plain forest is represented by the white ash, box elder, cottonwood, white elm, glaucous willow, sand bar willow, and speckled alder. Most of the trees that are characteristic of the cliffs are absent, tho the white birch, our most characteristic cliff tree is occasional. It is also possible that other of the upland trees may be represented at times. Thus it can be seen that this forest is quite heterogeneous as regards tree species.

The mixed forests are approaching the climax the time of whose establishment will be determined by the rapidity with which the necessary conditions are established. The most mesophytic, and most characteristic climax tree of our region, the sugar maple, is not common in the mixed forest and its appearance is governed by conditions which will be discussed later.

The more xerophytic slopes bear very interesting successional stages with telescoping reduced to a minimum. The lichen, moss, and fern stages are absent and grasses and herbs are the pioneers. A list of the dominant grasses and herbs will convince one that the exposed slopes support pioneer vegetation that includes practically all of the characteristic prairie plants of our region. The grasses dominate the exposed slopes in the beginning and include: Andropogon furcatus Muhl., Andropogon scoparius Michx., Bouteloua curtipendula (Michx.) Torr., Elymus canadensis L., Panicum capillare L., and Panicum virgatum L. The herbaceous plants are best represented by: Agastache foeniculum Ktze., Ambrosia psilostachya DC., Amorpha canescens Pursh., Artemisia dracunculoides Pursh., Artemisia frigida Willd., Artemisia ludoviciana Nutt., Asclepias sp., Aster laevis L., Aster multiflorus Ait., Helianthus scaberrimus Ell., Liatris scari-

osa Willd., Petalostemum purpureum (Vent.) Ryd., Potentilla arguta Pursh., Solidago nemoralis Ait., and Solidago rigida L.

On the steep slopes the prairie stage is capable of maintaining itself for a long period, perhaps indefinitely. The development of prairie on steep, exposed slopes has been noted by Miss Braun (2), Dachnowski (7), and Nichols (11). Exposure to desiccating agencies with the resultant low moisture content of the soil, not infrequent fires, and the difficulty that shrub and tree seedlings experience in competing with the rapidly growing grasses and herbs are the chief factors responsible for the perpetuation of the prairie. The prairie stage may be considered as an edaphic climax, especially on the steeper slopes, as Nichols (11) uses that term, in that it will persist as long as the factors that are at present in operation remain effective.

If conditions permit, xerophytic shrubs establish themselves on the prairie slopes and at times form small thickets. These are best represented by: Cornus sp., Rhus typhina L., Rosa sp., Symphoricarpus sp., and Xanthoxylum americanum Mil. This stage as a rule develops slowly and does not seem to be necessary for the establishment of the trees of the xerophytic forest that follow the prairie.

The pioneer tree of the xerophytic forest is the burr oak which in places constitutes a practically pure stand. This tree is very intolerant and the forest that it forms is quite open with the undergrowth still dominated by prairie grasses and herbs. Here again an edaphic climax is possible in that the oak forest of the south-facing slopes especially may endure for a long time. The burr oak is followed by the northern pin or scarlet oak which is slightly

less xerophytic and comes in as a result of the shade supplied by the pioneer burr oaks. Following the northern pin or scarlet oak stage there comes the red oak which is the least xerophytic of the oaks mentioned so far. The white oak is rare on the slopes as a result of the inhibiting influence of the more or less calcareous soil. The oak forest will remain until conditions become more mesophytic and the more tolerant trees find soil conditions suitable.

While the tendency of vegetational development in all places is toward the climax the progression is most rapid in the more favorable places, the north and east-facing slopes and especially the ravines. These habitats therefore have developmentally the most advanced vegetation. The degree of development attained may be considered as directly related to the degree of exposure to unfavorable influences, i.e. low moisture content of the soil and high evaporation as a result of direct exposure to the prevailing winds and to the most direct insolation.

Since the various successional stages upon all habitats considered are advancing with greater or lesser degrees of rapidity toward the climax this stage will now be considered. The climax forest of our region is composed of the basswood and the sugar maple. In other words these trees are the most mesophytic that the region as a whole will support. The basswood, already noted as a common tree on the exposed cliffs, is the better suited to endure unfavorable conditions and is the first to come in. The maple, is at a disadvantage in having more mesophytic requirements, but when the proper conditions prevail, it can easily exclude all of the other trees by reason of its extreme tolerance. Even in the case of openings in the climax forest the maple reproduction fills the gaps before other trees have had an opportunity to establish themselves.

In the course of my observations I noted the following facts with regard to the occurrence of the maple: on the west and south-facing slopes the maples are confined almost exclusively to the deep, narrow ravines, while on the east and north-facing slopes the maples, while best developed in the ravines, are coming in on certain of the more mesophytic talus slopes as well.

