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During the years of the journal's publication, the Butler University Botany Department had an active program of research and student training. 201 bachelor's degrees and 75 master's degrees in Botany were conferred during this period. Thirty-five of these graduates went on to earn doctorates at other institutions.

The Botany Department attracted many notable faculty members and students. Distinguished faculty, in addition to Cain and Friesner , included John E. Potzger, a forest ecologist and palynologist, Willard Nelson Clute, co-founder of the American Fern Society, Marion T. Hall, former director of the Morton Arboretum, C. Mervin Palmer, Rex Webster, and John Pelton. Some of the former undergraduate and master's students who made active contributions to the fields of botany and ecology include Dwight. W. Billings, Fay Kenoyer Daily, William A. Daily, Rexford Daudenmire, Francis Hueber, Frank McCormick, Scott McCoy, Robert Petty, Potzger, Helene Starcs, and Theodore Sperry. Cain, Daubenmire, Potzger, and Billings served as Presidents of the Ecological Society of America.

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FOREST SUCCESSION IN THE TROUT LAKE, VILAS COUNTY, WISCONSIN AREA: A POLLEN STUDY[1]

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The lake forest in Wisconsin, and at least in parts of Michigan, is characterized by a contrasted variation in the dominants controlling the crown cover in the stand; one consists of Pinus, in less favorable, sandy habitats, the other of species of the northern hardwoods (*Acer saccharum, Betula lutea, Tsuga canadensis,* and eastward also *Fagus grandifolia*), which occupy the better clay and loam soils. As pointed out in a previous study on the Gillen Nature Reserve (5), the hardwoods complex is the more recent invader in Vilas county and adjacent areas in Wisconsin and upper Michigan, perhaps even in the whole lake forest region as indicated by pollen profiles from New Jersey (8). Earlier pollen studies by Potzger and Wilson (9), Smith (11), and Moss (3) in Michigan and Indiana indicate that a simple Pinus dominance gave way to invasion by broadleaved genera, which in the lower latitudes consisted chiefly of Quercus. As pointed out for the Gillen Nature Reserve (5), the northern hardwoods (Tsuga, Betula, Acer [?]) replaced to a marked degree the long-time Pinus dominance which had superceded Picea, the first invader after glacial retreat. The present paper is another chapter in the study of vegetational history of the Vilas county, Wiseonsin neighborhood, stressing this time the area immediately adjacent to Trout lake, which as a whole is controlled by Pinus, and revolved in a Pinus dominance to the present time. Two smaller tracts of forest primeval are still existing at or near the lake, viz., the Point Woods T. 41 N., R. 6 E., Sec. 9, and the 60-acre tract owned by the Dairymen's Country Club, T. 42 N., R. 6 E., Sec. 6 (center). The constitution of these forests is shown in tables 1 and 2. Large acreage between Trout lake and for miles in all directions from the lake

[1]Contribution 125 from the botanical laboratory of Butler University, Indianapolis, Indiana; and notes and reports 109 from the Limnological Laboratory of the Wisconsin Geological and Natural History Survey, University of Wisconsin.

are today devoid of all climax forest cover, the vegetation consisting primarily of the low shrubs *Comptonia peregrina* and species of Vaccinium, with scattered clumps of Amelanchier, scrubby specimens of *Quercus borealis* var. *maxima* and luxuriant cover of *Pteridium aquilinum* var. *latiusculum*. There is no indication of an invasion by hardwoods, but all seems to be marking time for the day when Pinus will have advanced from centers of seed trees to take possession of areas where it constituted the dominant tree layer for many thousands of years. Areas adjacent to seed trees readily yield to re-occupation by Pinus. An eighth-acre tabulation in a recently invaded tract adjoining the Dairymen's Country Club forest, which had been completely denuded of trees, shows 108 stems of young *Pinus strobus* and 4 of *Pinus resinosa*. The next adjoining one-eighth acre supported 82 stems of *Pinus strobus* and 16 of *Pinus resinosa*. Species of broadleaved trees were limited to depauperate stems of *Acer rubrum*. In view of these facts, one wondered what the records in peat would show for this region. The analysis of deposits from five bogs included in this paper answers the question at least in part.

