

A PHYTOSOCIOLOGICAL STUDY OF TSUGA CANADENSIS  
AT THE TERMINATION OF ITS RANGE IN WISCONSIN

A thesis submitted to the Graduate School of  
the University of Wisconsin in partial fulfillment  
of the requirements for the degree of Doctor of  
Philosophy.

by

Harold Arthur Goder


Date July 25, 1955

To Professors: **Curtis**

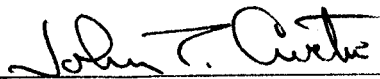
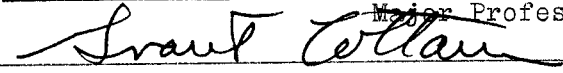
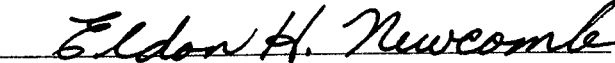
**Newcomb**

**Cottam**

This thesis having been approved in respect to form and mechanical execution is referred to you for judgment upon its substantial merit.

  
Dean

Approved as satisfying in substance the doctoral thesis requirement of the University of Wisconsin.

  
Major Professor  
  


Date Aug 5, 1955

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HAROLD ARTHUR GODER

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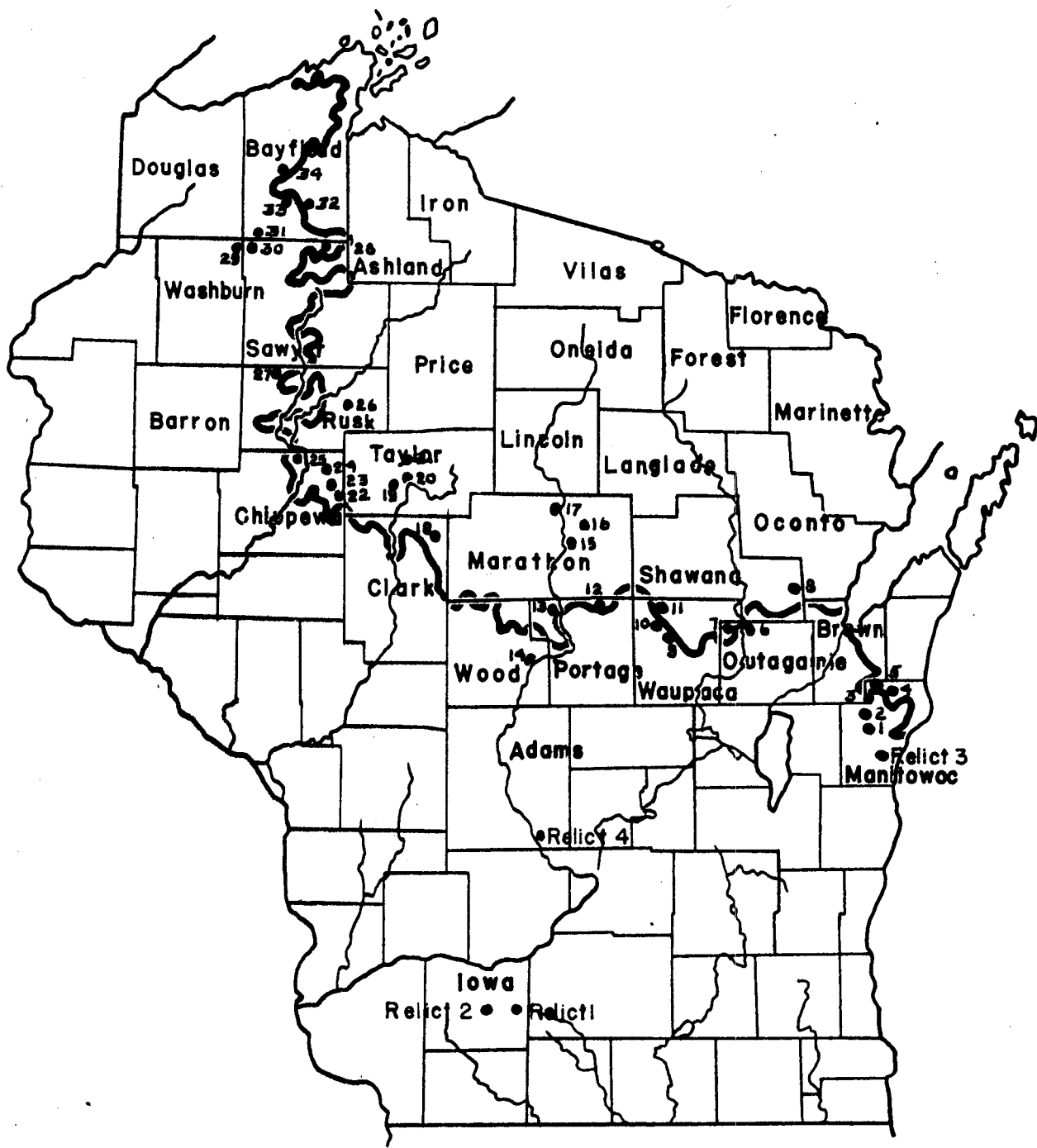
## INTRODUCTION

The presentation of this phytosociological study of eastern hemlock (Tsuga canadensis) is a second study of the behavior of an arboreal species at the termination of its range in Wisconsin. Ward (1954) completed a study of the beech forests (Fagus grandifolia) of eastern Wisconsin and their relationships to other upland forests.

Opportunities for future ecological study of *Tsuga* in Wisconsin will be limited to residual forest tracts, woodlots, and stands within the border because of encroachment of improvident forestry and agriculture practices. Therefore, this study records quantitatively the phytosociological aspects of remaining *Tsuga* stands along the western-most extension of this species in the United States. During summers of 1953 and 1954, 34 stands without severe allogenic disturbances were sampled along the border (Fig. 1). Each stand was upland and well drained. The stands were sampled in order to fulfill two objectives: to record the composition of arboreal species and to present a detailed study of *Tsuga* reproduction.

Records of pre-settlement vegetation were utilized to ascertain factors which limited the range of *Tsuga* and to study the past composition along the border. Surveyor's records were transcribed for each range of townships and each tier of townships along the entire border. Four hundred and sixty-five townships were analyzed.

Fig. 1. Tsuga canadensis border as drawn from surveyor's records, location of present day stands, and state political divisions. (in part)



## LITERATURE REVIEW

With the presentation of this literature review the author has endeavored to embody the work of investigators pertaining to arboreal vegetation, emphasizing the behavior of coniferous species. Numerous descriptive accounts of arboreal species at the termination of ranges have been published. These qualitative studies make the paucity of quantitative data more apparent.

Some early investigators were adamant in their knowledge of a single factor which affected plant distribution while others believed that multiple factors were responsible. Brockmann-Jerosch (1919) drawing his conclusions from a study of tree limits in the Swiss Alps stated, "tree limits do not depend on any single factor such as precipitation, wind, or snow, but rather the character of the climate which is a complex of single factors." He could not determine the responsible factor for tree limits because he recognized that one climatic factor by itself would not prevent tree growth. Good (1931) in his "Theory of Tolerance" concluded that each and every plant species is able to exist and reproduce only within a range of climatic and edaphic factors. Tolerance was further expanded by Mason (1936) when he stated, "in the life history of an organism there are times when in its development there is a critical phase which has a narrow tolerance range for a particular factor of the environment. The distribution of intensity span of this factor during the time the plant is in this particular phase limits the area in which the function can operate and hence governs the distribution of the species."

Local knowledge and herbarium data have been used as a basis for distribution maps. Munns (1938) presented distribution maps of 102 arboreal species but the exclusion of quantitative data restricts their value. Employing quantitative data derived from cruise or inventory figures, Halliday (1943) published maps using different degrees of shading to indicate population intensities. Finley (1951) completed pre-settlement vegetation maps of Wisconsin with descriptions of associated plant communities. In his literature review he discussed vegetation maps which had been prepared for the State of Wisconsin by various investigators.

Factors limiting the range of species have been discussed by many investigators. Transeau (1905) correlated climatic factors with centers of plant distribution. He concluded that plant distribution was controlled by four climatic factors which he considered of great importance to plant life - temperature, relative humidity, wind velocity, and rainfall. In a study of a southern outlier of T. canadensis (L.) (Carr.)<sup>1</sup> on the Warrior Plateau in northern Alabama, Segars (1951) reported that evaporation rates varied according to microclimate. The data suggests that high humidity has played an important role in the persistence of the species in the region. Other investigators who have studied factors limiting distribution of

1. Nomenclature from Gray's Manual of Botany, 8th Edition, 1950.

arboreal species are Adams (1920, New York); Livingston and Shreve (1921); Elanctet (1925, Great Slave Lake); Halliday (1943, Canada); and Brink (1949, British Columbia).

It appears that any marginal advance or retreat of vegetation is a local condition and does not occur throughout the entire border. Griggs (1914) concluded that along the northern border of the boreal forest the advance of a single individual is indicative of change because the movement is not obscured by competing vegetation. Competition along southern forest borders frequently masks fluctuations. Raup (1941) as a result of extensive investigations into boreal forest problems, reported that the entire forest border does not react the same.

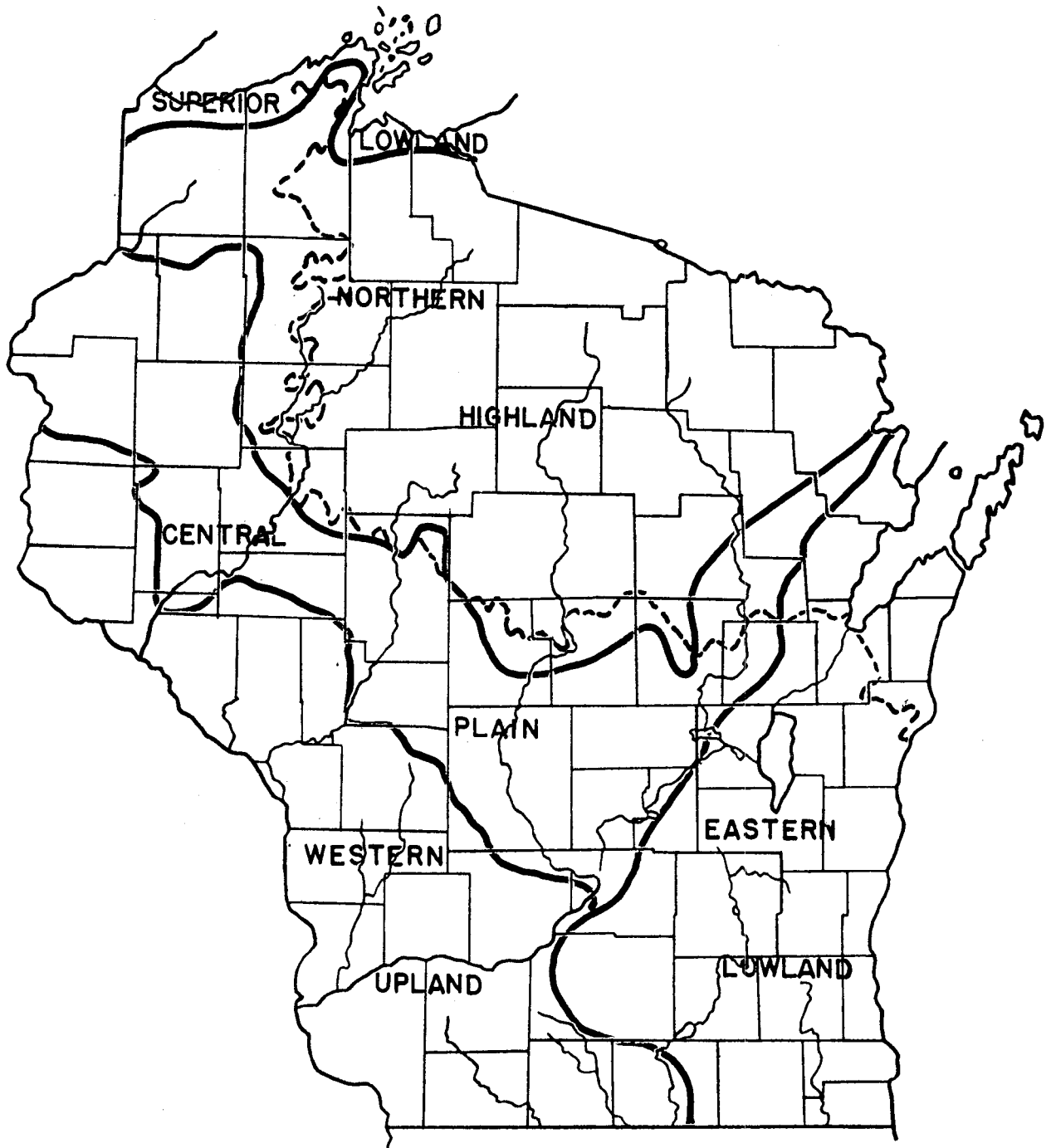
There are few quantitative studies relating a single species to other members of the community at the termination of a range. Within the northern hardwood forest in Wisconsin, investigations have been made by Stearns (1947) who studied the autecology of *Tsuga*, *Acer saccharum* Marsh, *Betula lutea* Michx. and several minor species. Stearns reviewed the literature of northern hardwood forests and classification of forest types. Potzger (1946) presented a phytosociology study of forest tracts in Vilas and Price Counties in Wisconsin, and Gogebic County, Michigan. Quantitative studies of stands which include *Tsuga* have been completed in Wisconsin by Brown and Curtis (1952), Christensen (1954), and Ward (1954).

The micro-relief of *Tsuga* stands has been noted by two investigators. Lutz (1940) who worked in New Hampshire, presented a paper

on the disturbance of soils by uprooted trees. In a detailed quantitative study he discussed the physical property and chemical changes which occur in the soil upheaval. He also reviewed early literature pertaining to windthrow conditions. Goodlett (1954) stated, "the present forests are growing on this micro-relief produced by past vegetation, and occupy all parts of the 'blow-down' landscape except the bottom of the pits, where they are almost universally absent."

Early literature describing the vegetation of the state has reference to *Tsuga*. Roth (1898) stated, "hemlock is confined to the gravelly loam and clay lands of the more humid half of north Wisconsin .... It is generally old timber with little indication of active reproduction. In the southern part of its area and on the heavier soils it grows to a height of 85 to 100 feet, with a diameter of 24 to 30 inches; in the northern counties and on the lighter gravel it is usually both shorter and smaller, frequently not over 60 feet high and under 20 inches in diameter."

Fig. 2. Tsuga canadensis border in relation to geographic provinces of Wisconsin (After Martin, 1932).



## PHYSICAL GEOGRAPHY

The diversified physical features of Wisconsin divide the state into five natural regions (Martin, 1932). The boundaries are delimited by variation of the underlying bedrock (Fig. 2). The Lake Superior Lowland is the northernmost geographical province, extending south to the highest abandoned beach line of Lake Superior. Lake deposits of Superior red clay overlies the Lake Superior sandstone bedrock. It is in the north central part of this province that Tsuga canadensis reaches its furthest westward extension along the south shore of Lake Superior.

The Northern Highland is part of an extensive buried peneplain spreading south from Hudson Bay. In Wisconsin the province covers 15,000 square miles. The topography slopes strongly southward and lesser east and west from maximum relief in the center. Cary ground moraine deposits, which predominate over the northern part of the peneplain, and undifferentiated moraine in the south cloak the igneous bedrock.

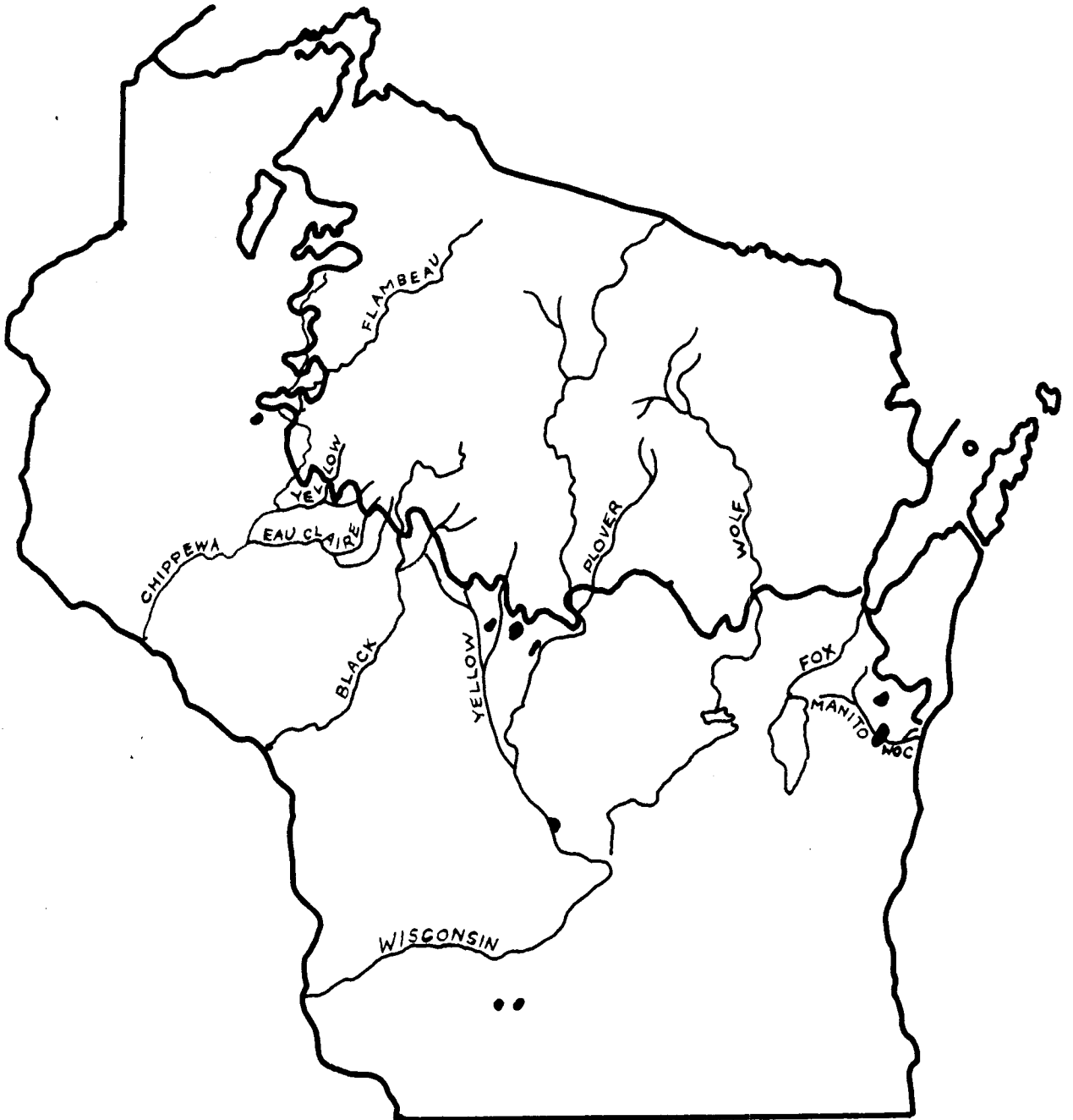
Noteworthy among the ascending features of the peneplain are several monadnocks. Illustrative of these are the quartzite Barron Hills. Lying adjacent to the western border of Tsuga, the Barron Hills extend in a northeast direction through Chippewa, Barron, and Sawyer Counties.

The southern border of Tsuga is north of the principal part of the Central Plain but spans a northeast extension in Waupaca and

Outagamie Counties. The underlying upper Cambrian sandstone is mantled by Cary end moraine and Valders ground moraine. The soil is enriched by glacial deposition of calcareous material from the region outside.

Water and glacial action have modified the topography of the Eastern Lowland. Deposits of unassorted till, stratified gravel, sand, and lacustrine clay overlie dolomitic and shale bedrock. Extending north from Milwaukee a band of red clay covers the Valders drift. The band broadens northward into Manitowoc County and the Green Bay-Lake Winnebago lowland. Here, along the western shore of Lake Michigan, Tsuga reaches its furthest extension southward in Wisconsin.

Fig. 3. Tsuga canadensis border in relation to drainage systems.



## DRAINAGE SYSTEMS

Topographic features due to glaciation determine drainage patterns within the range of Tsuga canadensis (Fig. 3). A great part of this area is drained by the Chippewa and Wisconsin River systems. The tributaries of the Chippewa River have their source in over 100 lakes distributed in the Northern Highland Province. The river flows south parallel to the western border of Tsuga into central Chippewa County where it courses southwest to the Mississippi River. Important tributaries of the Chippewa River are the Flambeau, Yellow, and Eau Claire Rivers.