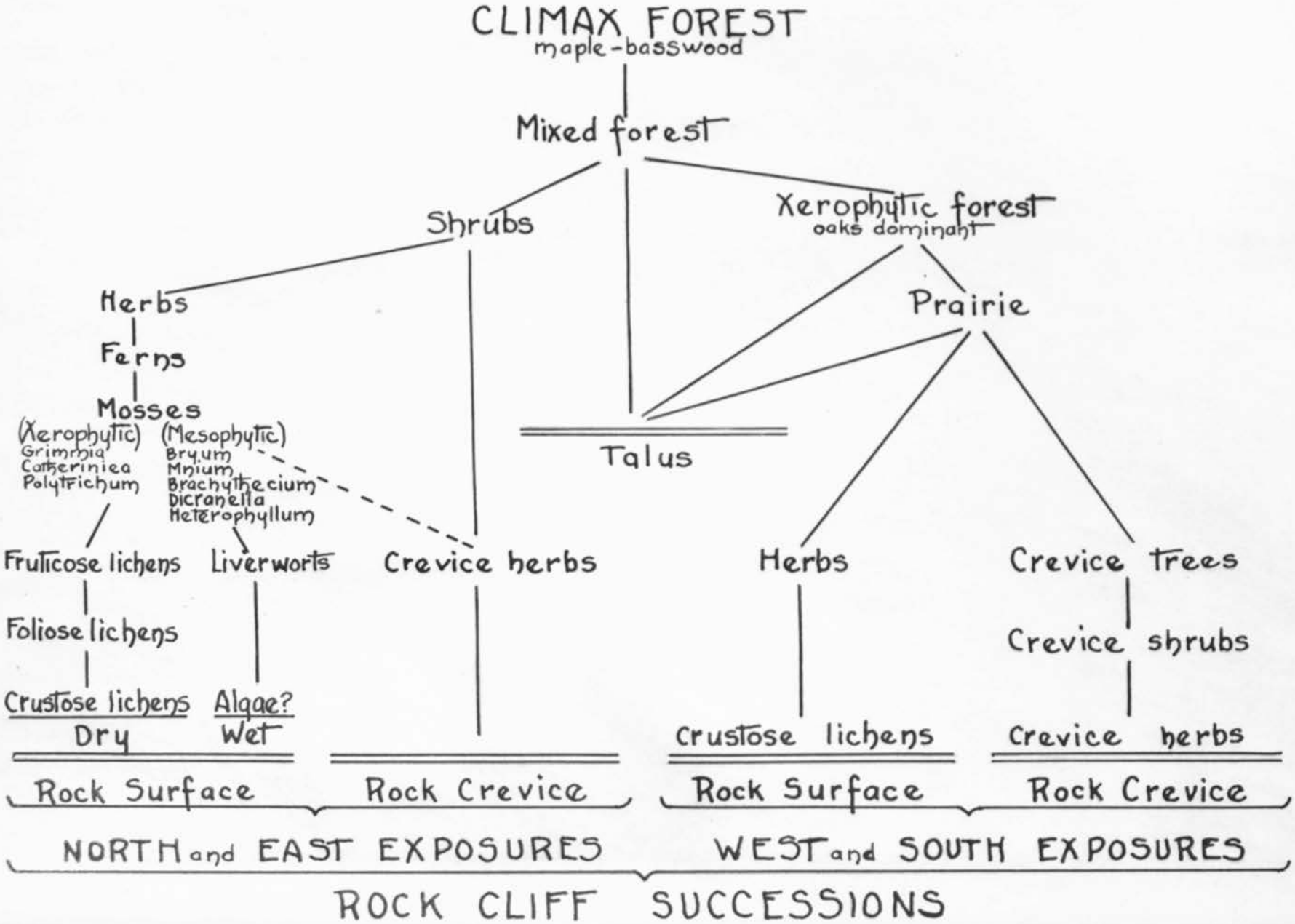
IV. SUMMARY.

The successional diagram sums up the lines of vegetational development on the habitats found along the river bluffs of our region. It should be remembered that deviations from the normal order are not uncommon as the result of some local factor whose influence is restricted to a limited area. The mass effect of vegetation is of prime importance, not the occurrence of infrequent phenomena.

The several successional lines as seen along the river bluffs are all progressing with varying degrees of rapidity toward the maple-basswood climax forest.

Local conditions upon the talus may result in the slowing up or even the total stoppage of the successional processes, so that any stage may become an edaphic climax. Thus the prairie, the xerophytic forest, and the mixed forest may be relatively permanent in places where conditions are unfavorable for further successional progress.

COURSES OF VARIOUS SUCCESSIONS ON ROCK CLIFFS OF THE MINNEAPOLIS REGION



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