TOPOGRAPHIC AND VEGETATIONAL FEATURES

Pleistocene deposits determine the surface geology of Vilas county. The topography is rolling with occasional stretches of level outwash plains. The high Winegar moraine is only about 12 miles north of Trout lake. The soil for the most part is sandy or gravelly, and so presents edaphic problems of inadequate water supply to plants. The landscape is pitted with numerous lakes and bogs. Now and then one encounters small patches of northern hardwoods, but as a whole it was and still is potentially a pine territory; and the absence of this crown cover is due to the complete destruction of older seed trees by lumbering and subsequent fires.

BOGS STUDIED

For lack of convenient specific names, four of these depressions have been designated by alphabetical terms.

Bog A (*Forestry Bog Lake*). This little bog is less than one-eighth of a mile north of the Wisconsin Limnological Laboratory, on the State Forest Headquarters property, T. 41 N., R. 6 E., Sec. 8 (ne. quarter). A small open pool occupies the center, but most of the mat is covered by a scrubby growth of *Larix laricina* and *Picea mariana*. In 1937 L. R. Wilson and E. F. Galloway (14) studied

an incomplete core of approximately 15 foot depth in the same bog, but did not penetrate to the original lake bottom.

The boring for the present study was made about forty feet southeast of the pool, approximately in the center of the depression. With the assistance of Mr. V. E. McKelvey, geologist with the Wisconsin Geological and Natural History Survey, we were able to exert sufficient pressure on the borer to penetrate the layers of fine sand over-lying coarse sand. Sediments were mixed with fine reddish sand at the 24-foot level and became very sandy at the 27-foot level, which condition persisted to the 31.5-foot level. Boring at Bog A represents the deepest one made in Vilas county bogs.

Bog B. The small, deep-set kettle hole promised a deeper layer of organic matter than the 6.5 feet which we obtained. The depression is only about 200 feet across, the peat has solidified completely and is now covered by straggling growth of *Picea mariana.* It is 0.2 mile southwest of the intersection of highways M and N, on the east side of highway M (T. 40 N., R. 6 E., Sec. 30 [ne. quarter]).

Bog C. The area covered by this bog is approximately 1,000 by 2,000 feet. It is an ice-block type depression flanked by steep slopes which at some places reach an elevation of 50 to 75 feet above the mat. The bog is in a late stage of filling, with a pond approximately 100 to 150 feet across occupying the eastern section. A quaky mat, densely capped with Sphagnum, covers the major portion of the depression. *Picea mariana* and *Larix laricina* form a dense forest about the rim, and have even invaded the mat in straggling colonies. The first core was taken about 50 feet west of the pond and sand was struck at 17 feet. A second boring about 15 feet west of the open water yielded additional peat samples to a depth of 24 feet. The bog is located on the east side of highway M, 1.4 miles north of U. S. 51 (T. 40 N., R. 6 E., Sec. 31 [nw. quarter]).

Bog D (Cardinal Bog). The beautiful little bog on the property of the Cardinal Resort is located at T. 41 N., R. 6 E., Sec. 14. It is hidden even from the nearby U. S. 51 by a dense encircling forest made up of *Picea mariana, Larix laricina* and *Abies balsamea.* An open pond about 75 feet across occupies the center. The boring was made approximately 10 feet from the open water, along the northern edge of the pond. Total depth was 22 feet.

Grassy Lake Mat. The mat covering the southwest border of Grassy lake may be described in superlative terms with respect to quakiness. A luxuriant growth of Sphagnum forms the carpet layer

while *Camadeaphne calyculata* and *Myrica gale* at times form dense thickets, yielding in some places to Larix. Boring was begun close to the open lake but moved progressively shoreward when eight feet yielded no sample. A complete core was finally secured approximately 100 feet southwest of the open water. The exact location is T. 42 N., R. 6 E., Sec. 4 [sc. corner]).