The Wisconsin River emanates from Lac Vieux Desert on the Wisconsin-Michigan border and flows south and southwest into the Mississippi River. The Plover and Yellow River join the Wisconsin River just south of the border of Tsuga. Another tributary of the Mississippi River is the Black River which flows directly southwest from its source in Taylor County.

The principal drainage system in eastern Wisconsin is the Fox River and independent streams which flow into Green Bay and Lake Michigan. The Fox River system consists of the Fox and Wolf River headwaters, Lake Winnebago, and the lower Fox. In the headwaters are several lakes which lie in the Central Plain. Another important stream which flows into Lake Michigan is the Manitowoc River.

Waterways, upon leaving the resistant rocks of the Northern Highland, cross sandstone of the Central Plain and form cascades. This fall line is comparable to the fall line of the coastal

plain in eastern United States. It was along this line that sawmills arose, utilizing the available source of water power and forests of the Northern Highland. Cities located along the fall line include St. Croix Falls, Chippewa Falls, and Wisconsin Rapids.

## SOILS

Three sand areas are found in the northern part of the state. In the northwest, the "St. Croix Barrens" extend across Washburn, Douglas, and Bayfield Counties in a band 10-20 miles wide. A projection spreads east into central Sawyer and southern Bayfield Counties. The sandy soil was derived largely from Lake Superior and Potsdam sandstone by glacial and water action.

A north central sand area extends north from Langlade and Lincoln Counties into Oneida and Vilas Counties. The transported mantle has its origin in sandstone rocks of northern Michigan.

Two soil series are represented in the above regions. The soils of the level portion are Plainfield sand and fine sands, and the rougher morainic portions are of the Vilas Series. Within the sand areas are limited regions of heavier textured soils.

Sandy soil in Marinette and Oconto County is partly derived from upper Cambrian sandstone and in part by action of water on glacial drift. Granitic rocks lying outside of the area contribute to the composition of the sand (Whitson, 1912). Therefore, this type has a higher content of feldspar, hornblende, mica, and other minerals than the above soil series. The soil is classified in the Vilas-Omega-Hiawatha Series.

The difference in degree of fertility among the three series is not great. Each is characterized by low humus content, low water holding capacity, high radiation, and deflation. Available nutrients

are concentrated in the organic fraction of the soil.

Adjacent to Lake Superior and south of the Bayfield Ridge are areas of podzolized lacustrine clay. The Superior red clay loam of eastern Wisconsin is more weakly podzolized and variable than the clay area bordering Lake Superior. Interspersed in the clay region are sites of Superior loam and fine sandy loams.

The remaining soil types within the border of Tsuga are represented in moderately leached podzolic loam phases of the Kennan, Spencer, Antigo, Marathon, and Miami loam and silt loam Series. Podzol phases of Kennan, Spencer loams and silt loams, Iron River Series are classified as loam podzols (Wilde, 1949). Throughout the area of upland silt loam the subsoil contains sand and gravel to produce good drainage. The petrographic origin of much of the loam soil is granitic rocks.

The ectorganic fraction of friable ~~mull~~humus is composed of twigs and leaf matter. It is not uncommon in stands along the southern border of Tsuga in Wisconsin. The matted mor humus is confined to coniferous stands along the northwestern part of the border and within the range of Tsuga. The ectorganic layer is compacted by masses of fungus mycelia growing throughout partially decomposed litter (Wilde, 1949).

## CLIMATE

Latitude, distance from large bodies of water, altitude, and weather are primary factors determining regional climate. Soil, vegetation, and topography are secondary.

There is relatively little variation in altitude within the Tsuga range in Wisconsin, but it is enough to show slight variations in temperatures at the same latitude. For example, Park Falls in Price County has an elevation of 1494 feet and mean annual temperature of 40° F.; Spooner, Washburn County which lies at an elevation of 1095 feet has a mean annual temperature of 41° F.

Large bodies of water counteract the influence of altitude and weather. Lakes Superior and Michigan affect weather factors inland for approximately 25 miles. Isotherms which trend east and west curve south along the western shore of Lake Michigan, while lines of fall and winter temperatures reverse this direction and bend sharply northeastward.

The most variable weather occurs during the months of November and March. These are transitional months between seasons. Winter is dominated by three air masses bringing cold dry air from the Arctic, cold dry air from the West, and moist warm air from the Gulf region. Decreases in temperature are concomitant with anticyclonic eddies of Arctic air pushing across the state.

Precipitation in winter is mostly in the form of snow although winter rains are not uncommon in the south. Convergence of continental and Arctic air masses brings about an increased amount of

snowfall in the extreme northern part of the state. The annual snowfall within the state ranges from 60 inches in the north to 30 inches in the south. In the northern part, the ground is covered with one to three feet of snow from December 1 to April 1. Winter thaws frequently clear the ground of snow in southern counties.

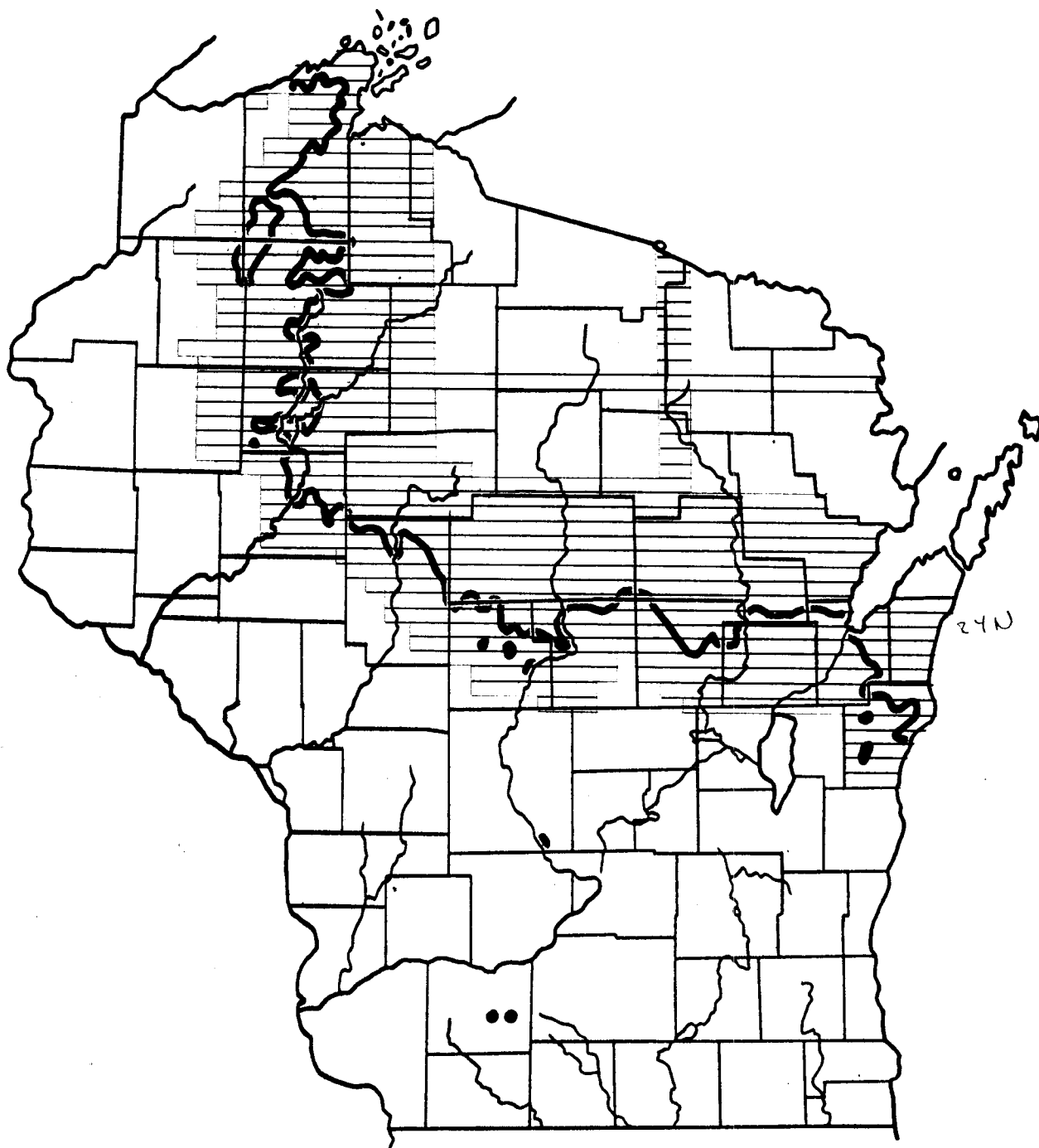
Decreased snowfall and more precipitation in the form of rain accompanies spring into Wisconsin during May. Temperatures increase as tropic air streams modify the cold masses of polar air and the west-east flow of air decreases. The mean date of the last frost within the Tsuga border is about May 15, which may be altered by the maritime influence of the Great Lakes. Temperatures remain cool in the northern part of the state until warm southern air masses penetrate the region.

Surface summer winds are laden with moisture from the Gulf of Mexico. A mixing of the southern air masses with Arctic masses over the coniferous forests of the state contribute to an increased amount of rainfall. Weather stations within the Northern Highland Province report a mean annual rainfall which is 1 inch greater than that reported by stations of adjacent provinces. Sixty to 70 per cent of the total rainfall occurs from May to September, inclusive. June has the heaviest rainfall.

The range of Tsuga in Wisconsin lies between July isotherms of 66° and 70° F. Southwest winds during July and August bring high summer temperatures to the state, but if the wind shifts to the northeast cold air from the lakes cause a decided drop in temperature.

The greater frequency of Arctic air masses in late August contribute to decreases in temperatures. It is during this month that droughts occur because of the predominance of dry air masses. Resurgences of tropical air masses may send the temperature soaring. The mean date of the first killing frost within the Tsuga border is September 20, concluding a 130-day growing season.

Fig. 4. Townships utilized from surveyor's records.



## METHODS

Surveyor's Records

Several sources may be utilized in studying the ecology of a species along its border. The data for this report were taken from surveyor's records and present day field studies. Surveyor's records were used to determine the status of *Tsuga* in Wisconsin before settlement. Field work included the study of the arboreal vegetation in 34 stands whose location was determined by corresponding and talking to county foresters, cruising along roads, and talking to people in areas where *Tsuga* was reported by the surveyors.

The utilization of vegetational records taken from early land surveys is a valuable experience in acquiring knowledge of pre-settlement vegetation. The field books of the land survey of Wisconsin are available for evaluation in the Public Land Office, Wisconsin State Capitol Building, Madison, Wisconsin. Previous to the investigator's employment of the records for the present study, it was necessary to locate the townships in which the range of *Tsuga* terminated. Examination of vegetation maps indicated the approximate boundary.

Using these border locations, data were copied directly from the original field books for two townships exterior to the border and six townships within the border. For comparison of data, it was decided to transcribe the notes for an east-west transect along Townships 36 and a north-south transect along Section 12 from the western and southern border, respectively, to the Michigan state line

(Fig. 4). A total of 465 townships was utilized. The following information recorded by the surveyors along interior north-south lines and exterior lines was transferred onto mimeographed township forms: the names of the surveyors and the year in which the township was surveyed, the survey book number, the township number and range, and the species and diameter of all trees along with the link distance that each was located from the section or quarter section corner. Letter abbreviations were used to denote species. If four witness trees were utilized at a section corner instead of two, the data for each tree were recorded.

The recorded diameters taken from the surveyor's records were converted to dominance (basal area). The basal areas, number of individuals in each size class, and the number of points of occurrence for each species were transferred to data summary sheets. Each quarter and section corner counted as one point of occurrence.

The Importance Value (Curtis, 1951), which is a summation of the relative per cent frequency, density, and dominance was calculated for each species. Relative per cent frequency, density, and dominance are determined by dividing the total value of each into the species individual value.

Supplementing the above data, the average distance between trees was calculated for even-numbered tiers of townships along the western border of *Tsuga*, even-numbered ranges of townships along the southern border, and all townships of both transects. In townships where two witness trees were utilized, the distance from the corner to the tree

in links is equal to the mean distance in feet between trees. If four trees were recorded at a point, the mean of the four link distances was converted to feet. In addition to the mean basal area which was calculated for all species, the mean basal area of *Tsuga* was computed separately. The mean basal area is determined by dividing the total dominance of a species by the number of individuals contributing dominance.

Assuming that the mean area of an individual tree takes the form of a hexagon (Cottam, 1949) the mean area of the individual is calculated by multiplying the square of one-half the distance between two trees by 3.4644. The number of trees per acre was determined by dividing the mean area into the number of square feet per acre (43,560).

Thirty-four townships were selected for comparison with 17 present day stands. Two townships were chosen for each stand in order that the number of points of occurrence would be approximately equal. Adjacent townships were selected on the basis of similarity of topography, nearness to the border, and distribution along the border. The townships selected were examined for vegetation homogeneity by application of a Chi-square test. Each township was divided into four equal units and the expected and observed values were calculated for the species with the greatest density in all four units. The probability of each township was then determined from a Chi-square table. The five per cent level was arbitrarily chosen as the lowest level of acceptance.

### Present Day Survey

Criteria used in selecting stands for field study were: presence of Tsuga, no allogenic disturbance during the growth of the stand, well drained location, an area not less than 10 acres, and nearness to the border. Sixty stands were examined but only 34 were sampled. Stands were usually rejected because of size or disturbance.

The sampling method provided data for 100 trees. Briefly, the "Wandering Quadrant"<sup>1</sup> method is as follows: at a predetermined number of paces the closest tree is selected as a starting point. A 45 degree half-angle of inclusion is determined along a compass line. The distance from the tree at the starting point to a second tree within the angle is measured. Using this same scheme three distances are measured and recorded. At the end of the third distance the basal area and species of tree is recorded. Employing this tree as the center of four quadrants the basal area and species of the nearest tree in each quadrant is measured and recorded. At this point three distances and five basal areas have been recorded. The procedure is continued until 100 trees and 60 distances have been tallied.

At each quadrant point the presence of seedlings<sup>2</sup> and saplings<sup>3</sup>

1. Acknowledgment is made to Dr. Grant Cottam for the development and suggestion of this method.
2. Seedlings unless otherwise noted are greater than one year old and less than one foot tall.
3. Saplings are greater than one foot tall and less than 12 d.b.h.

within a 30 foot radius was noted.

Using the quadrant method (Cottam, et al. 1953), the location of the trees,<sup>1</sup> saplings, and seedlings were checked on a form sheet according to the following locations: mound, pit, intervening area, log, stump. One hundred forty eight quadrants were studied in each stand. Distances between mounds and mound areas were also recorded.

Density of germinated seedlings<sup>2</sup> on mounds and intervening areas was sampled with 100 one-foot square quadrats. A wooden quadrat frame with an inside measurement of 12" was utilized. In order to locate the position of the quadrat, a hunting knife was tossed into the air; the point of the blade indicating the position of the lower left corner of the quadrat. The criterion for the selection of the area was the absence of exposed rotten wood.

Along with seedling counts, the cone density of the previous reproduction season (1953) was recorded. These cones were distinguished from older cones by their sepia coloration. Cones were gathered from the ground and brought into the laboratory for analysis.

Coniferous logs and stumps were examined and measured but were not differentiated into species. Measurements included area, zone of decay, and circumference of solid core. An estimated per cent moss cover and residual bark was recorded along with a description of each log or

1. Trees are greater than 12 d.b.h.
2. Germinated seedlings are seedlings which had germinated during the 1954 growing season.

stump. The density of seedlings and germinated seedlings was recorded for all species on each log and stump. Moss and wood collections were brought into the laboratory for identification and analysis. Identification and recording of the presence of herbaceous species was made in the field. Notes were made of the basal area of windthrown T. canadensis.

Along with soil and humus collections, profile measurements for both mound and intervening areas were made. Three separate samples were taken from each horizon and combined into one for laboratory analysis. Larger samples of five stands, from which cone collections were also made, were collected for greenhouse experiments. The direction of ground slope was also recorded.

At predetermined intervals along a compass line, 10 light meter readings were taken just before finishing a stand. Another reading was taken upon arrival in an open clearing.

In the autumn of 1954, three relict stands in southern Wisconsin were visited. *Tsuga* cones and soil collections were made in each.

### Laboratory

Field data for trees and saplings were transferred to data summary sheets. Importance Values, number of trees per acre, average distance between trees, and average basal areas were computed for each stand. One additional statistical treatment was utilized - a Continuum Index (Brown and Curtis, 1952). A Continuum Index is computed by multiplying the Importance Values of each species by a climax adaptation value.

Low adaptation values are related to pioneer species and high values to climax species. The summation of Continuum Indices range from 300 to 3000. Homogeneity was ascertained in each stand by application of a Chi-square test. Only those stands with a probability greater than 5 per cent were used in further analysis.

Cones were air dried. The seeds of two cone samples were extracted by hand. In the remaining samples, seeds were removed by agitating cones in a paper bag. The cones were then examined and seeds lodged in the scales were removed with forceps. The extracted seeds were examined for injury; all damaged seeds were discarded. Seeds were dewinged by flailing in a small paper sack and winnowing, except in one sample in which the seeds were retained with intact wings. The seeds from the apical part of the cones were kept separate from seeds of the basal portion in two samples. Seeds were placed in labeled screw top vials and stored at  $4^{\circ}$  C.

Samples of 100 cones were measured with a vernier caliper. An analytical chain balance was used to weigh cone and seed samples.

Each sample of seeds was divided into several lots of 50 to 400 seeds and given various combinations of treatments. Samples were stratified for 80 days in screw top vials in a mixture of garden loam and sand whose estimated water content was slightly above field capacity. Thirty-three samples of stratified and three non-stratified samples were stored at  $4^{\circ}$  C. Two stratified samples were stored at  $-22^{\circ}$  C.

At the close of the period of stratification the seeds were

Fig. 5. Germination Chart (Modified from Baldwin, 1942)

Type of Germinator

Germination Temperature

Date of Stratification

Stratification Period (days)

Special Seed Treatment

Number of Seeds Tested

Preliminary Reports		Days since
Date	Remarks	start

5

10

15

20

25

30

35

40

45

50

55

60

65

70

75

planted. A one-half inch layer of pea gravel was used for drainage. Seeds collected from a stand were planted at a depth two times the diameter at the broadest point of the seed in soil from the same stand and in soil from at least two other stands, or in garden loam. A part of the same type of soil used in planting was sifted over the seeds and covered with a thin layer of screened sphagnum moss. The containers were kept in the greenhouse. A syringe containing commercial fungicide diluted 1/4 teaspoon to each quart of distilled water was used in watering.

Daily germination was marked with colored toothpicks. Different colors or combinations of colors were used for each five day period of the test. The total number of seedlings germinating during each five day period was recorded on a germination chart (Fig. 5). The cotyledon number of each seedling was also noted.

Germination tests were concluded after 60 days. The energy period (the number of days in which the majority of germination occurs), germination energy (per cent of seeds germinating in the energy period), and germination capacity (total per cent of seeds which had germinated when test was discontinued) were then determined for each sample (Baldwin, 1942).

Soil and humus samples were air dried, pulverized, and shifted through a 2 millimeter sieve. Water holding capacity and pH were determined for each sample. Standard Hilgard cups were used for determination of water holding capacity. The pH was determined electrometrically with a glass electrode Beckman pH meter. Thirty

grams of soil were placed in a 50 milliliter beaker and enough glass distilled water was added to make a thin paste which would flow without jarring. The mixture was allowed to stand for 30 minutes with occasional stirring. After the glass electrodes were completely immersed in the paste, the pH reading was taken. Wood and humus samples were analyzed for water holding capacity and pH similarly.

## RESULTS

In order to analyze the data in a coherent manner the results of the investigation are presented in units. Each unit includes a particular phase of investigation and is concluded with a discussion.

Surveyor's records were utilized to project data in several ways. The information was first used to portray population intensities of Tsuga. The Importance Value of Tsuga in each township was placed on a base map. The values were arbitrarily divided into four groups. Each group was assigned a color and the corresponding numbered township on the base map was colored with crayon. Identically colored townships were connected with isolines. The completed map gives a perspective of the population of Tsuga at the termination of its range as recorded by the surveyors from 1836 to 1859 (Fig. 6).

To explain the transition of arboreal species across the range of Tsuga, several transects along the western and southern border were analyzed (Fig. 7).

### Results of Transects Along the Western Border

Seven species were plotted for each range along Township 36 (Fig. 8). Abrupt decreases in the Importance Values of Tsuga occurred

Fig. 6. Population intensity of Tsuga canadensis within townships analyzed.

IMPORTANCE VALUE

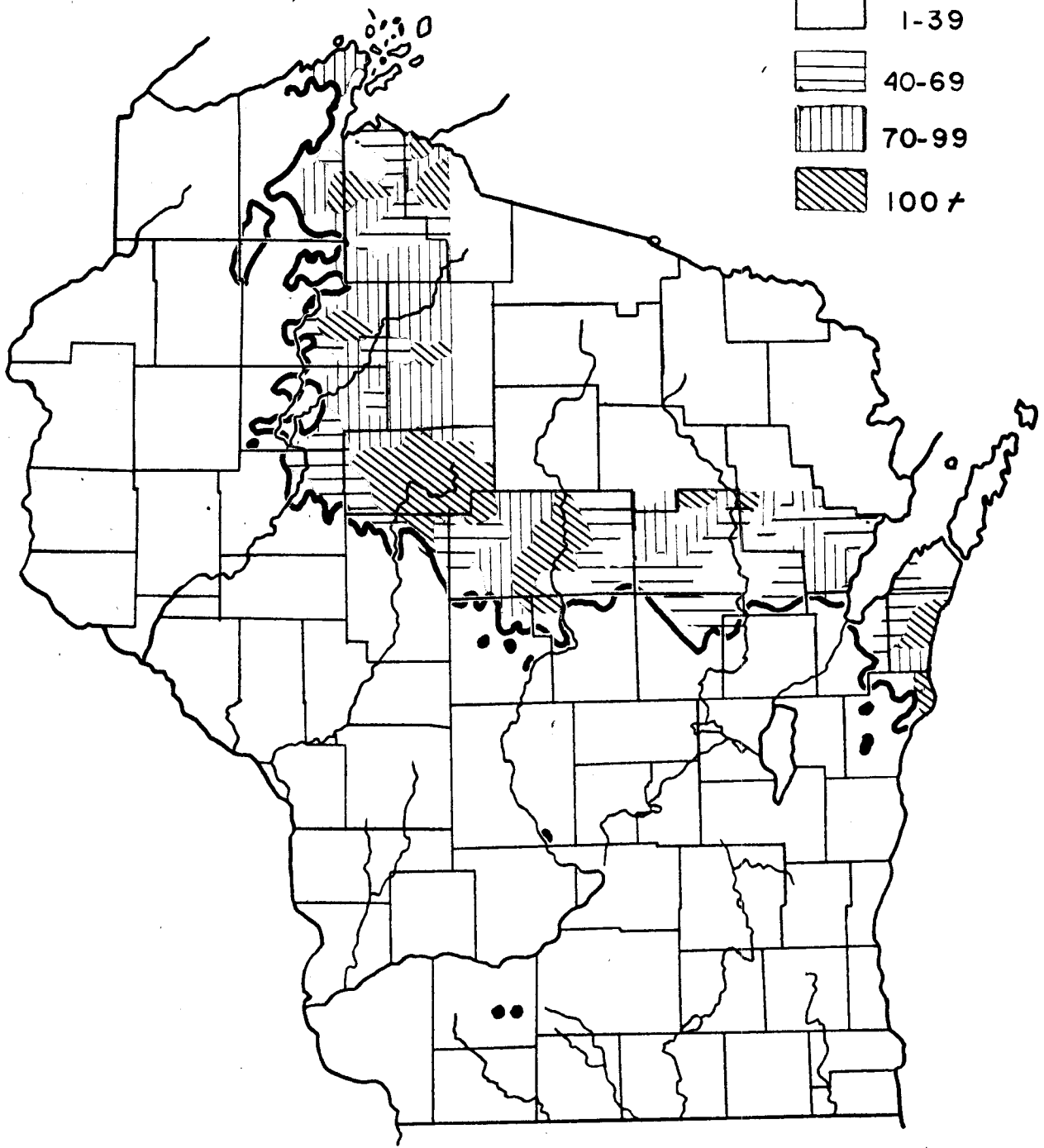
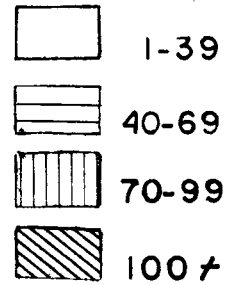
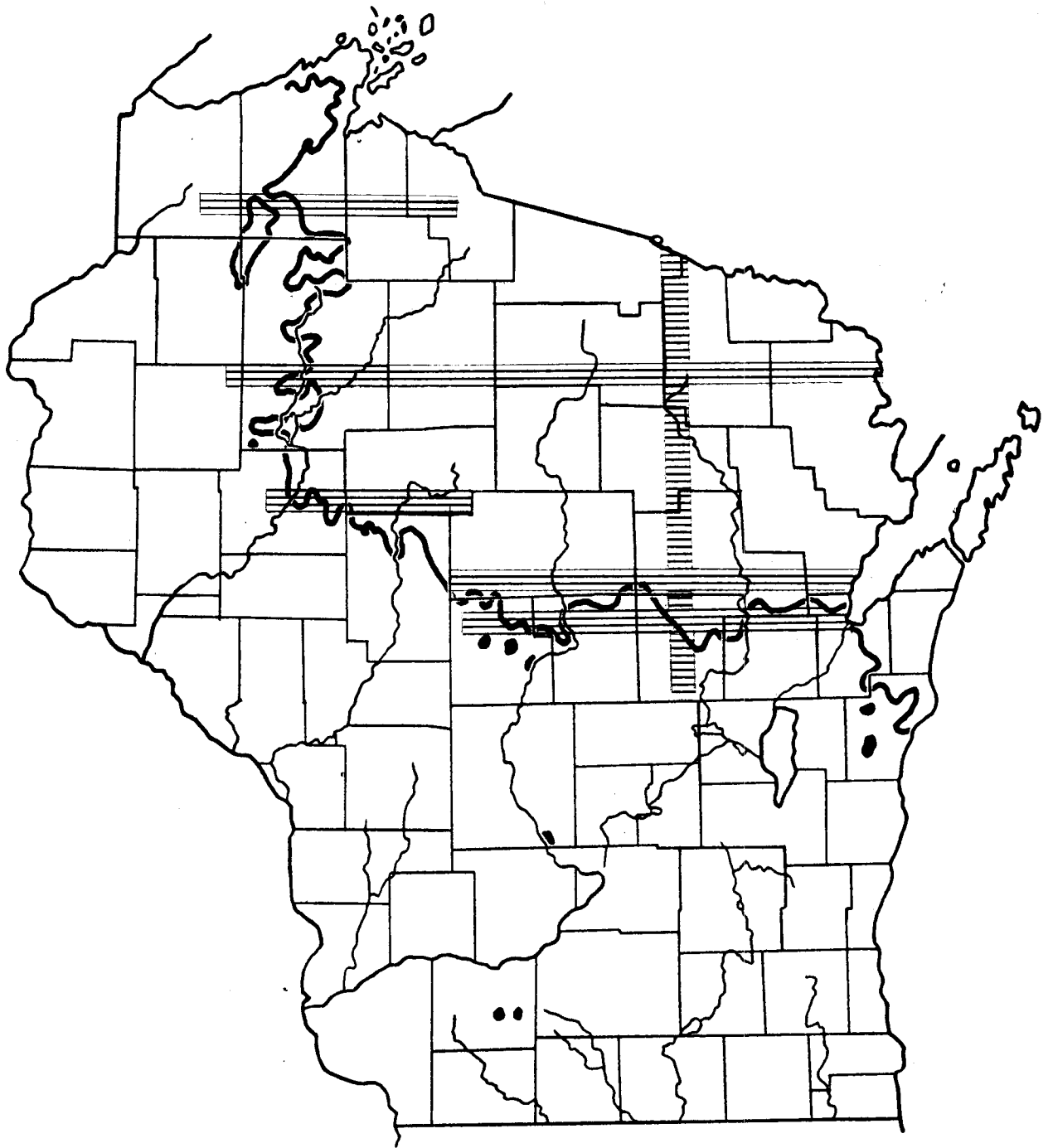


Fig. 7. Transects analyzed in relation to border of  
Tsuga canadensis.



within the border. Correlating Tsuga decreases were increased values of Pinus Spp. and Populus Spp.<sup>1</sup> The Importance Values of A. saccharum were generally less than Tsuga and conformed with its sharp decrease in Ranges 6E to 11E and 18E to 20E. West of the Chippewa River (Range 7W) A. saccharum was dominant. Fluctuating Importance Values of Tilia americana L. parallel A. saccharum Importance Values.

A transition from closed to open canopy recurred within the border. The greatest distance between trees was recorded in areas where Importance Values of Tsuga decreased. At the periphery of these areas the canopy began to close (Table 1).

Table 1. Mean Distance in Feet Between Survey Trees (Township 36)

Range	4E	5E	6E	7E	8E	9E	10E	11E	12E	13E
Distance	20	40	39	28	63	67	42	17	14	15

East of the Chippewa River an acute decrease of Importance Values of Tsuga took place. An open canopy was recorded west of the river in contrast to closed conditions east of the river (Table 2).

1. Populus tremuloides Michx. and P. grandidentata Michx.

Table 2. Mean Distance in Feet Between Survey Trees (Township 36)

Range	11W	10W	9W	8W	7W*	6W	5W	4W
Distance	28	25	22	17	18	25	18	16

\* Chippewa River

West of the river Pinus strobus L. was the dominating coniferous species. East of the river its importance decreased rapidly. Disjunct occurrences of Pinus banksiana Lamb. and Pinus resinosa Ait. appeared where Tsuga had low Importance Values.

The number of trees in each dominance class adds to the transitional picture of past conditions (Fig. 9). Within the border, the majority of Tsuga were in the 12-80 or 81-320 dominance class. P. strobus occurred in all three classes but the 81-320 size class was most frequently represented. Extending west along Township 36 the mean basal area of Tsuga decreased gradually to the termination of the border, whereas other species reversed this phenomenon (Fig. 10).

A transect of ranges along Township 44 indicates high Importance Values of Tsuga west to Range 6W, a decrease in Range 7W, and an increase in Range 8W (Fig. 11). Low values of Tsuga, A. saccharum, and T. americana occurred in Townships which were located on sandy soil. P. strobus and Populus spp. retained high Importance Values west of the Tsuga border but decreased as Tsuga values increased. The mean basal area of terminal Tsuga trees was 188 square inches (Fig. 12).

Fig. 8. Importance Values of arboreal species along a  
transect of ranges in Township 36.

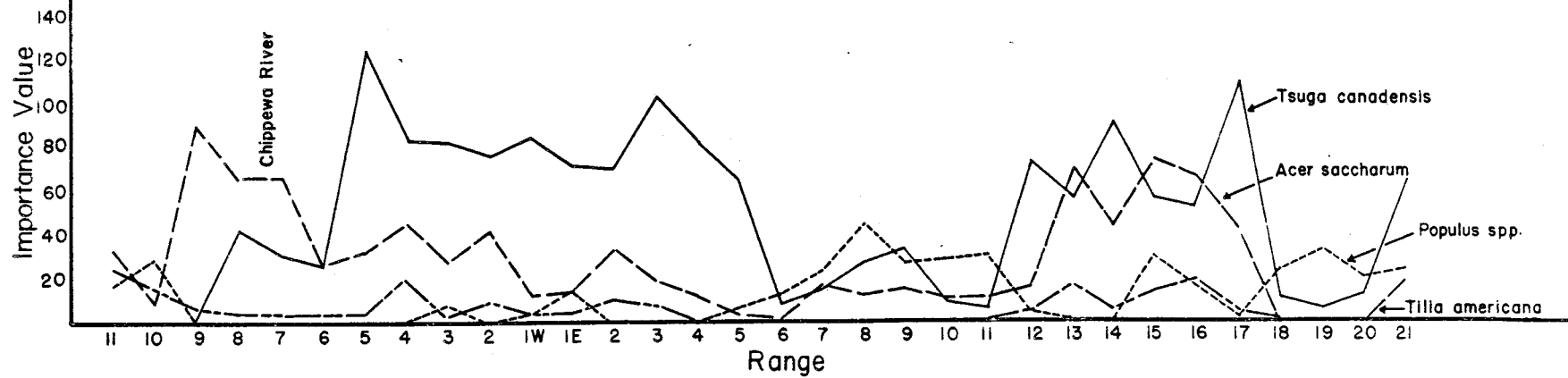
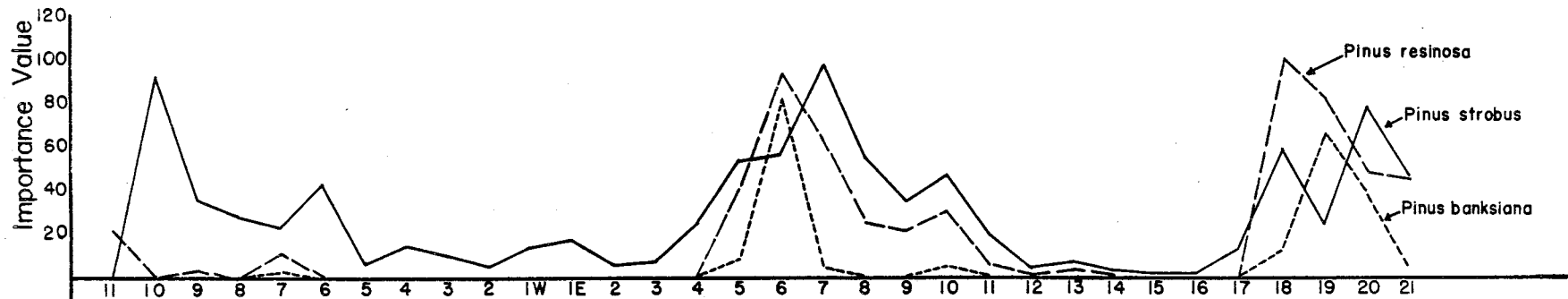


Fig. 9. Number of trees in each dominance class along a  
transect of ranges in Township 36.

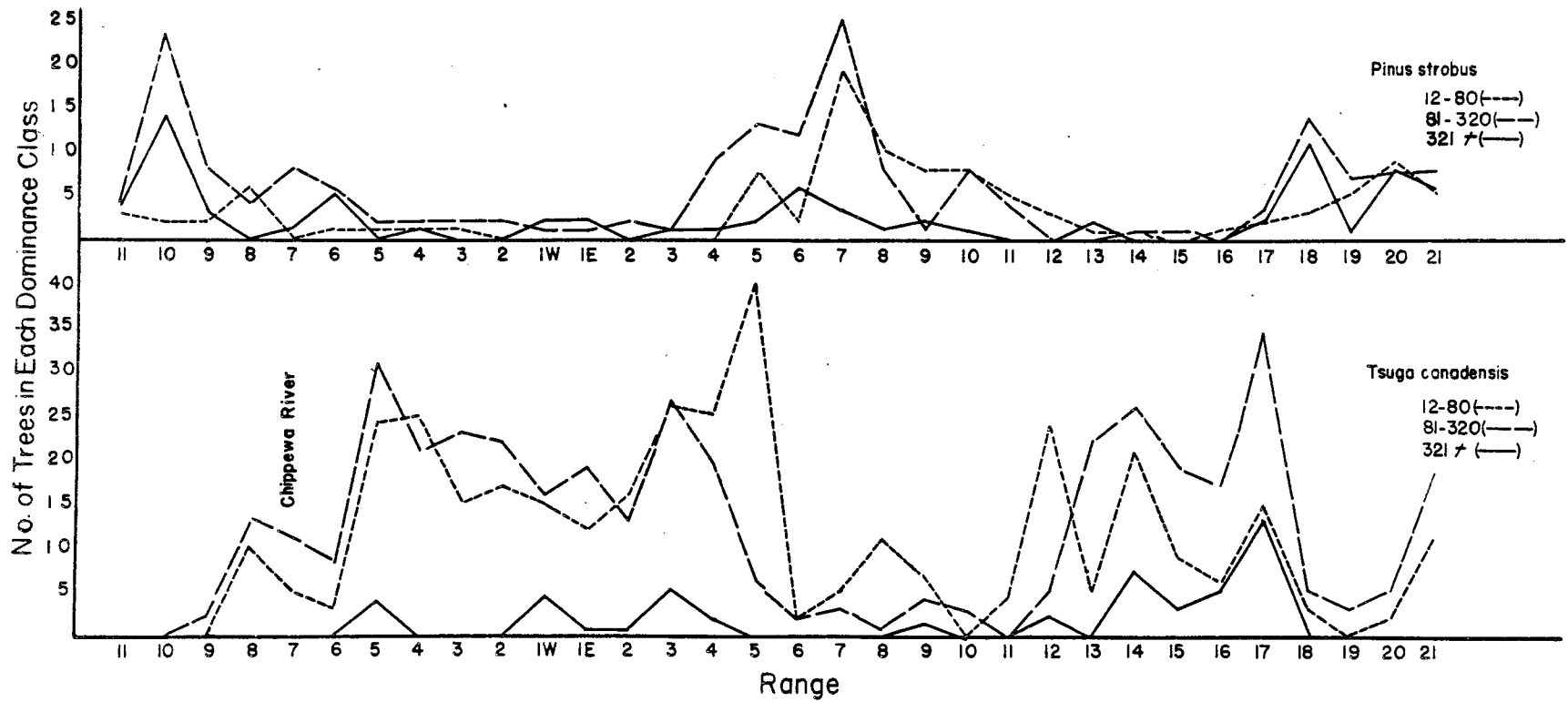


Fig. 10. Mean basal area of Tsuga canadensis and all other species along a transect of ranges in Township 36.

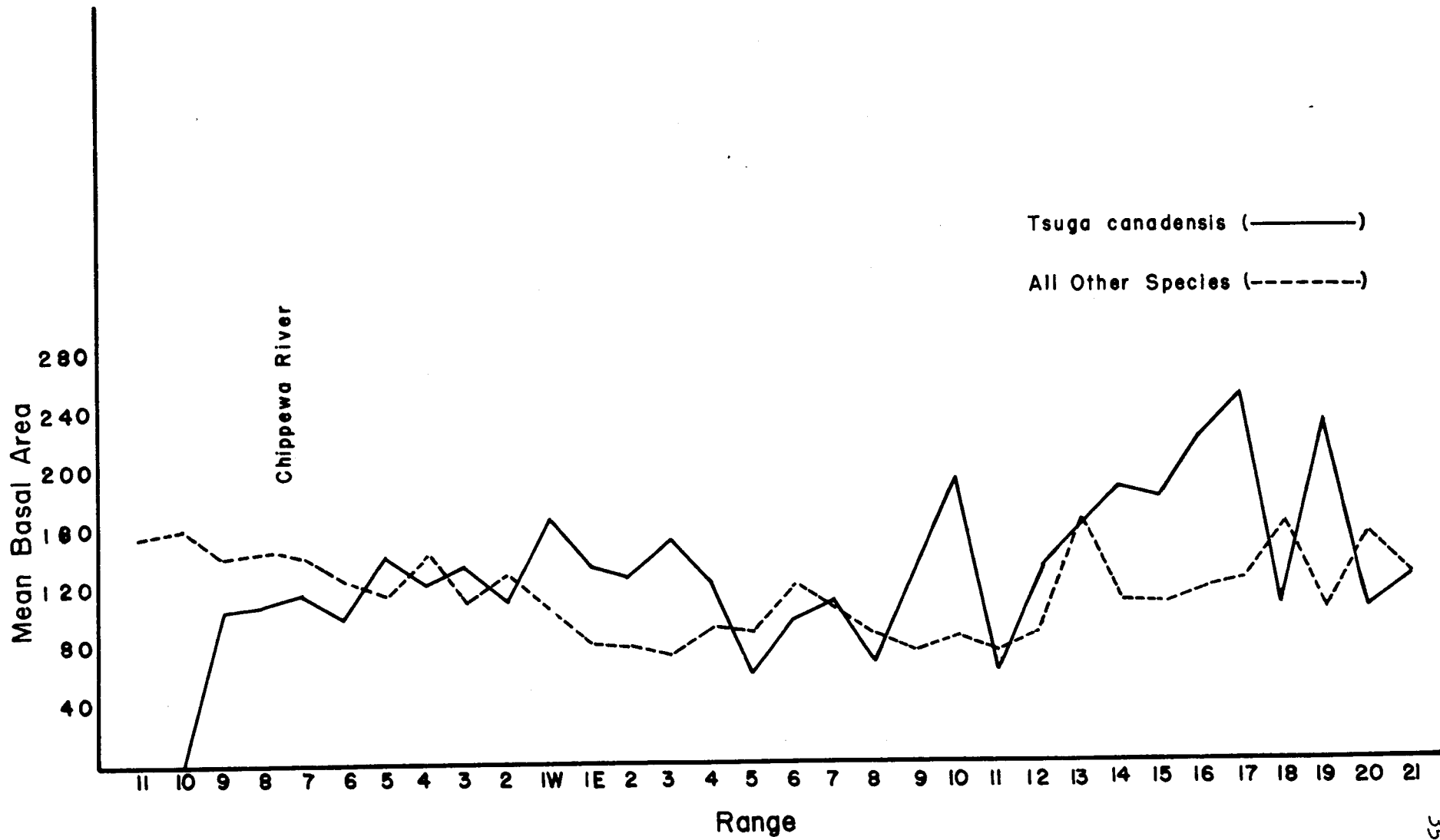


Fig. 11. Importance Values of tree species along transect  
of ranges in Township 44.