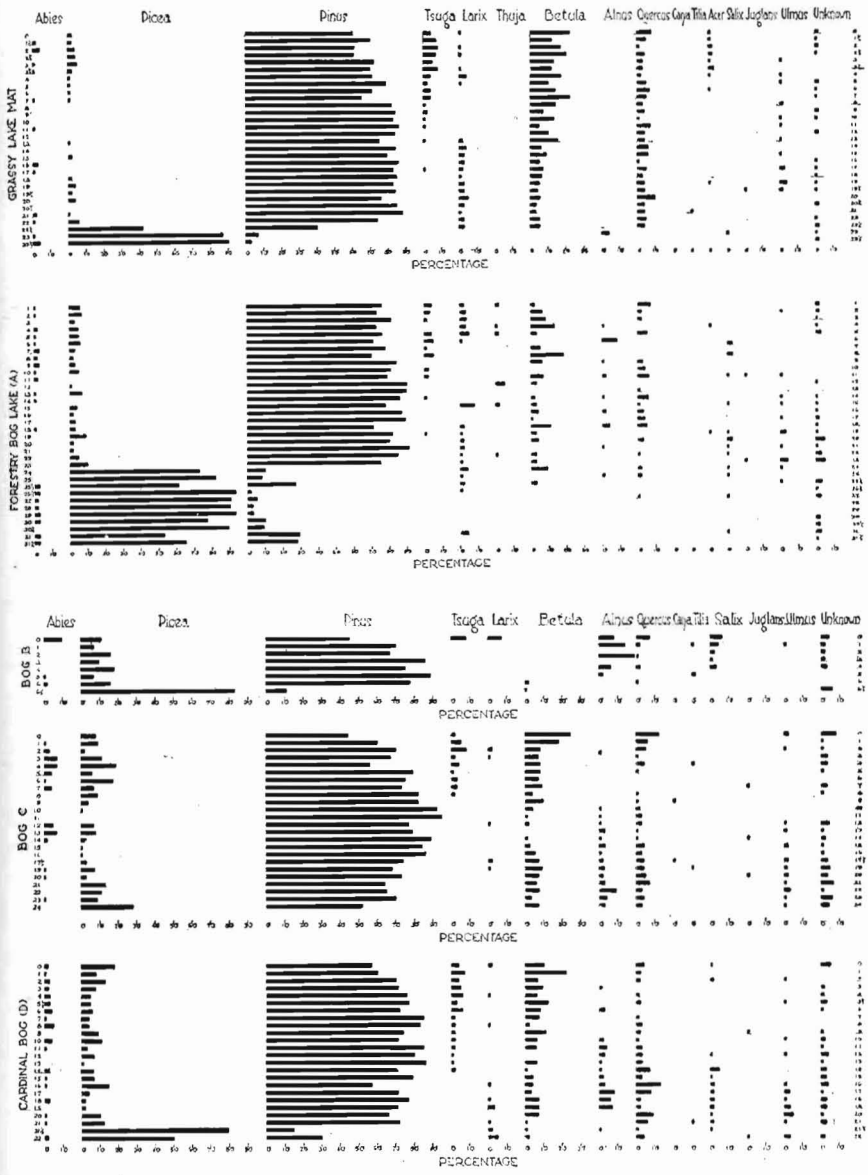
METHODS

Samplings were taken with the movable sleeve, cylinder-type borer. A small portion of sediment was removed from the center of the inside cylinder and placed into a properly labelled bottle. In the laboratory, separation of the peat was accomplished according to the Geisler (2) method. Glycerine jelly was used as mounting medium. Since the forest complex in this part of Wisconsin is so simple, only 100 pollen grains were counted for each foot-level. Recordings kept in two 50-grain tabulations showed an almost identical percentage representation of the leading genera. An attempt was made to separate the pollen of *Pinus banksiana* from that of the other two pines, but the recommended diagnostic characteristics did not prove satisfactory in this study when check counts were made by several workers in our laboratory. Our experiences were similar to those reported by Deevey (1) in his work in Connecticut. For this reason we list Pinus only generically. Prompted by an inquiry from Dr. L. R. Wilson of Coe College on our method of separating Abies from Picea, and a subsequent detailed study of the pollen of these two genera, we came to the conclusion that the differentiation between the two on size of pollen, as given in Sears (10), which we had followed in previous work, is not tenable, certainly not with *Picea canadensis*, and led to the erroneous high percentages for Abies given in our previous publications. A check count was made in the present study on all earlier tabulations, and this places Picea into great prominence in the lower levels while Abies becomes of minor importance. No doubt the same change in importance of Abies in favor of Picea will be true for published records of Indiana lakes and bogs.

RESULTS

With some difference in degree and apparent duration of control, all bogs except C show an initial Picea dominance, with Pinus present from the beginning. We consider the condition as to degree and

length of dominance of Picea in bog A as typical for the region, and that in the other depressions the lowest part of the profile is missing either because of borings omitting layers of sand with pollen, (see



levels 26 to 31.5 for bog A) or because the boring could not be made in the originally deepest part of the old lake basin. This latter type of defect is likely to be true for boring in bogs C and D, where a pond of considerable size still occupied the central area of the depression. A study in progress now indicates proof of such errors in borings and the incorrect conclusions drawn from such results.