Fig. 12. Mean basal area of Tsuga canadensis and all other  
species and number of trees per acre along  
transect of ranges in Township 44.

Fig. 13. Number of trees in each dominance class along  
transect of ranges in Township 44.

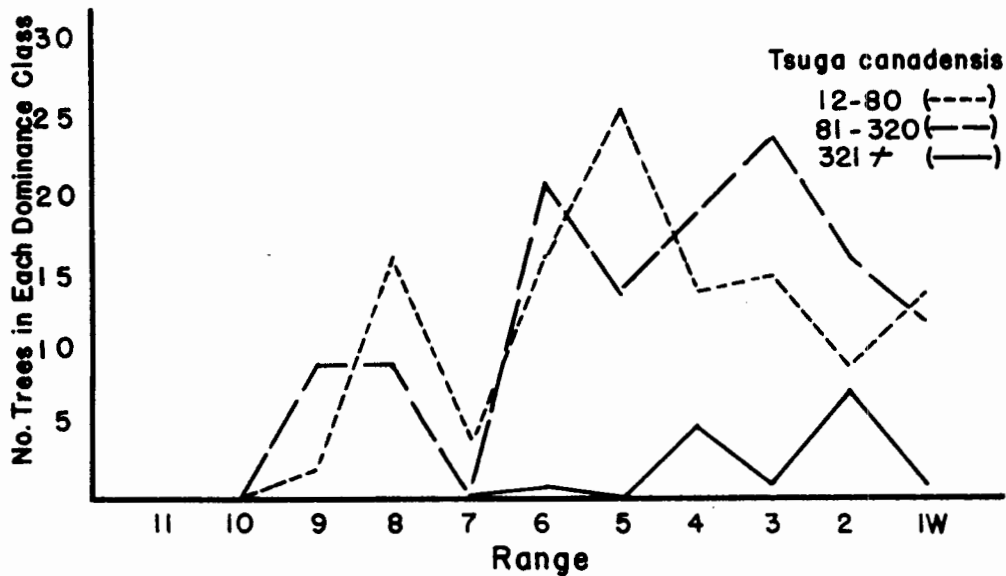
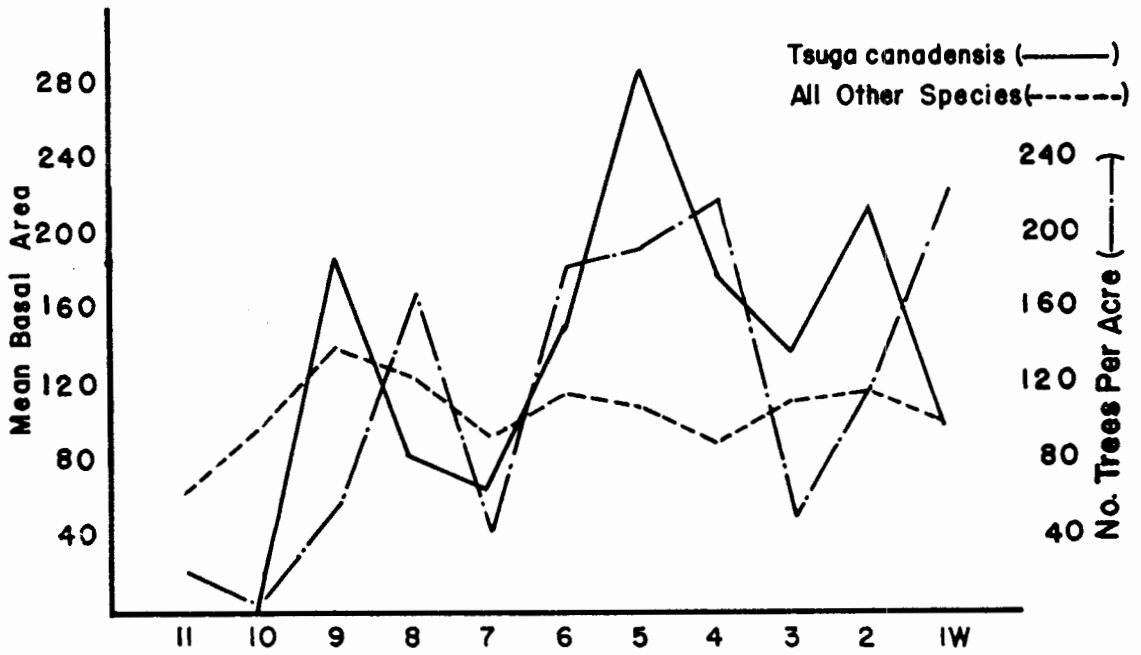
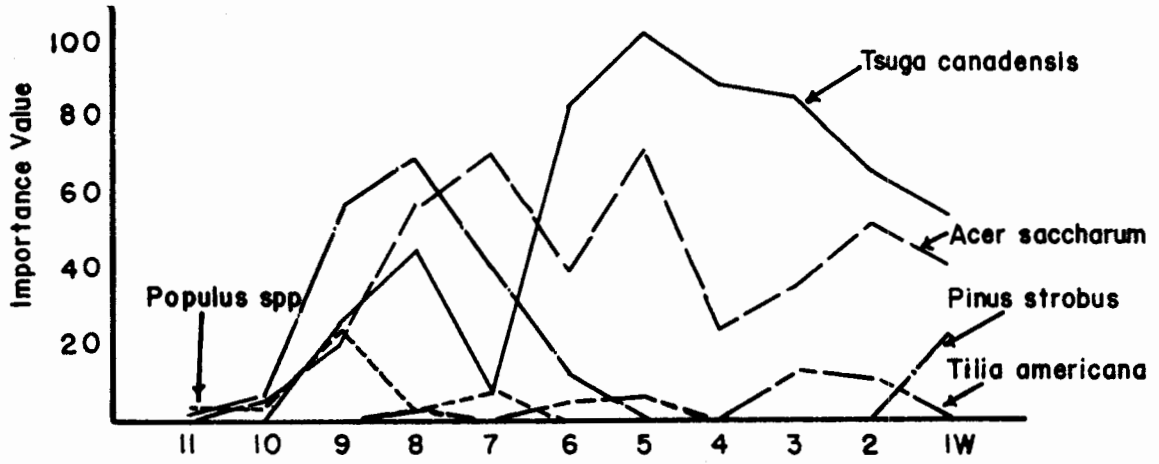


Fig. 14. Importance Values of tree species along transect  
of ranges in Township 30.

Fig. 15. Mean basal area of Tsuga canadensis and all other  
species and number of trees per acre along  
transect of ranges in Township 30.

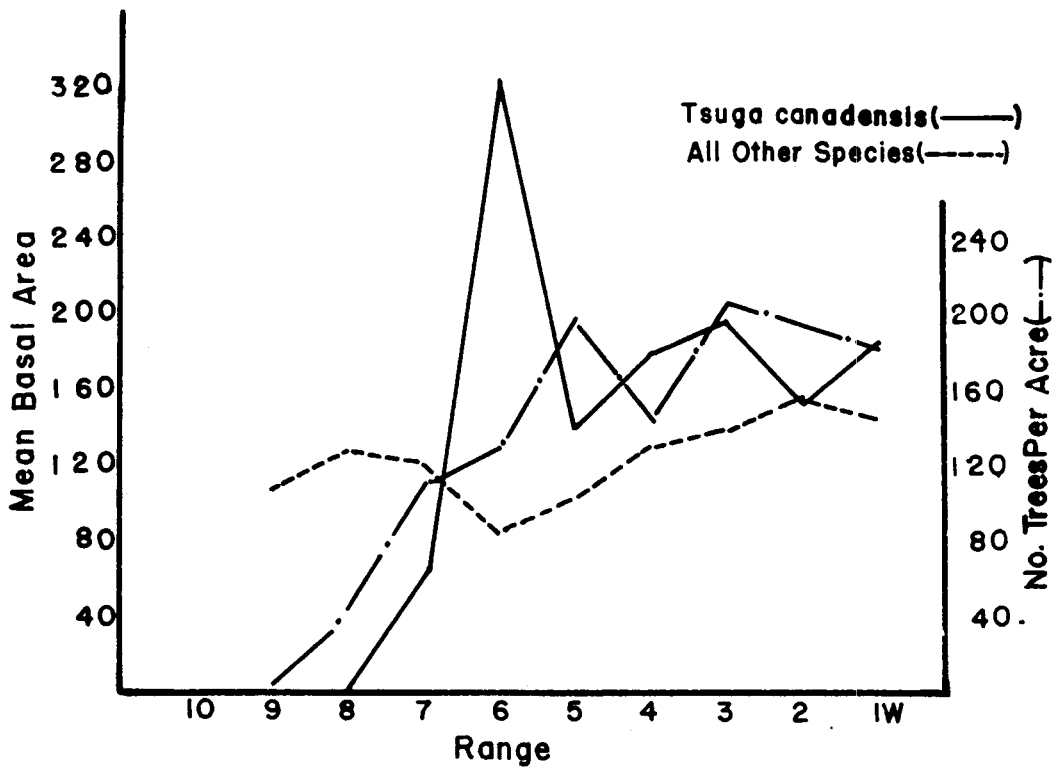
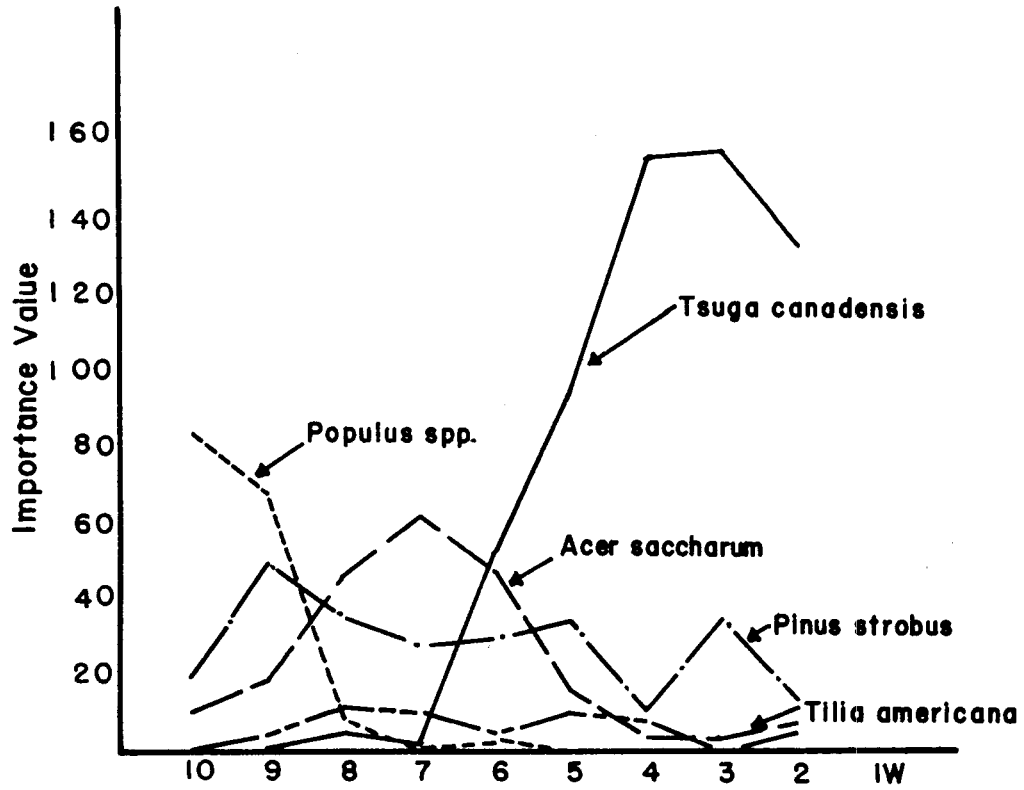
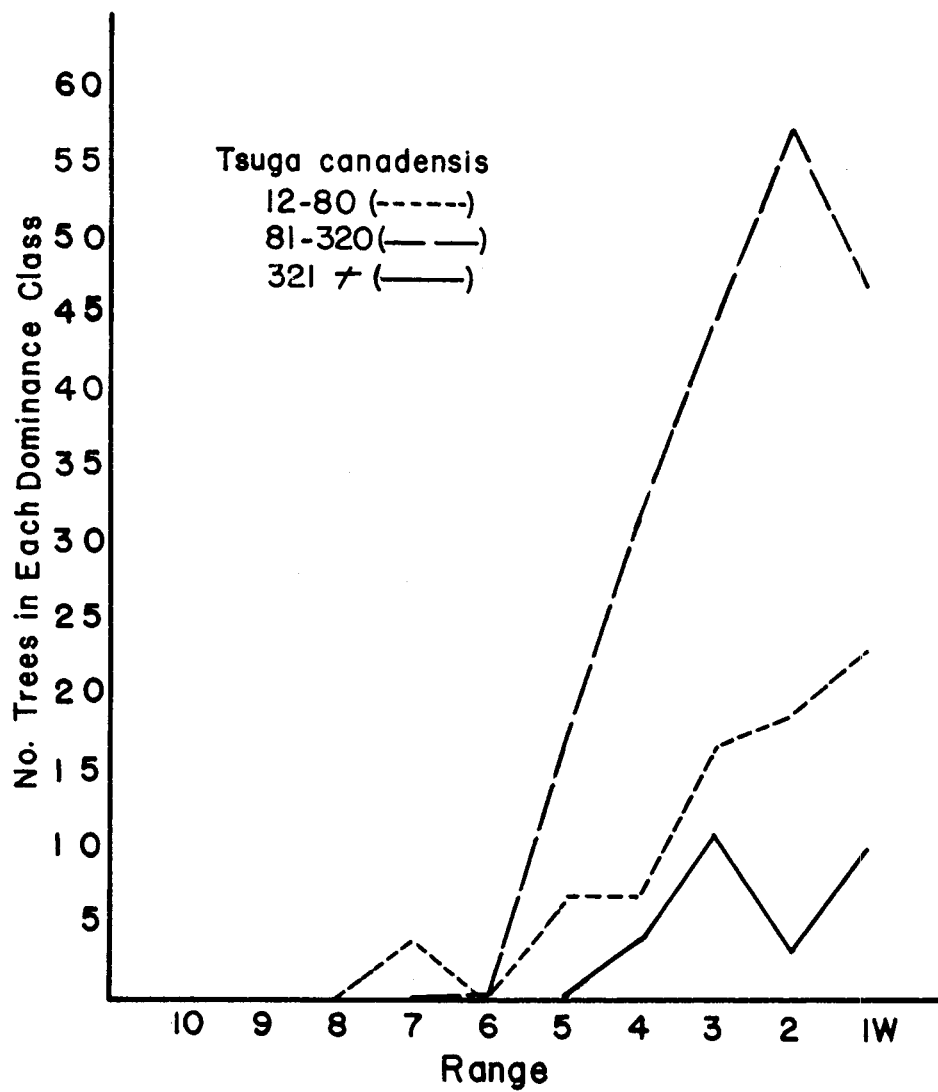


Fig. 16. Number of Tsuga canadensis in each dominance class along transect of ranges in Township 30.



The number of trees which made up this mean can be ascertained in Fig. 13. The largest size class of *Tsuga* in Township 44 terminated at the periphery of the northwest sand area. The two smaller size classes occurred in high values west of this region on loam soils of the Kennan Series.

Graphical presentation of five species along Township 30 indicates high Importance Values of Populus spp. west of the Chippewa River (Fig. 14). *Tsuga*, which was not recorded west of the river, increased acutely to the east. At the termination of the border the mean basal area of *Tsuga* was 60 square inches (Fig. 15). There was a progressive decrease in the number of trees in each size class (Fig. 16). The largest size class terminated 12 miles east of the river, the 80-320 class 6 miles east of the river, while the smallest size class continued to the river.

### Discussion

The population map depicts the variability in distribution of *Tsuga* at the termination of its range. The largest area of high concentration occurred on morainic deposits in Taylor County. Much of this particular region has rough topography which would be an effective fire barrier.

The western extension of the range along the south shore of Lake Superior and continuing south and east into Ashland County had a low density of *Tsuga*. The dominant species were P. strobus, Picea glauca Moench, and Abies balsamea (L.) Mill. Competing with the coniferous

species were Populus species. What factors were responsible for this community of species? Hutchinson (1918) stated that A. balsamea and P. glauca prefer moist soil and cool summer temperatures. These species are not fire resistant. Other investigators have concluded that fire is necessary for the perpetuation of P. strobus and Populus spp. (Mitchell, 1935; Maissurow, 1941; Brown, 1952; and Spurr, 1954). If fire was responsible for the presence of Populus and P. strobus, a protecting factor must have been present for the persistence of Tsuga and post-climax species. The area is deeply entrenched by post-glacial streams with ravines 40 to 100 feet deep (Martin, 1932). Provided conditions were favorable for fire to sweep across the expanses, the ravines would have been refugia for P. glauca, A. balsamea, and Tsuga. Repeated fires would have established the Populus-Pinus grouping in unprotected areas. Within the border of Tsuga along Township 50 only 2.7 per cent of all Tsuga recorded by surveyors occurred as a witness tree with P. glauca or A. balsamea. This disassociation infers that the species did not grow together. Owen (1852) stated that Tsuga was found at the bases of ridges and A. balsamea in swamps.

Low Importance Values of Tsuga on lacustrine clay suggests that an edaphic factor may have been partly responsible for the limitation of the species. Wilde (1946) stated, "planting is often handicapped by the unfavorable physical properties of the soil, heaving, and high content of lime in the substratum." At a later date (1949) he concluded, "rain water percolates with great rapidity through the channeled clay profile, so that only a small portion is retained in the surface layer. This, in connection with the high hygroscopicity

of the soil, presents a serious obstacle for invasion of the area by deciduous or coniferous species of high moisture requirements." The drying out of the humus layer would present highly inflammable material for burning.

Sharp decreases in Importance Values along Township 36 must be accounted for by a disturbance since there are no severe topographic changes along the transect. High Importance Values of P. strobus and Populus spp. occurred in the eastern and north central sand plains. The occurrence of these species on sandy soils suggests that the area was susceptible to burning. Consequently, the favorable habitats for Tsuga establishment would have been destroyed. Interspersed areas of heavier soils or a protective feature of the topography enabled Tsuga to persist in low numbers. The disjunct occurrences of P. banksiana and P. resinosa further support the fire theory.

Tsuga terminated at the eastern edge of the sand barrens which cross Bayfield County. Fire was the primary reason for the sharp transition. High values of P. strobus and Populus spp. were recorded outside of the boundary. The open canopy was favorable for establishment of P. strobus. Shirley (1934) concluded that P. strobus requires 20 per cent light intensity for satisfactory survival and 43 per cent for optimum survival and good growth. The presence of only a few large P. strobus in areas of Tsuga predominance indicates poor establishment of P. strobus under a closed canopy.

Historical accounts of fires add to the picture. During a geological survey of 1952, Owen reported that in the sandy regions of

northwest Wisconsin large areas had been overrun by fires. Murphy (1931) speaks of legends in which Ojibwa Indians burned the sand barrens for better growth of blueberry crops. Graham (1941) concluded that between 1400 and 1600 A.D. fires destroyed a greater part of the forest cover existing in the Great Lakes Region.

Barring drastic topographical and edaphic changes, what would have prevented fire from penetrating the conifer stands? Roth (1898) concluded, "fires stop of their own accord after they have run a moderate distance, evidently finding obstacles which gradually reduce their power." Surface fires entering a mesic stand would soon burn out because of moist humus conditions.

The separated extension of the border in southern Bayfield and northern Sawyer Counties was at one time connected to the main border. High Importance Values of Populus spp. north and east of the extension indicate that the area had been burned before being surveyed.

The southern part of the western boundary of *Tsuga* parallels the Chippewa River. East of the river *Tsuga* had high Importance Values which decreased immediately to the west. Grayish brown loams of the Kennan Series predominate east and west of the river. A severe change in topography occurs west of the river because of a monadnock range, the Barron Hills. *Tsuga* extended west of the river in low values and had a secondary high value in the foothills. Low values adjacent to the river may be accorded to fires burning along the river bottoms. Projections and absence of the border west of the river would be expected of a boundary ravaged by fires of varying intensity and amplitude. The

river would have provided a formidable, although not impassible, barrier to fires approaching from the southwest. Fire brands could have easily blown across the river. The diffuse boundary implies that fires took place east of the river but were either of rare occurrence or of short duration.

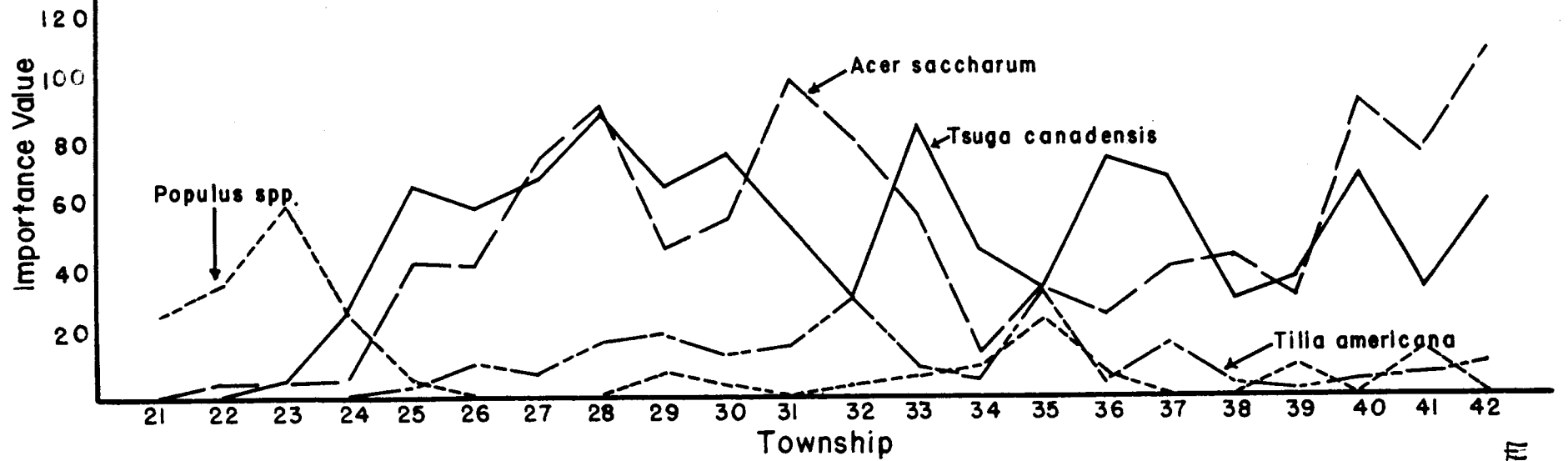
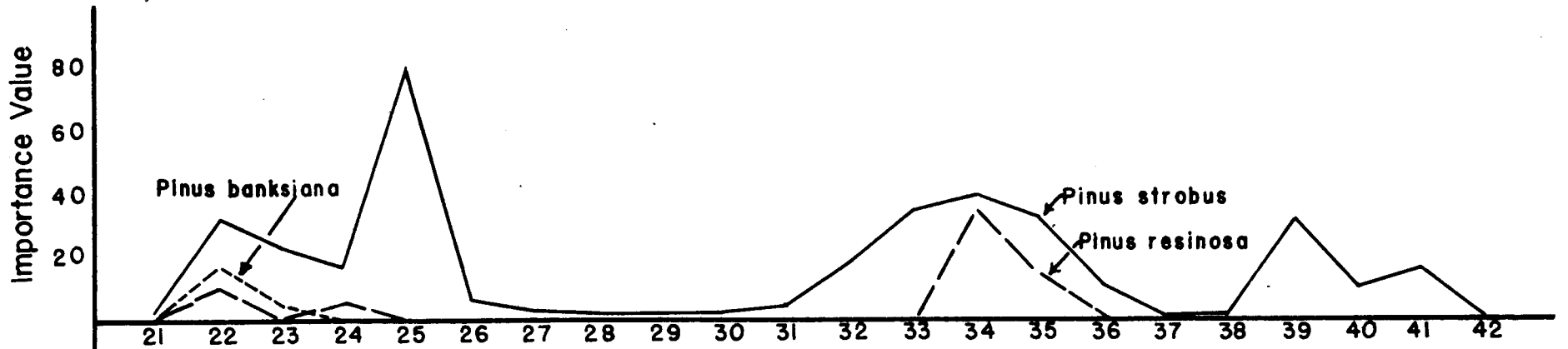
The *Tsuga* recorded west of the river were smaller trees. Lack of large trees at the border indicates instability. It appears that there were periodic invasions of *Tsuga* across the river during reduced incidence of fire. In the intervening fireless periods, *Populus* spp. were succeeded by *P. strobus*. Later, suitable micro-reliefs for the establishment of *Tsuga* were created by windthrown trees.

#### Results of Transects along Southern Border

Graphical presentation of a north-south transect (Range 12E) indicates abrupt transitions of *Tsuga* similar to those occurring along the east-west transects (Fig. 17). Correlated with decreases in Importance Values of *Tsuga* were consistent increases of *Pinus* spp. and *Populus* spp. An intergradation of *Tsuga*, *Pinus*, and *Populus* took place at the periphery of sand areas. *A. saccharum* and *T. americana* had similar trends along the transect. At the limits of its range (Township 23), *Tsuga* suddenly terminated along with *A. saccharum* and *T. americana*.

The two smaller size classes of *Tsuga* were represented at the border (Fig. 18). Trees of the 321<sup>+</sup> size class were not recorded at the termination of the range. *P. strobus* was present along the transect in the three size classes, but the number of trees in the 81-320 size

Fig. 17. Importance Values of arboreal species along  
transect of townships in Range 12E.



class predominated (Fig. 19). The mean basal area of *Tsuga* within the border varied from 80 to 280 square inches. Terminal trees had a mean basal area of 144 square inches (Fig. 20). An increase of the mean basal area of other species was recorded from north to south along the transect.

The abrupt termination of the range and opening of the canopy is exemplified in the mean distance between survey trees (Table 3).

Table 3. Mean Distance in Feet Between Survey Trees (Range 12E)

Township	21	22	23	24*	25	26	27	28
Distance	172	55	42	16	21	20	19	22

\* Border

Immediately south of the border the mean distance increased greatly.

A transect (Fig. 21) extending east from Range 1E to Range 21E along Township 27 denotes high Importance Values for *Tsuga* west of the Wisconsin River (Range 7E) and west of the Wolf River (Range 15E). Low values were recorded in Ranges 9E and 16E. East of the rivers *P. strobus* and *Populus* spp. showed substantial increases. *P. banksiana* was not reported along the transect.

Along an east-west transect (Township 24), which includes ranges within and outside the *Tsuga* border, Importance Values of *Tsuga* again peaked west of the Wisconsin and Wolf Rivers (Fig. 22). In an area outside the range of *Tsuga*, immediately east of the Wisconsin River,

Fig. 18. Number of Tsuga canadensis in each dominance class along transect of townships in Range 12E.

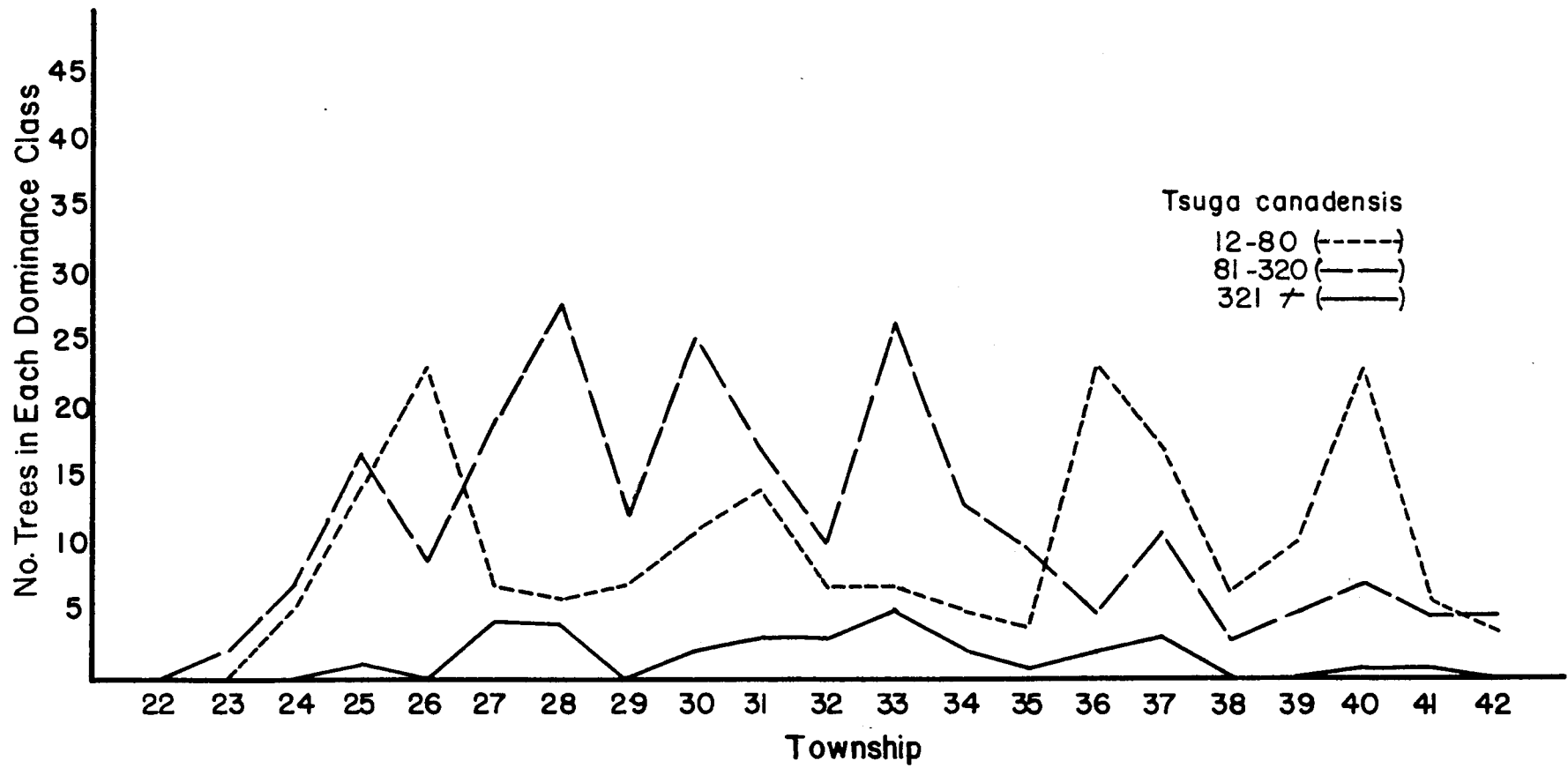


Fig. 19. Number of Pinus strobus in each dominance class  
along transect of townships in Range 12E.

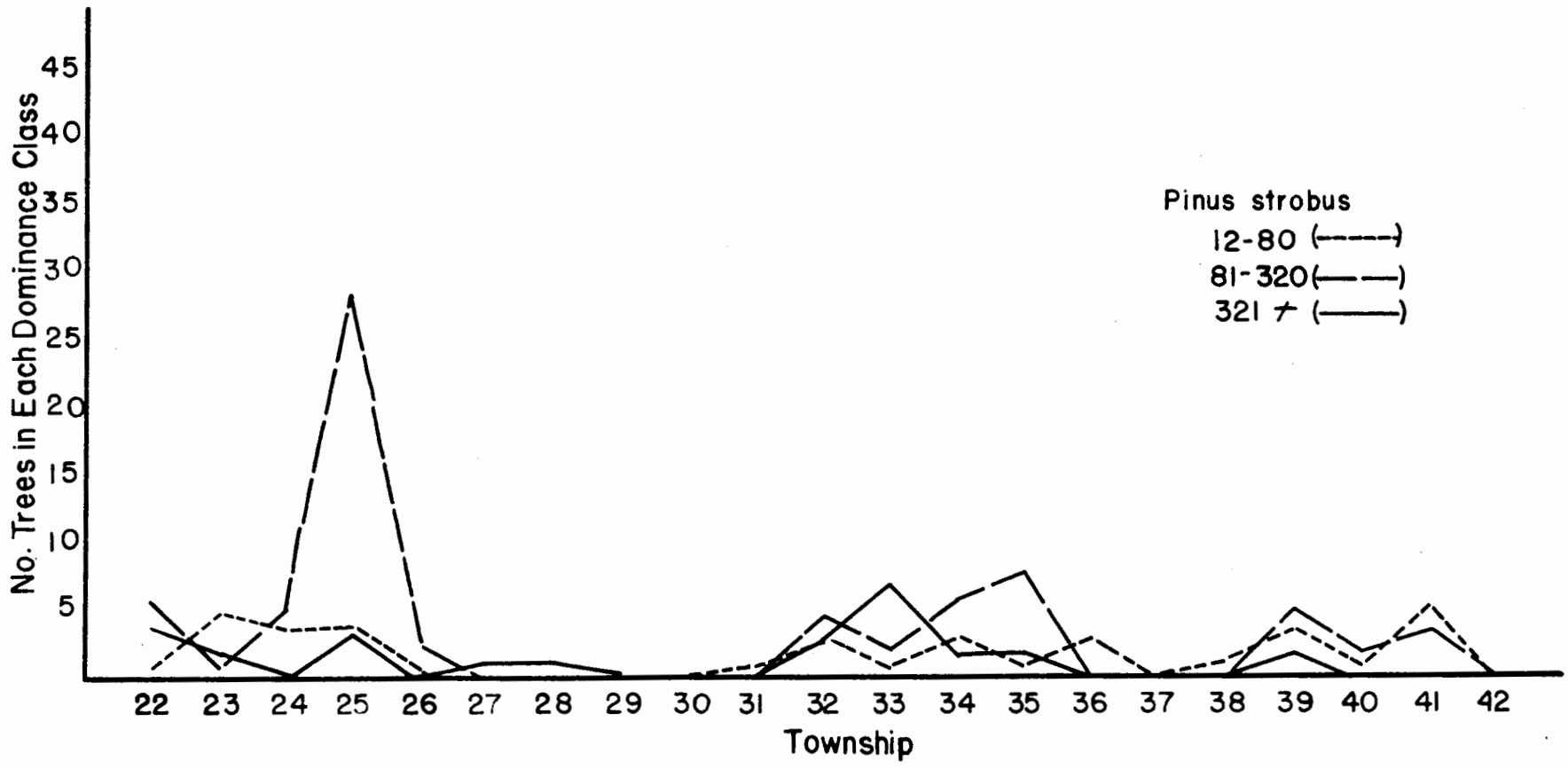


Fig. 20. Mean basal area of Tsuga canadensis and all other species along transect of townships in Range 12E.

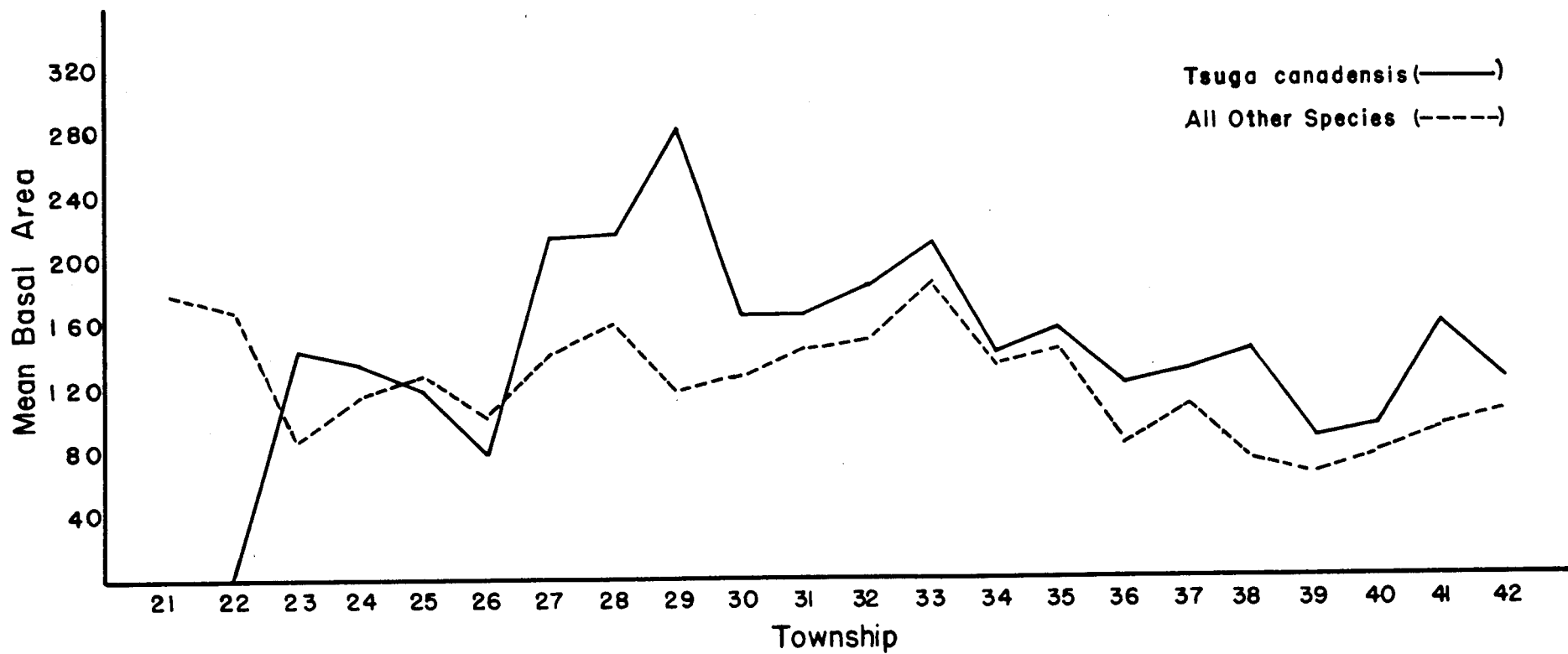
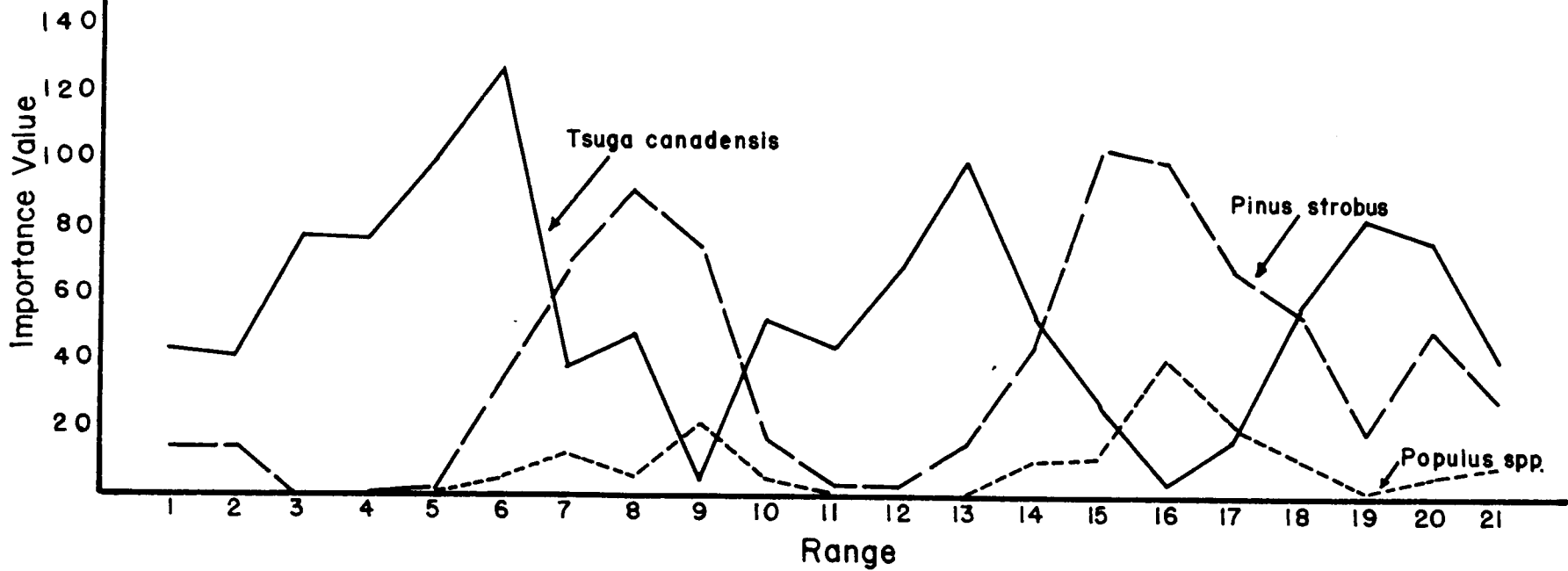
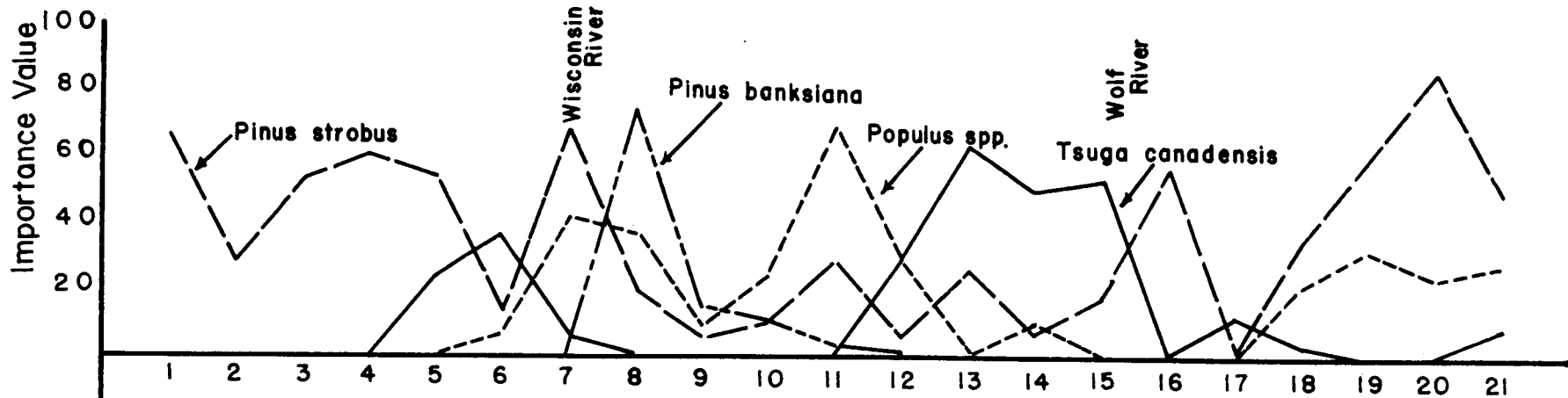


Fig. 22. Importance Values for arboreal species along  
transect of ranges in Township 24.