The story of vegetational succession is short in the Trout lake area. Pinus succeeded Picea and held its dominance to the present day (tables 1 and 2). It differs from that of the Gillen Nature Reserve (5) which is about 15 miles north, in that the northern hardwoods have not yet invaded. Tsuga is represented by a very small percentage in all five pollen profiles (figs. 1 and 2), the Betula pollen present resembles mostly that of *Betula papyrifera,* and thus would be part of the Pinus dominance complex, playing an important role during periods of decline of a stand, or after catastrophic destruction of a forest. The most striking single feature of all five profiles is the long and complete dominance by Pinus.

Quercus could best be characterized as an early invader, and persisting as a non-aggressive constituent of the arboreal layer. Tables 1 and 2, likewise, reflect such a sociological status for this genus.

DISCUSSION

Northern Wisconsin and Michigan offer a splendid opportunity for pollen workers to obtain actual facts on the behavior of the two forest-cover types controlling larger or smaller areas in the lake forest region, and to ascertain whether the complex of conifers and broadleaved genera moved as an entity or whether the broadleaved element was a later intrusion into the uniform coniferous dominance, controlled by climate, and whether localized areas with least favorable soil conditions had experienced fluctuation in forest dominance. The study in the Gillen Nature Reserve (5) was concerned with the former question and this paper with the latter. The initiation of a cool-dry following a cool-moist climate of the Picea dominance apparently favored Pinus to the extent that it almost completely replaced Picea. No doubt because of greater height it reduced light on the forest floor and so interfered with the development of seedlings of the intolerant Picea. The striking "sudden" disappearance of Picea marks, perhaps, the decline of the then existing uniform stand and the culmination of compensating reproduction of the genus.

Increase of Picea towards the upper foot-levels of the bogs evidently indicates more solidified mats and invasion by *Picea mariana*.

In the sandy Trout lake region, Pinus maintained dominance to the present day, but increased aggression of broadleaved genera made itself felt. This was pointed out by Wilson and Galloway (14). It is interpreted by us as marking the initiation of moderating climate at which the northern hardwoods invaded and assumed control in more favorable places. Tables 1 and 2 show that *Acer saccharum, Acer rubrum, Betula papyrifera* and *Quercus borealis* var. *maxima* have a fair representation in the small-size classes, but they maintain more a position of second layer trees in the dominant pine stands. In the newly invaded denuded areas east of the forest on the Dairymen's Club property, broadleaved species were wanting. To judge from the pollen profiles of the Gillen Nature Reserve (5) we must conclude that the climatic change which initiated Pinus dominance has more recently undergone further changes by way of moderated temperature and increased moisture, which favored an invasion by the broadleaved forest. This injects the problem of climatically controlled dominance for the region. Weaver and Clements (12) say, "The lake forest consists of a single association in which *Pinus strobus, P. resinosa* and *Tsuga canadensis* are the climax dominants." Nichols (4) takes a still broader view of the climatic climax when he calls it "a mesophytic forest comprising a mixture of evergreen coniferous and deciduous broadleaved trees," which involves all species, both needleleaved and broadleaved, alike. However, as soon as pine constitutes almost pure stands on sandy stretches he no longer considers them climaric climax, but calls them a "physiographic climax." This would perhaps best fit the "postclimax" of Weaver and Clements (12). Whitford (13) separates the two elements, considers broadleaved with Tsuga as co-dominant as climatic climax, and pine in the hardwoods association as "relics of a previous pine forest." Pollen profiles support this latter view. All profiles from southern Michigan, Minnesota, Wisconsin, some from Indiana and New Jersey (8) show a period of complete dominance by Pinus and a partial or entire replacement by broadleaved genera. From studies of pollen profiles of bogs in the various states mentioned above, as well as from observations during boyhood days in Presque Isle county, Michigan, the senior author has always been impressed with the fact that Tsuga is not a co-dominant with Pinus but rather characteristically forms a part of the later invading northern hard-

woods crown cover (see figures 1 and 2, and tables 1 and 2). The results of pollen studies force to the conclusion that Pinus in the lake forest at present plays a role of postclimax, controlled by edaphic factors. In the southern extension of the range of this forest Pinus is today being replaced by Quercus, as a survey now in the making will show. This is but a repetition of the fate of Pinus from Indiana northward as shown with so monotonously uniform regularity in all pollen profiles. As Potzger and Friesner (6) pointed out, the boreal and the buffer lake forest with it, are moving northward, giving way to the climatically favored southern broadleaved element. In more rigorous sandy habitats, as about Trout lake, Pinus is still favored by edaphic factors, as the vast treeless areas easily yielding to Pinus invasion, when centers of germule dissemination are available, show. The status of the pine and northern hardwoods in Wisconsin and upper Michigan is similar to Quercus-Carya and mixed hardwoods in central Indiana, as discussed by Potzger and Friesner (7). There edaphic factors, primarily soil moisture, maintain a Quercus-Carya dominance in a climatically-favored mixed hardwoods region.