Fig. 21. Importance Values for arboreal species along  
transect of ranges in Township 27.



P. strobus and Populus spp. suddenly increased along with a disjunct occurrence of P. banksiana. The southwestern periphery of the border lies north of tributaries of the Yellow, Hemlock, and Poplar Rivers in Township 24, Ranges 3E and 4E.

### Discussion

Transects extending through the southern boundary indicate transitions approximating those of the western border. Low Importance Values of Tsuga are accompanied by high Importance Values of disjunct Pinus spp. and Populus spp. At the southern limits of the border in Portage County, peak Importance Values of Populus spp. and P. banksiana evidence the frequency of fires. In the southwest part of the range, extending southeast from Chippewa County, a natural barrier to the approach of fires was the mesh of tributaries of the Yellow, Hemlock, and Poplar Rivers. The border of Tsuga lies north of this drainage area.

An example of the effectiveness of water barriers is the southwest coursing of the Wisconsin River in Portage County. Yellowish or gray sands prevail on both sides of the river. Within the pocket formed by the meander of the river (Township 23, Range 7E) Tsuga was recorded by the surveyors. Immediately east of the river, in an area accessible to northward spreading fires, Tsuga was not recorded. It is evident that the river was a factor in preventing the progress of the fires. Outliers of the southern border were similarly protected from fire by streams.

Tsuga skirted the northern boundary of lacustrine clay deposits

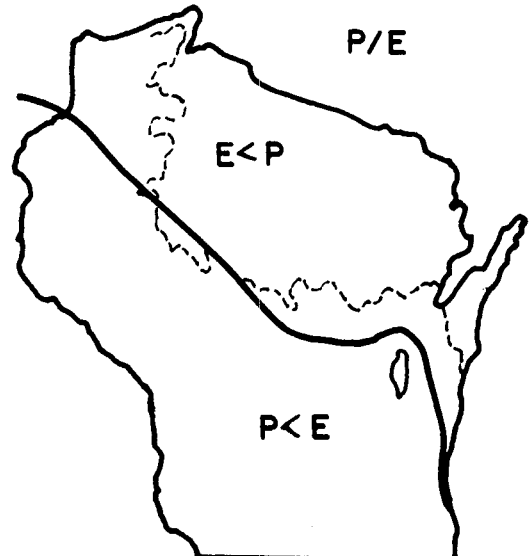
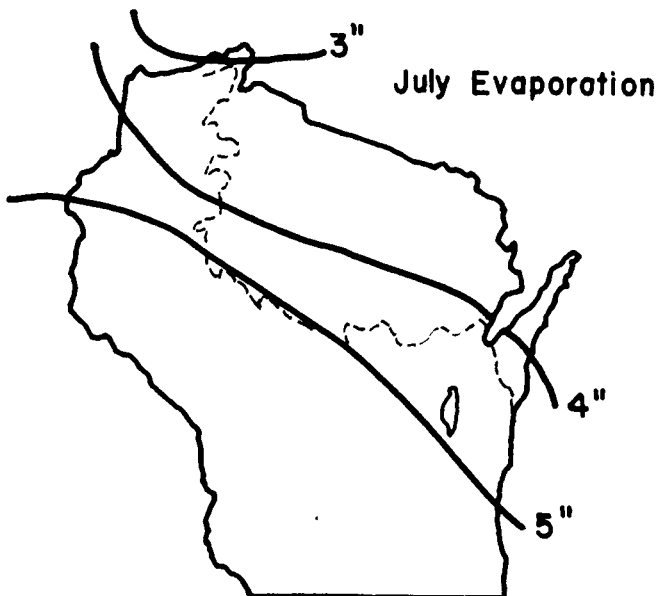
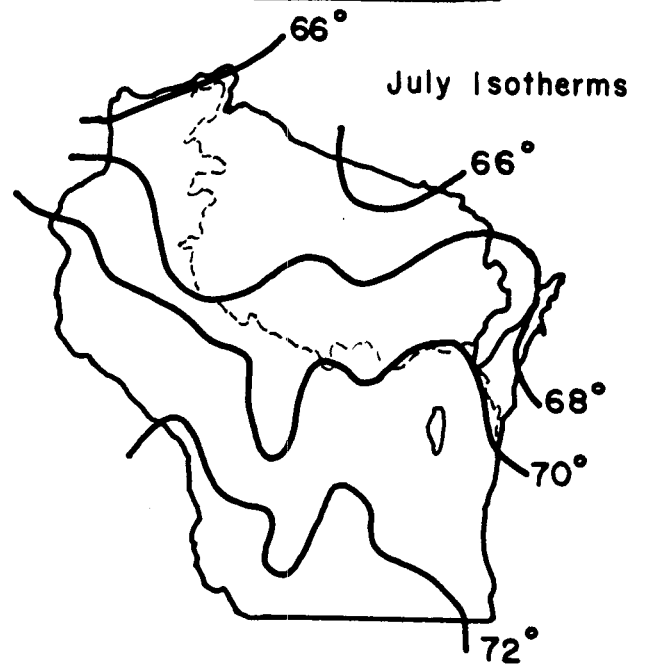
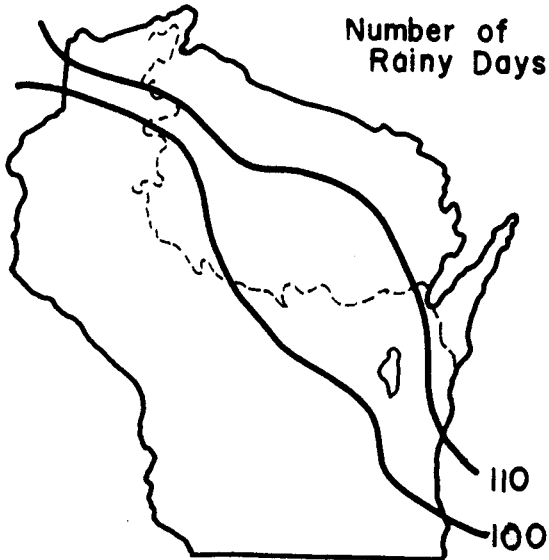
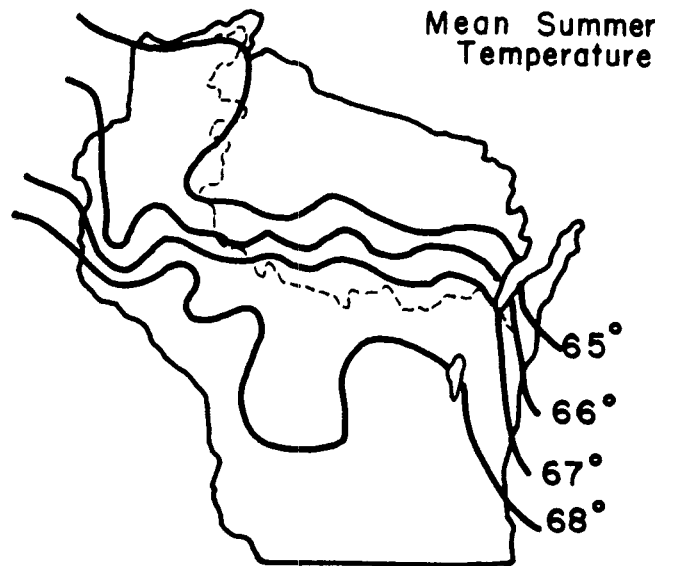
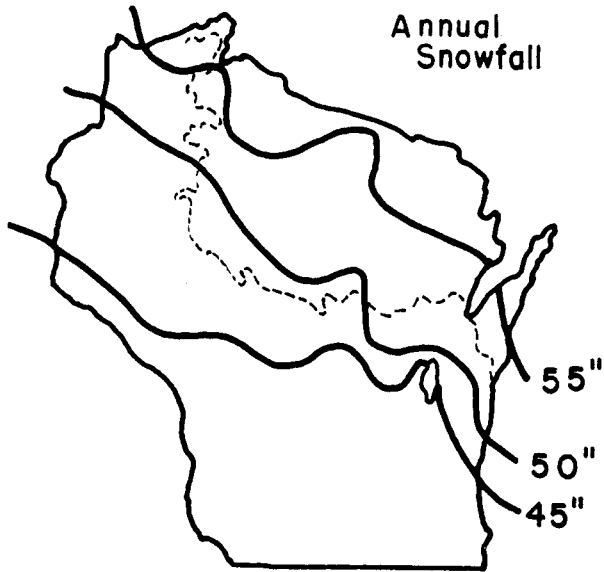
in Brown County and then extended south into Manitowoc County on the same soil type. The density of Tsuga was closely correlated with changes in soil type. The greatest concentrations in Manitowoc County occurred on loam soils of the Miami Bellfontaine Series. Humus of these heavier soils would diminish the effects of fire.

Surveyors reported the presence of Tsuga along the Lake Michigan shore as far south as Sheboygan County. Even today a few scattered Tsuga are found within 50 feet of the shoreline in this vicinity. Kenoyer (1933) stated that 85 per cent of the Tsuga used as witness trees in southwestern Michigan were within 10 miles of the Lake Michigan shore.

#### Discussion of Climatic Factors and General Summary

At the present time insufficient micro-climatic studies do not permit precise correlations of climatic factors and the border of Tsuga. General suppositions can be made that the range of Tsuga in Wisconsin is within gradients of greater rainfall (P), cooler summer temperatures, lower evaporation rates (E), and greater winter snowfall (Fig. 23). The complex of climatic factors functions in varying degrees along the border. The southeastern boundary of Tsuga bends sharply southward along the shore of Lake Michigan, closely paralleling temperature and moisture gradients. A correlation of the boundary with the isopleths would suggest that temperature and precipitation are effective in limiting the species range. The occurrence of outliers on north facing bluffs and in deep cool ravines in the southern

Fig. 23. Relation of the border of Tsuga canadensis to climatic factors (after Climate and Man, 1941; Curtis, 1950, and Ward, 1954).



part of the state further implies that temperature and moisture may be important climatic factors limiting the range of *Tsuga*.

Snow depth may be important when considered in conjunction with ground freezing. The *Tsuga* boundary lies north of the 45" snowfall isoline. *Tsuga*, a shallow rooted species, is susceptible to frost. Hough (1945) in observing 291 *T. canadensis* seedlings and saplings on the northern Allegheny Plateau recorded 49 per cent as frost damaged. In an area where snow mantles the ground before freezing conditions occur, coniferous trees are protected from frost injury and are assured of a supply of ground moisture during cold weather. Bay (1952) stated that 24" of snow provides enough protection to prevent frost penetration at  $-21^{\circ}$  F.

In summary, conclusions can be drawn from the surveyor's records that the border of *Tsuga* was affected by edaphic, fire, and climatic factors. Along the south central and northeast parts of the border, which lie adjacent to sand plains, soil conditions favored surface fires. One of the consequences of repeated fires was the consumption of reproduction habitats. The density of *Tsuga* on lacustrine clays was similarly influenced by combined effects of soil and fire. River systems were the principal barriers to the progress of fires. Topography and moist soil conditions diminished the effects of fire.

The close correlation of certain climatic factors with segments of the border may be mere coincidence since the boundary does not conform to any one gradient along its entire extent.

Table 4. Tabulation of the composition of arboreal species in present day stands.

Species	Number of Stands of Occurrence	Mean Importance Value	Range Importance Values	Mean Freq. % Seedlings	Mean Freq. % Sapling
<i>Tsuga canadensis</i>	34	135.2	11.5 - 243.0	14.6	21.6
<i>Acer saccharum</i>	29	48.2	3.8 - 166.1	33.8	27.1
<i>Betula lutea</i>	32	35.9	3.3 - 101.5	15.1	15.6
<i>Acer rubrum</i>	26	17.1	3.3 - 68.5	12.7	9.6
<i>Ulmus americana</i>	20	8.4	3.2 - 49.1	1.3	0.9
<i>Tilia americana</i>	17	7.0	2.9 - 30.0	3.2	4.4
<i>Thuja occidentalis</i>	10	7.0	4.0 - 24.0	0.8	0.8
<i>Quercus rubra</i>	11	5.0	3.0 - 44.0	4.0	3.3
<i>Pinus strobus</i>	7	4.3	3.5 - 66.3	0.2	1.3
<i>Betula papyrifera</i>	10	2.9	3.9 - 16.7	0.2	0.6
<i>Ostrya virginiana</i>	8	1.7	3.3 - 13.6	-	0.6
<i>Populus grandidentatum</i>	5	1.6	2.7 - 17.0	0.6	0.4
<i>Populus tremuloides</i>					
<i>Pinus resinosa</i>	1	0.4	12.9	-	-

### Composition of Arboreal Layer from Present Day Survey

Owing to selective cutting, a peculiar situation exists in residual stands along the border of *Tsuga*. In several stands investigated the degree of disturbance has reduced the importance of *Tsuga* from a dominant to a minor species. Stands which have a high density of *Tsuga* are undisturbed; accordingly, the stands which were sampled had high Importance Values of *Tsuga*. Twenty seven stands were dominated by *Tsuga* and seven by *A. saccharum*. Except for minor regional fluctuations the border of *Tsuga* in 1954 was geographically similar in its location to that recorded by the surveyors in 1845.

### Results

In the 34 stands sampled, *Tsuga* had a mean Importance Value of 135.2 out of a total value of 300. Co-dominant with *Tsuga* are *A. saccharum* and *B. lutea* (Table 4). *B. lutea* was ranked second in importance to *Tsuga* in only one stand. Occurring as a constant associate of *Tsuga*, *B. lutea* was recorded in 32 of 34 stands.

*Tsuga* saplings were recorded in 27 stands. A frequency of 81.8 per cent for sapling reproduction was recorded in the stand which had the highest Importance Value of *Tsuga* - 243.0. The frequency range of saplings was 1.9 to 81.8 per cent; seedling frequency ranged from 4.0 to 54.6 per cent.

*A. saccharum* occurred in 29 of 34 stands. Both *Tsuga* and *A. saccharum* do not occur in the same stand with equal Importance Values. *A. saccharum* saplings were recorded in 30 stands. The highest *A. saccharum* reproduction occurs in stands in which that species is

dominant.

Ostrya virginiana (Mill.) K. Koch and Acer rubrum L. are important understory trees but seldom reach tree size. A. rubrum reproduction was recorded in 27 stands. O. virginiana reproduction was negligible.

T. americana and Ulmus americana L. were present in over one-half of the stands. Neither reach high Importance Values. T. americana reproduction was observed from both seed and stumps.

P. strobus and P. resinosa seldom occur where *Tsuga* has high Importance Values. P. resinosa was only recorded in one stand. Reproduction of the pines is limited by the closed canopy. They represent a subclimax of long duration because of their longevity.

Betula papyrifera Marsh and Populus spp. are successional after disturbance. The low frequency of reproduction of these species is indicative that the stands are undisturbed.

Within a stand of *Tsuga* the light intensity is low. In 33 stands the light intensity within the stands was less than 5 per cent of the light outside the stands.

### Discussion

In stands at the termination of the border, *Tsuga* reproduction occurred in 32 stands. Stands in which no reproduction or little reproduction was recorded were noted as having a lack of available germination habitats. Sapling establishment occurs principally on mounds, stumps, and logs. The successful survival of trees from such a group would tend to make islet groupings of younger trees among older trees (Plate 1). If the canopy should close before the saplings express

dominance the individuals remain suppressed. The ability of *Tsuga* to endure suppression has been noted by other investigators (Graham, 1941; Stearns, 1947). Stearns concluded that suppression, not climatic change, accounted for variations in annual ring width because of the failure of slow and rapid growth to coincide in time in different individuals within the same stand. The majority of stumps in the stands portray the remains of an overstory of *P. strobus*. Removal of the pines released the understory of *Tsuga* from suppression.

*A. saccharum* does not reproduce well under a heavy canopy of *Tsuga*. Stearns (1947) in applying association tests found a negative relationship between *Tsuga* and *A. saccharum*. It is not until edaphic or environmental factors are changed that other species can become established in a stand of *Tsuga*. This process may be hastened because of the susceptibility of *Tsuga* to windthrow. Further investigation is needed to determine the changes which occur within a stand of *Tsuga* to cause an exclusion of other species.

The replacement of dominant species by subdominants is inappreciable. These minor species occur in micro-areas where the canopy has been opened by catastrophes. In the favorable conditions created these species become established, forming islet groupings within the larger stands. By reason of catastrophes there are continual rotations of species in a stand. The trend of succession toward a pure stand is, therefore, momentarily halted.

Table 5. Comparative composition (Importance Values) of tree species as shown in surveyor's records and present day field studies.

Species	Composition 1834-1858*	Composition 1954**
<i>Tsuga canadensis</i>	55.4	134.4
<i>Betula lutea</i>	52.9	37.1
<i>Acer saccharum</i>	33.7	53.1
<i>Pinus strobus</i>	24.5	2.2
<i>Ulmus americana</i>	11.7	9.2
<i>Populus spp.</i>	8.6	1.5
<i>Acer rubrum</i>	7.3	14.8
<i>Tilia americana</i>	6.5	8.4
<i>Abies balsamea</i>	5.4	5.1
<i>Fraxinus americana</i>	5.3	8.7
<i>Betula papyrifera</i>	3.1	3.0
<i>Ostrya virginiana</i>	2.9	2.2
<i>Quercus rubra</i>	2.0	4.0
	<hr/>	<hr/>
Total	219.3	283.7
Other species	80.7	16.3
	<hr/>	<hr/>
	300.0	300.0

\* Importance Values based upon 34 Townships

\*\* Importance Values based upon 17 Stands

### Pre-settlement Composition versus Present Day Composition

A comparative study of pre-settlement and present vegetation was completed to ascertain changes in composition along the Tsuga border. Other Wisconsin investigators have also used surveyor's records for similar comparisons: Thomson (1940) studied relic prairie areas in central Wisconsin; Fassett (1944) the Brule River Basin; Cottam (1949) oak-openings in southern Wisconsin; Stearns (1949) vegetational studies in Northern Wisconsin; Ward (1954) beech border in eastern Wisconsin; and Zicker (1955) vegetation of Jefferson County, Wisconsin. Cottam was the first to apply quantitative methods to the data.

### Results

In this study, the recorded species (Table 5) were reported in both surveyor's records and present day field work. Values for surveyor's records represent the mean values of two townships. The greatest change in Importance Values, since the time of the survey, has occurred principally among the dominant species (Table 5). Pioneer species have decreased in importance in the past 120 years.

Since the time of the survey there has been a substantial decrease in the distance between trees and an increase in the number of trees per acre (Table 6). The mean basal area of Tsuga is generally less in 1954 than 1845. Only four present day stands have a larger basal area of Tsuga than was recorded by the surveyors.

### Discussion

The significantly increased Importance Value of Tsuga denotes

Table 6. Comparative mean basal area, mean distance between trees (in feet), number of trees per acre from surveyor's records and present day field study.

Stand No.		Mean B.A. Excluding Tsuga	Mean B.A. Tsuga	Mean Dist. Btw. Trees	No. Trees Per Acre
1	1834	90.0	190.0	18.2	163.0
	1954	140.1	55.0	15.4	213.2
7	1850	133.6	162.4	18.8	197.0
	1954	130.4	60.8	11.2	401.0
8	1845	141.0	177.0	16.0	227.0
	1954	113.2	95.5	13.9	261.0
10	1852	92.0	135.4	63.0	93.1
	1954	74.6	64.4	9.4	571.7
11	1852	118.0	128.2	26.6	80.0
	1954	114.1	171.9	14.8	229.6
12	1853	106.0	221.8	56.1	18.9
	1954	127.4	89.0	9.3	586.5
13	1851	132.3	278.2	17.0	175.4
	1954	145.9	94.0	12.5	322.9
18	1853	149.6	225.6	20.4	129.1
	1954	69.4	58.0	12.0	349.3
21	1853	130.0	131.9	33.0	46.5
	1954	87.0	102.5	13.9	260.3
23	1849	123.6	160.7	17.1	174.9
	1954	76.6	93.3	11.6	373.8
25	1857	143.0	191.1	26.5	83.7
	1954	46.8	93.9	11.5	383.0
30	1855	109.2	187.8	27.1	107.1
	1954	35.6	99.3	11.9	354.0
31	1853	153.4	112.2	21.7	122.5
	1954	38.2	116.2	12.3	331.4
33	1857	89.6	86.3	15.3	235.2
	1954	256.1	97.8	12.5	321.9
36	1856	120.3	95.0	22.1	103.2
	1954	85.4	132.1	14.0	258.1
38	1858	104.0	158.1	25.4	111.3
	1954	84.1	159.4	15.0	222.9
40	1858	93.4	151.5	26.1	113.7
	1954	65.2	90.3	12.6	320.9

that the species has been reproducing along the border. Improvident cutting of P. strobus and the tanning industry at the turn of the century could have affected *Tsuga* in several ways. The removal of the overstory of P. strobus would have released *Tsuga* from suppression. Pine slashings left to decay after lumbering would increase the number of suitable germination habitats. *Tsuga*, which was never valued as a wood producing species, was felled and stripped of bark; the residual wood was left to rot. This practice not only provided more habitats for establishment but most likely caused a decline in the density of mature trees. Stearns (1949) concluded that the per cent of *Tsuga* in the large size class (321+) had increased within the past 100 years in Forest County, Wisconsin. The instability of a species at the border of its range could effect a decrease in the large size class. The number of trees in each dominance class discloses the greatest difference in the smallest (12 - 80) class (Table 7).

Table 7. Per Cent *Tsuga* in Each Dominance Class

Size class	1945*	1954
12 - 80	36.6	51.6
81 - 320	54.8	44.5
321+	8.6	3.9

\* Mid-date of surveys

The high per cent of trees in the 12 - 80 size class in present day

stands may be a recovery from the decimation at the turn of the century. The decrease in the large size class cannot be attributed entirely to windthrow. On the basis of field records the greatest amount of windthrow occurs in the 81 - 320+ size class. Fifty-one windthrown *Tsuga* trees which were measured had a mean basal area of 199 square inches. Only one windthrown tree was recorded in the 320+ size class. Damage is also incurred by the partial pulling down of small trees as larger trees topple over. Two such conditions were noted in the field in which the large windthrown trees had a mean basal area of 225 square inches and the young trees 57 square inches.

The capacity of *A. saccharum* to reproduce in low light intensities is reflected in increased Importance Values. *T. americana* is maintained by its ability to sprout from stumps.

A reduction of *P. strobus* occurred as the canopy closed. The decreased mean distance between trees, accompanied by closing of the canopy, precluded successful establishment of *P. strobus*. When a catastrophe occurs in a stand the canopy is broken. It is in such areas that islets of *P. strobus* can become established.

Owing to the phenomena of catastrophe, longevity, and great size *Tsuga* is able to maintain itself in mixed forest types along the border. Other investigators have concluded that within the border of *Tsuga*, the species has decreased since the time of the survey. Ward (1954) stated that *Tsuga* had not reproduced and had declined in eastern Wisconsin. In Forest County, Wisconsin *Tsuga* has decreased in density from 34.3 to 27.7 per cent in the last 100 years (Stearns, 1947). Nineteen

of 34 stands occurred on level ground, 12 on north slopes, 2 on eastern slopes, and 1 on a western slope. Upon the basis of this evidence it appears that *Tsuga* is not restricted to favored micro-reliefs along its border.

#### Field Collections of Seeds and Cones, Greenhouse Experiment

Cone data (Table 8) are arranged according to geographical location of stands. Cones collected from stands along the western border and from relict stands tend to be heavier than cones from along the southern border. There is a slight trend toward longer cones along the western border.

Seed weight varies from stand to stand (Table 9). Heavier seeds were obtained from relict stands than from stands within the border. The seeds from relict stands, collected from *Tsuga* trees in the fall of 1954, were produced that year. Seeds gathered from the remaining stands were from the 1953 reproduction season. Since the cones from which these seeds were extracted had already fallen, it is conceivable that the majority of heavier seeds may have already been shed.

Seed samples used for planting were given various kinds of treatments (Tables 10 and 11). The earliest germination occurred 20 days after the seeds were planted. The energy period of samples was dependent on the seed source and treatment. The 25 day longer energy period of dewinged seeds implies that wing removal injures the seed coat and delays germination. The energy period of apical and basal seeds of Relict 1 was 30 days. Germination capacity of the

Table 8. Tabulated data of field collected cones  
(mean per 100 cones).

Table 9. Tabulated data of field collected seeds  
(grams per 1000 seeds)

Stand Number	Weight Air Dried Cones (Grams)	Length (Centimeters)	Range in Length
2	14.5	1.8	1.5 - 2.4
7	22.3	1.5	1.2 - 2.0
9	16.7	1.5	1.2 - 1.9
23	19.6	1.6	1.3 - 2.1
25	29.7	2.1	1.5 - 2.8
26	20.5	1.7	1.4 - 2.1
29	25.8	1.9	1.3 - 2.6
39	28.0	1.9	1.4 - 2.3
Relict I	25.5	1.7	1.3 - 2.0
" II	21.9	2.0	1.7 - 2.4
" III	22.4	1.9	1.3 - 2.3
" IV	21.7	1.8	1.4 - 2.2

Stand Number	Weight
2	1.0
7	1.0
9	1.0
23	0.8
25	1.2
26	0.7
28	0.9
29	0.9
39	1.1
Relict I	1.9
" I (apical)	1.3
" I (basal)	1.7
" II	1.1
" II (apical)	0.8
" II (basal)	1.3
" III	1.2
" IV	1.1

Fig. 10. Tabulation of Germination Data (garden soil)

Origin of Soil (Stand Number)	Origin of Seed (Stand Number)	Type of Seed Treatment	Number of seeds in test	Germinative Energy (%)	Energy Period (Days)	Germination Capacity %
Garden Loam	7	Non-stratified 4° C. 80 days	100	--	--	--
" "	7	Stratified 4° C. 80 days	150	2.7	25	2.7
" "	26	Stratified -22°C. 80 days	50	--	--	--
" "	26	Stratified 4° C. 80 days	100	--	--	--
" "	28	Non-stratified 4° C. 80 days	400	0.8	45	1.0
" "	28	Stratified 4° C. 80 days	1000	0.1	25	0.1
" "	Relict 1	Stratified 4° C. 80 days (apical)*	194	1.5	30	2.1
" "	Relict 1	Stratified 4° C. 80 days (basal)**	100	11.0	30	17.0
" "	Relict 1	Stratified 4° C. 80 days (winged)	150	6.0	25	12.0

\* Apical- toward top of cone  
 \*\* Basal - toward base of cone

Origin of Soil (Stand Number)	Origin of Seed (Stand Number)	Type of Seed Treatment	Number of seeds in test	Germinative Energy (%)	Energy Period (Days)	Germination Capacity %
Garden Loam	Relict 1	Stratified 4° C. 80 days (dewinged)	140	1.4	50	1.4
" "	Relict 2	Stratified 4° C. 80 days (apical)	77	--	--	--
" "	Relict 2	Stratified 4° C. 80 days (basal)	50	2.0	45	6.0
" "	Relict 2	Stratified -22° C. 80 days	50	2.0	55	2.0
" "	Relict 2	Stratified 4° C. 80 days	50	12.0	25	14.0
" "	Relict 3	Non-stratified 4° C. 80 days	200	0.5	50	0.5
" "	Relict 3	Stratified 4° C. 80 days	400	3.5	50	4.3

Table 11. Tabulation of Germination Data (field soil)

Origin of Soil (Stand Number)	Origin of Seed (Stand Number)	Type of Seed Treatment	Number of Seeds in Test	Germinative Energy (%)	Energy Period (days)	Germination Capacity %
2	2	Stratified	250	2.0	25	3.6
2	28	4° C. 80 days	400	1.5	30	1.8
7	7	" "	150	0.7	35	2.0
7	Relict 4	" "	130	2.3	25	2.3
7	26	" "	183	-	-	-
7	28	" "	1000	0.4	30	0.5
23	23	" "	100	-	-	-
23	Relict 1	" "	150	2.7	40	3.3
23	" 2	" "	50	-	-	-
23	" 3	" "	400	0.7	35	2.0
28	28	" "	400	3.3	30	4.8
28	Relict 3	" "	400	1.5	25	2.8
28	" 2	" "	250	1.2	25	2.8
39	39	" "	55	5.5	30	5.5
39	Relict 1	" "	50	8.0	25	14.0
39	" 3	" "	400	6.8	25	10.8
Relict 1	Relict 1	" "	100	8.0	25	15.0
1	" 1	Stratified	50	12.0	50	16.0
		-22° C. 80 days				
1	26	Stratified	200	0.5	30	0.5
		4° C. 80 days				
1	39	" "	55	7.3	25	7.3
3	Relict 3	" "	400	12.8	30	19.8
3	23	" "	200	6.0	30	8.5

apical seeds was 2.0 per cent and the basal seeds 17.1 per cent (Table 10). The higher germination capacity is correlated with heavier seed weight.

Freezing prolongs the energy period and reduces germination capacity. Replicate samples stratified at  $-22^{\circ}$  C. had a 30 day longer energy period than samples stratified at  $4^{\circ}$  C. (Table 10, Relict 2). Seed lots from other sources, treated similarly, also had longer energy periods.

Seeds remaining in cones collected from the ground have a lower germination capacity and longer energy period than seeds collected in cones from trees (Tables 10 and 11).

Comparable samples and treatments of seeds demonstrate unequal germination capacities when planted in soils collected from several geographical locations. The origin of soil, pH, and germination capacity per cent for seeds collected from Relicts I and III are presented in Table 12.

Table 12

Seeds collected from Relict I		
Origin of Soil	pH	Germination Capacity (%)
Relict 1	4.6	15.0
Stand 39	4.3	14.0
Stand 23	4.0	2.0
Seeds collected from Relict III		
Relict III	6.0	19.8
Stand 39	4.3	10.8
Stand 28	4.0	2.8
Stand 23	4.0	3.3
Garden Soil	8.0	4.3

Seeds presented higher per cents of germination when planted in soil collected from stands on which the parent trees were growing than in other soils. Similar trends in other seed samples and plantings were noted (Table 11).

Cotyledon counts of 318 seedlings gave a mean of  $3.05 \pm .08$   $\sigma = .29$ . Butts and Buchholz (1940) found the mean cotyledon number of 217 counts of Tsuga canadensis to be  $4.24 \pm .08$   $\sigma = 1.19$ . The seed source was not identified.

#### Discussions and conclusions.

In order to simulate natural conditions in the greenhouse experiments, soil collected in the field was utilized. A marked decrease occurs in germination capacity in soil more acid than pH 4.3. Evidence in the literature as to the effect of pH on germination is conflicting. Baldwin (1942) concluded from a survey of the literature that a mildly acid reaction has a favorable effect on germination. Wilde (1946) reported a pH of 4.5 to 6.0 as most favorable for germination of forest tree seed. It appears that the range of pH for optimum germination of Tsuga seed is between 4.3 and approximately 6.0. The experiment contained too few samples to be treated statistically.

The germination ability of a seed is correlated with its position in the cone. In the central part of the cone the seeds are heaviest and have the highest germination capacity. Dewing of the seed decreased germination capacity 10.6 per cent.

Toumey (1942) stated that Tsuga canadensis has a low degree of viability. In 20 years of seed testing, the shortest germination time was 20 days which is the same as determined in the present investigation. The average germination capacity ranged from 21 per cent to 79 per cent. Environmental factors would vary the germination capacity of seed lots from year to year. The viability of seeds which are more than one year old would be important in off-seed years.

#### Results - Log and Stump Data

The characteristics of 61 logs and 37 stumps examined in the field were utilized in constructing indices of decay classes. Five stages of decay were designated for logs and stumps. Decay classes are designated with the letter D.

#### Index for logs:

- D1. Fallen tree with needles, cones, and twigs present; branches and bark intact.
- D2. Fallen tree with no needles, cones, or twigs present; distal ends of large branches present; bark intact without evidence of sloughing; decay of wood not initiated.
- D3. Fallen tree with proximal ends of large branches present; bark sloughing but intact patches present; decay of wood may be initiated.
- D4. Fallen tree with proximal ends of large branches present; presence or absence of patches of bark; decay of wood well advanced; solid core present inside rotted shell; wood moist to touch, fracturing into small pieces.
- D5. Fallen tree incompletely outlined; no indication of branch positions, decay of wood complete; no solid core present; wood residue dry and crumbly.

## Index for stumps:

- D1. Stump with freshly exposed surface; bark intact.
- D2. Stump with more than 50 per cent bark present; outer core of wood solid on exposed surface.
- D3. Stump with more than 50 per cent bark present; outer core of wood not solid on exposed surface.
- D4. Stump with less than 50 per cent bark present; outer core of wood solid on exposed surface.
- D5. Stump with less than 50 per cent bark present; outer core of wood not solid on exposed surface.

The density of germinated *Tsuga* seedlings and per cent moss cover was obtained for each log and stump. The number of germinated seedlings was computed on the basis of 50 feet of log length and 21 square feet of stump area. The density of germinated *Tsuga* seedlings in each Decay Class of both logs and stumps parallels the per cent moss cover through Class 4 (Figs. 24 and 25). Maximum germination occurs on logs in Class 4. A decrease in the number of germinated seedlings occurs in Class 5. Mortality rates of seedlings on logs are high but as indicated in Table 13, survival does take place.

On stumps, the density of germinated seedlings is highest in Class 5 (Fig. 25). Classes 3, 4, and 5 exhibit increasing decay and exposure of greater surface area for germination. Maximum successful survival is found on stumps in Class 4 (Table 14).

The small number of A. saccharum and B. lutea logs examined precluded making separate indices of decay. Therefore, the above Decay Classes were used for comparison (Table 15.).

Fig. 24. Mean number of germinated Tsuga canadensis seedlings in each Decay Class per 50 feet of fallen tree trunk and mean per cent moss cover.

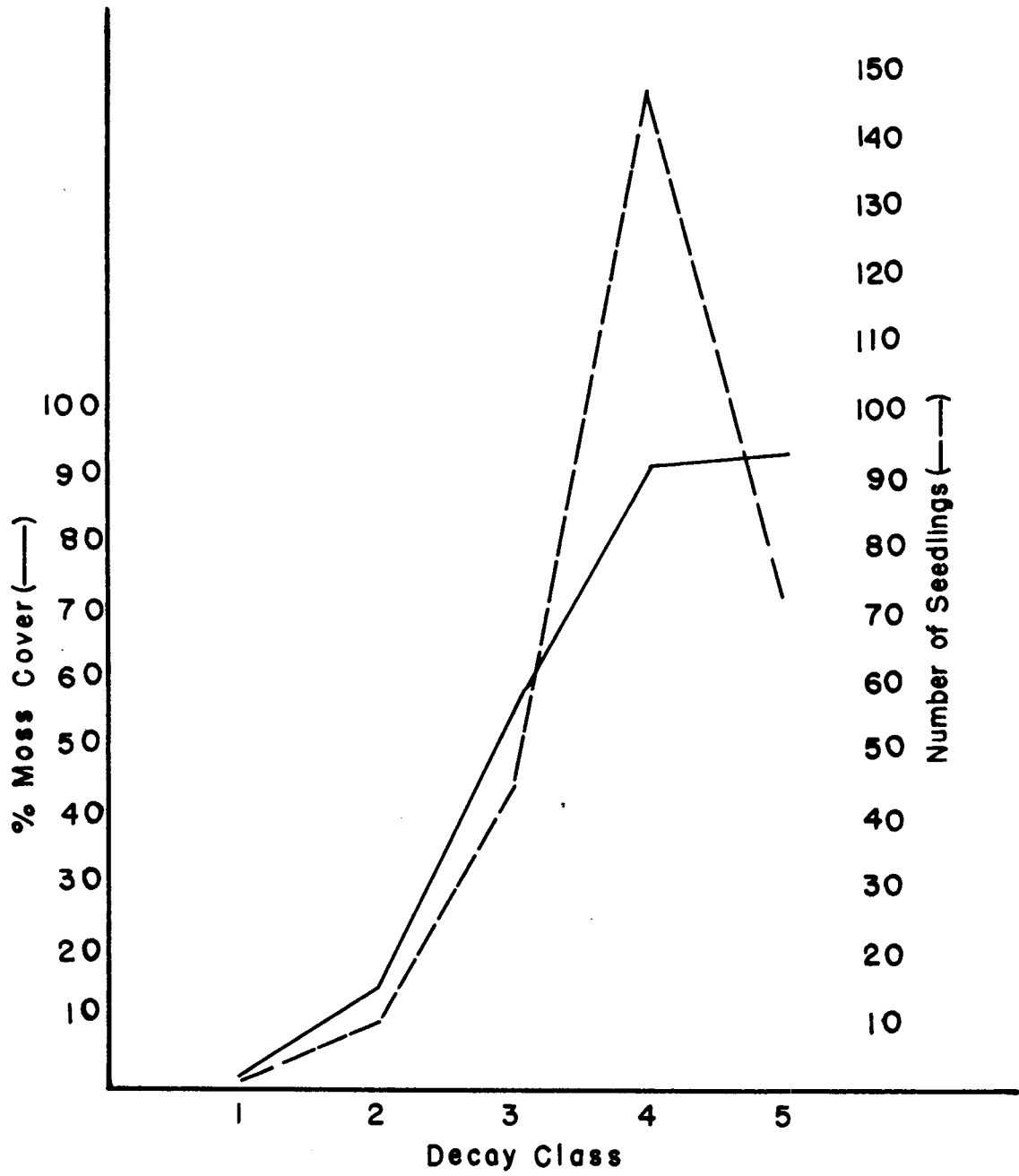


Fig. 25. Mean number of germinated Tsuga canadensis seedlings in each Decay Class per 21 square feet of stump area and mean per cent moss cover.