The rather elusive time element entering the discussion of any pollen profile is interesting, but always a factor modified and often distorted by the method of deposition itself as well as by imperfections in the sampling technique. Here enters especially the old question, has the core penetrated to the original ancient lake bottom? All the instruments used in bog boring work known to the authors fail to take samples at all in sandy layers, or only under various difficulties, at least when the sand is very coarse. In this respect the Wilson (15) sampler, used in lake borings, is the most satisfactory instrument to date, for it can take samples in sandy sediments. From bog studies in Wisconsin and lake sediments from Minnesota, Michigan and Indiana, the senior author has come to the conclusion that in sandy regions pollen of early invaders was deposited with fine sand long before much organic matter and eventually peaty deposits participated in the filling process. For that reason we feel that conclusions affixing time of duration to the Picea climax are, to say the least, of very doubtful value, unless layers of fine sand are included in the core. In the present study we feel that in all but bog A the length of time indicated by foot-level persistence of Picea is too short, due, very likely, to some errors in the sampling process. While the story of vegetational history is to all appearance complete in the

shallow bog B, the time scale is much compressed, with the probability present that some parts of the time of deposition are wanting.

SUMMARY

1. The paper reports on a pollen study of five bogs in the region adjacent to Trout lake, Vilas county, Wisconsin.

2. Forest succession was uniformly in all bogs from Picea to Pinus, and Pinus held complete dominance to the time represented by the top-most level.

3. Decline of Picea and ascendency of Pinus was sudden. This is interpreted as interference with reproduction in Picea when Pinus replaced the old stand.

4. Diagnostic characters recommended by several workers for separating pollen of *Pinus banksiana* from other species of Pinus were found unsatisfactory when check counts were made of the same foot-levels by several workers in our laboratory and for that reason Pinus is listed again as a genus only.

5. When the region considered in this study is compared with that occupied by the Gillen Nature Reserve, 15 miles north of Trout lake, the former area lacks the more recent climatically favored northern hardwoods succession. The status of Pinus is described as one of postclimax, maintained by edaphic factors.

6. The difference in numbers of levels in the several bogs where Picea showed dominance was explained on basis of incomplete cores, either because of missing layers of sand which constituted much of early sediments, or inability to make borings in the deepest part of the old lake basin because of open ponds.

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TABLE I

Composition of the Point woods at Trout lake based on 20 100-square-meter quadrats.

Species	Size-classes of stems							
	Below 1 inch	1-5	6-10	11-15	16-20	Above 20	Total	% F. I.
Abies balsamea	18	5	1				24	35
Acer rubrum	36	54	4				94	90
A. saccharum	62	95	4				161	60
A. spicatum	1						1	5
Alnus incana	1						1	5
Amelanchier sp?	18	15					33	60
Betula lutea		1					1	5
B. papyrifera		11	2				13	60
Corylus rostrata	374						374	90
Lonicera sp?	17						17	30
Picea canadensis		1					1	5
Pinus resinosa		5	4	42	28	9	88	100
P. strobus		43	4	4	2		53	60
Quercus borealis var. maxima	6	36					42	55
Thuja occidentalis		1					1	5

TABLE II

Composition of the pine woods on Dairymen's Country Club property based on 50 100-square-meter quadrats.

Species	Size-classes of stems							
	Below 1 inch	1-5	6-10	11-15	16-20	Above 20	Total	% F. I.
Abies balsamea	97	205	2				304	74
Acer rubrum	57	103	7				167	74
A. saccharum	10	71	11				92	60
Amelanchier sp?	2	3	1				5	10
Betula papyrifera	2	21	3		1		27	16
Corylus rostrata	101						101	44
Pinus resinosa	1	1	5	21	41	9	78	70
P. strobus	10	5	20	38	42	18	133	94
Prunus pennsylvanica		1					1	2
P. virginiana	4	14					18	16
Quercus borealis var. maxima	1	4	3				8	12
Tsuga canadensis			2				2	4