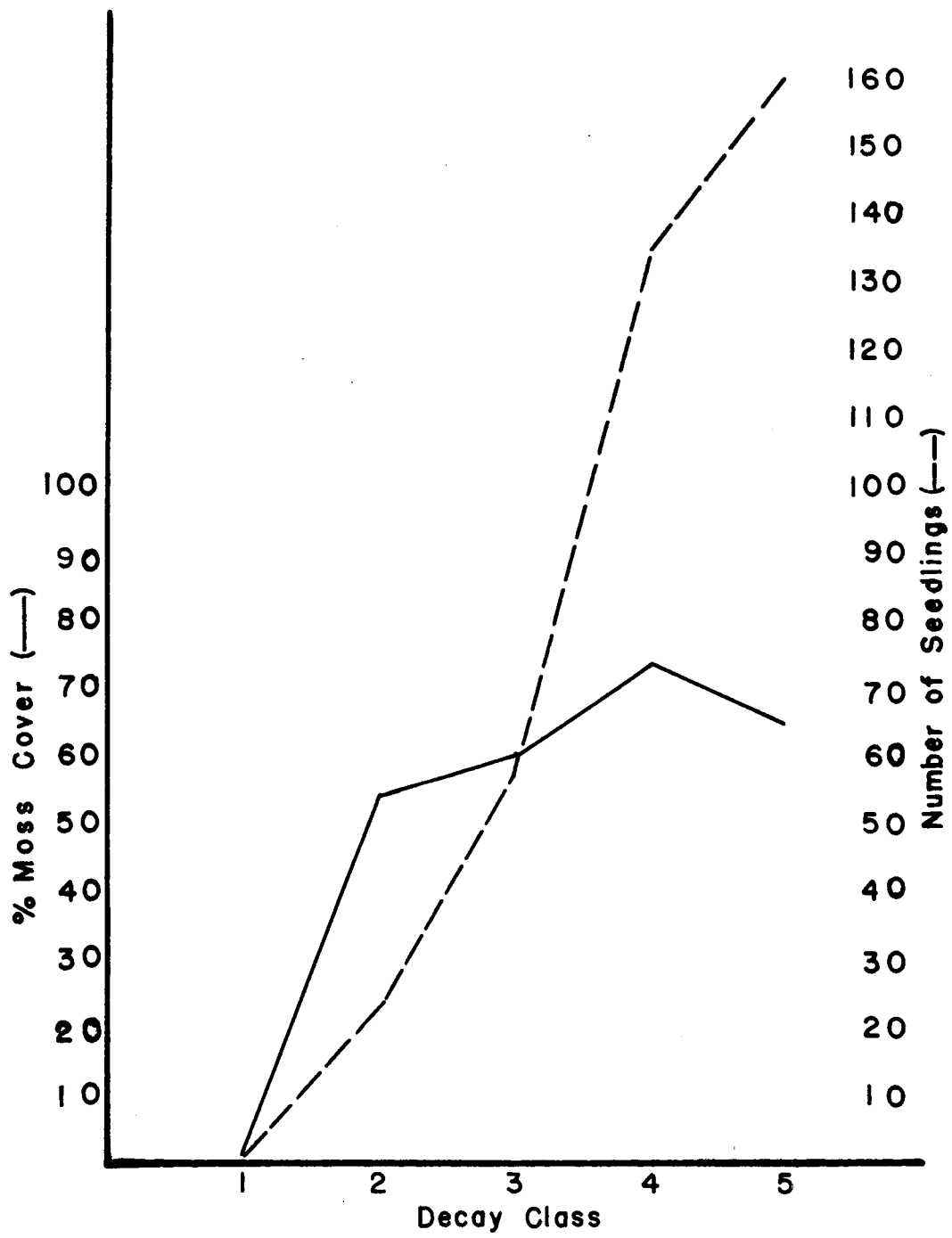


Table 13. Number of seedlings greater than one year old per 50 feet of fallen coniferous tree trunk.

Table 14. Number of seedlings greater than one year old per 21 square feet of coniferous stump area.

Table 15. Number of germinated seedlings per 50 feet of fallen Acer saccharum and Betula lutea tree trunk.

		DECAY CLASS						
1	2	3		4		5		
No.	Sp.	Age (yr)	No.	Species	Age (yr.)	No.	Sp.	Age (yr)
1	A.rubrum	1	12	T.canadensis	2	17	T.canadensis	2
			11	" "	3	10	" "	3
			4	" "	6	8	" "	5
			2	" "	9	5	" "	26
			49	B. lutea	1	2	B. lutea	2
			3	" "	3	8	" "	3
			1	A.rubrum	2	10	A. rubrum	2
						2	" "	3
						3	" "	10
							1 A.sacchrum	2

		DECAY CLASS						
1	2	3		4		5		
No.	Sp.	Age (yr)	No.	Species	Age (yr)	No.	Sp.	Age (yr)
8	T.canadensis	2	5	T.canadensis	2	1	T.canadensis	3
5	" "	3	7	" "	3	1	" "	6
			4	" "	6			
			6	" "	7			
			1	" "	12			
			10	B. lutea	2	2	B. lutea	4
			2	" "	3	1	" "	5
			1	" "	4			
			1	" "	5			
							1 A.rubrum	3

Species	Comparable Decay Class	Mean Number of Seedlings	
		Tsuga canadensis	Betula lutea
Acer saccharum	1	0	0
(based upon 4 logs)	3	9	253
Betula lutea	2	6	46
(based upon 9 logs)	3	15	850
	4	8	37
	5	59	1679

Mosses are rarely present in D1. Hypnum reptile and Mnium spinulosum were collected from logs of Class 2.<sup>1</sup> In addition to these two mosses, Brachythecium spp., Holocodium proliferum, and Plagiothecium spp. were identified from D3. The above genera and Dicranum flagella and rugosum, Leskea sp., Mnium cuspidatum, Pohlia nutans, Polytrichum Ohioense, Pylaisia sp.; and Thuidium sp. were collected from logs in Decay Class 4. Mosses on logs of Class 5 included Dicranum flagella, Georgia sp., Hypnum sp., Mnium spinulosum, Polytrichum Ohioense, and Thuidium sp. In addition, the liverwort, Bazzania trilobata, was identified from this Class. Generally, mosses formed the thickest mat in Decay Class 4. The number of moss species reached a maximum of 13 in D4 and diminished to six in Class 5.

Herbaceous plants were not found on logs until Decay Class 4. In this Class Maianthemum canadensis, Trientalis borealis, Coptis trifolia, Cornus canadensis, Clintonia borealis, and Oxalis montana<sup>2</sup> were noted. The genera recorded in Class 5 were Maianthemum, Cornus, and Oxalis.

The water holding capacity of wood and bark samples collected in the field was determined. Two B. lutea bark samples had a mean water holding capacity of 172 per cent. Wood from the same logs had a mean capacity of 686 per cent. Five Tsuga bark samples had a mean water holding capacity of 123 per cent and nine samples of wood 397 per cent.

1. Acknowledgment is made to Dr. R. I. Evans for aid in identification of mosses.

Nomenclature from Grout, A. J. Moss Flora of North America. 1936-1939.

2. Nomenclature from Gray, A. Manual of Botany, 8th Edition, 1950.

## Discussion

Intensity of log decay varies according to species and the location of the log in relation to the ground surface. It is not uncommon for a decayed B. lutea to remain standing long after death. Once such a tree falls it takes only a short period for the wood residue to disappear, leaving the dessicated shell of xeric bark. Tsuga seldom decays in a standing position. Later Decay Classes of fallen logs are of shorter duration than earlier classes.

A depression in the bark of a fallen tree is a requisite for seed germination. Germination on B. lutea is restricted to fissures in the bark and exposed wood. Commonly the exposed wood is located at the butt end of the fallen trunk. Fractured bark of Tsuga presents a greater area for retention and subsequent germination of seeds. Observational studies of the germination of Tsuga within the border conclude that fallen logs are a vital factor in the perpetuation of the species (Hough, 1943; Potzger, 1946).

Sernander (1936) and McCullough (1948) presented Decay Classes for germination of Picea abies and Picea Engelmannii, respectively. The number of Classes presented by these two investigators were too numerous to be used successfully in the present investigation.

In considering logs and stumps as favorable germination habitats, density of germinated seedlings varies according to the different micro-areas on these substrata. In descending order the most favored areas are: (1) mats of moss, (2) moist exposed wood, and (3) bark free from moss. Moss growth is indicative of a mesic micro-environment. Wood which has a high water holding capacity benefits

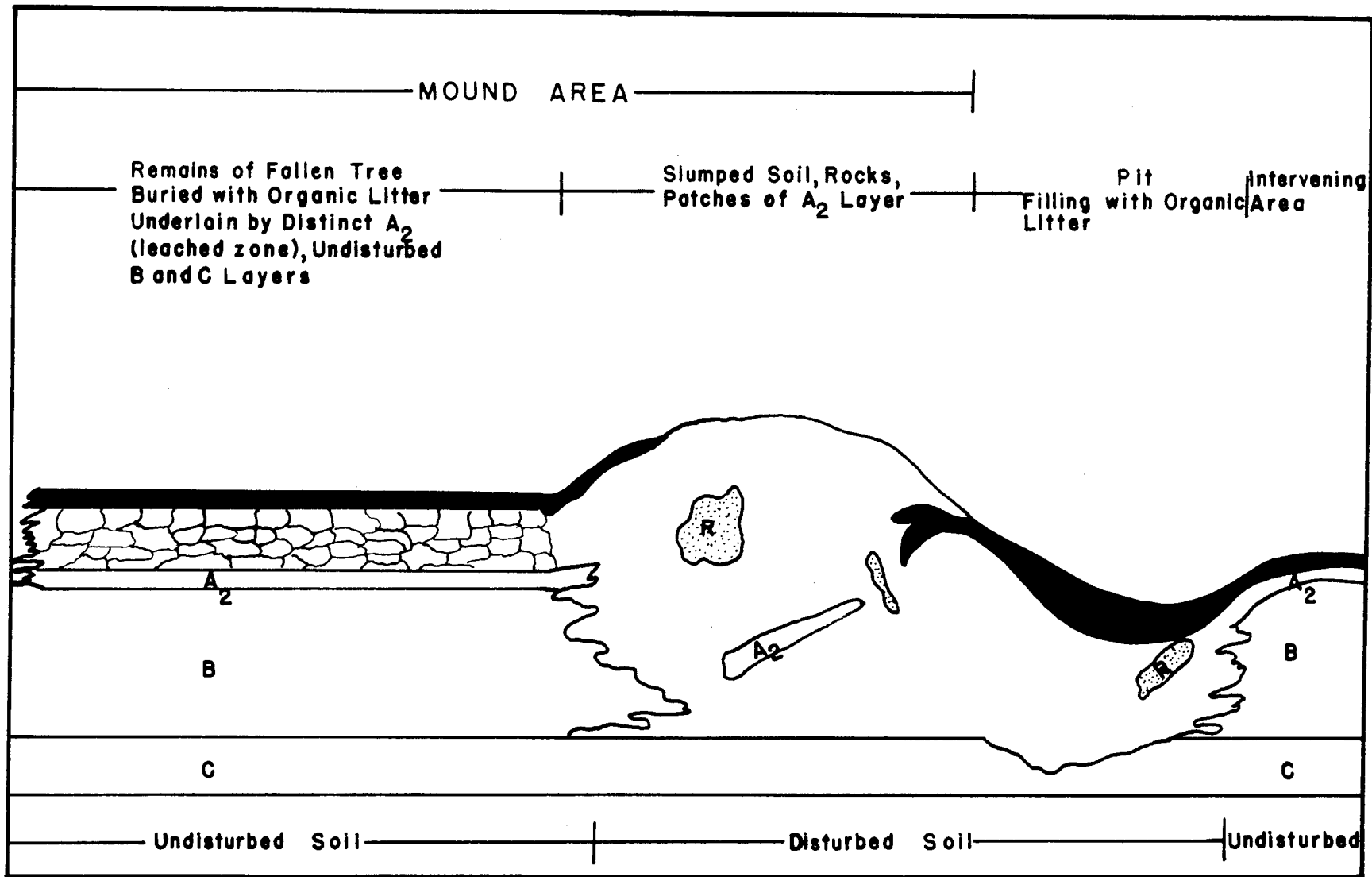
germination and successful survival. Residual bark which has a lower water holding capacity than wood appears to be least favorable to germination.

#### Results - Mound and Intervening Areas

Various names have been given to mounds which contribute to the micro-relief in a stand of Tsuga: "Indian-graves", "clay-mounds", and "tip-ups". Tsuga, a shallow rooted species, is susceptible to windthrow. When a tree is windthrown a pit is formed by the extraction of roots and adhering soil and rocks. The extent of the root system determines the amount of earth upturned. Decay of the roots of the fallen tree and weathering loosens the upturned soil material which falls and forms a mound on the side of the pit toward which the tree fell (Plate 2). The mound contains disturbed soil layers and buried debris (Fig. 26). Annual increments of organic matter gradually bury the fallen trunk. If successful germination occurs on the windthrown log, the direction of windthrow is evidenced even after decay of the log by straight lines of mature trees (Plate 3). Germinating areas which exist today as logs and stumps will in the future presumably become buried with litter and appear as mounds. The origin of mounds is not differentiated in this report.

Infrequently large areas of Tsuga are windthrown, but more commonly only a few trees in a stand are windthrown each year. Such blowdowns alter the micro-relief from year to year. Mounds which have a high content of rock material resist erosion for longer periods than mounds composed of finer soil particles (Plate 4).

Fig. 26. Diagram of mound profile in podzolized  
loam soil.



Therefore, mound height and area do not necessarily correlate with mound age. The minimum age of a mound may be told by the age of the oldest tree growing on the mound. Without increment borings, the basal area of a tree is only an estimation of mound age. Uneven age classes of *Tsuga* are usually present on any one mound (Plate 5).

In all stands except number 13 the greater number of cones and germinated seedlings was recorded on mound areas (Table 16). Inasmuch as cones are retained on the tree well into winter, it is conceivable that most cones drop during inclement weather. To determine the increase of weight due to imbibed water, 100 air-dried cones were weighed and put into a beaker of water. Within 20 minutes the weight increased from 18.1 grams dry weight to 43.3 grams wet weight. In an eight hour period the weight increased to 46.9 grams.

The cone drop of a mature isolated *Tsuga* tree was studied. Cone counts were determined for each square foot along four linear transects (Fig. 27). The greater number of cones along the south and east transects indicate a prevailing northwest wind. Maximum cone fall occurs within 15 feet of the trunk.

Mean distances between mounds and mean number of mounds per acre are indicative of disturbances within stands along the border of *Tsuga* (Table 17).

*Tsuga* seeds which germinate on mounds, logs, and stumps are those most likely to survive (Table 18). Rarely are trees, saplings or seedlings found in the pit region. Even though seed germination is high in the intervening areas successful survival does not occur, as indicated in the seedling column of Table 18. It can be inferred

Table 16. Mean number of Tsuga canadensis cones and germinated seedlings per square foot of mound and intervening area.

Table 17. Mean number square feet per mound, mean distance between mounds, and mean number mounds per acre.

Stand Number	Cones		Seedlings	
	Mound	Intervening	Mound	Intervening
7	6.9	4.3	1.0	0.4
11	12.1	7.0	5.6	1.6
12	5.4	3.3	2.2	0.6
13	1.8	3.7	0.4	0.8
14	8.3	5.6	13.4	9.2
15	9.7	3.4	3.9	1.6
23	10.2	6.8	12.0	8.1
25	7.5	3.7	1.3	1.3
28	20.2	14.3	12.0	2.2
43	9.2	8.9	1.0	0.5

Stand Number	Mean Square Feet	Mean Distance (in feet)	Mean Number per Acre
7	109.0	11.2	401.1
11	64.0	13.9	264.2
12	45.0	12.6	316.8
13	75.0	8.8	649.1
14	79.0	9.6	545.8
15	-	-	-
23	117.0	10.2	483.4
25	52.0	7.0	1027.3
28	59.0	12.0	337.9
43	-	11.4	386.9

Fig. 27. Number of Tsuga canadensis cones from isolated  
Tsuga canadensis tree per square foot along  
four linear transects.

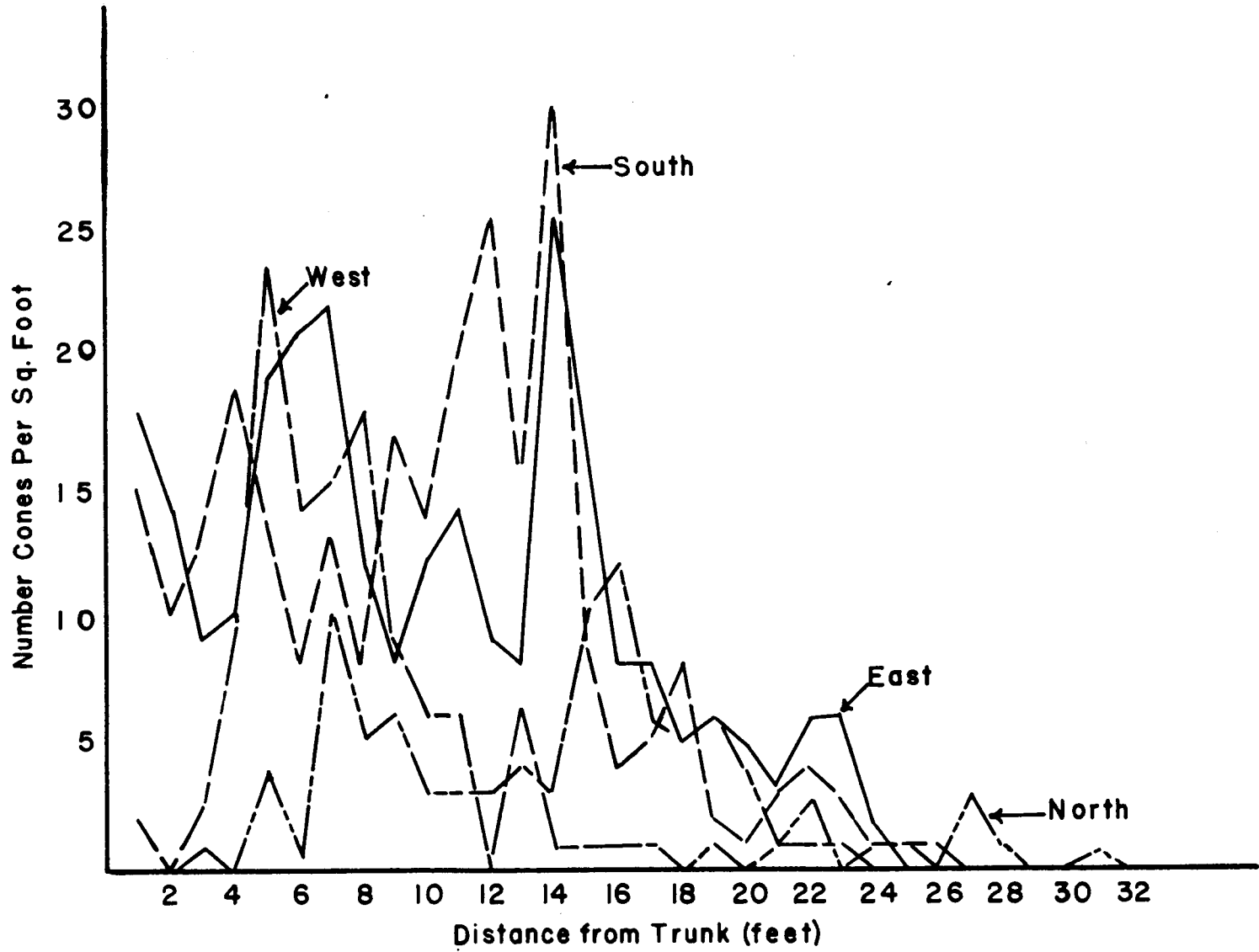


Table 18. Tabulation of successful germination per cent of Tsuga canadensis according to mound, pit, intervening, log, or stump area.

Stand Number	Trees					Saplings					Seedlings				
	M	P	I	L	S*	M	P	I	L	S	M	P	I	L	S
7	94.0	0.0	2.0	4.0	0.0	57.4	0.0	5.7	13.2	23.7	29.9	0.0	0.0	39.5	30.6
11	83.6	.7	9.8	0.0	5.9	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
12	90.9	0.0	3.9	3.9	1.3	85.1	0.0	0.0	14.9	0.0	0.0	0.0	0.0	0.0	0.0
13	97.1	0.0	2.9	0.0	0.0	99.6	0.0	0.0	0.0	0.4	100.0	0.0	0.0	0.0	0.0
14	100.0	0.0	0.0	0.0	0.0	98.4	0.4	0.0	0.0	1.2	98.4	0.0	0.0	0.0	0.0
23	96.0	0.0	0.0	4.0	0.0	88.7	0.0	0.0	7.0	10.6	56.2	0.0	0.0	12.5	31.3
25	100.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
28	93.0	0.0	3.0	4.0	0.0	100.0	0.0	0.0	0.0	0.0	1.8	0.0	0.0	.6	97.6

\* M = Mound  
P = Pit  
I = Intervening  
L = Log  
S = Stump

Table 19. Mean depth of humus ( $A_0$ ) layer on mound  
and intervening area (inches).

Stand Number	Mound	Intervening
7	3	4
11	$\frac{1}{2}$	$2\frac{1}{2}$
12	$1\frac{1}{2}$	4
13	$\frac{1}{4}$	2
14	1	$3\frac{1}{4}$
15	$\frac{1}{4}$	$2\frac{1}{2}$
23	-	-
25	-	-
28	1	$2\frac{1}{4}$
43	$1\frac{1}{2}$	2

from the tree data that conditions at one time in the past were favorable for successful establishment in the intervening areas of several stands. Observations indicate most successful survival of *Tsuga* is on sides of mounds rather than the apex (Plate 6).

Accumulations of litter occupy intervening areas (Table 19). Mounds, which are more exposed to ground winds, because of the scarcity of herbaceous vegetation, have a thinner organic layer. The higher water holding capacity of humus collected from intervening areas is due to greater amounts of undecomposed organic matter (Fig. 28). The trend toward alkalinity on both mounds and intervening areas as Continuum Index Values increase is caused by greater accumulations of non-acid deciduous tree litter (Fig. 29).

### Discussion

Cones mature in a single season, abscising and falling in winter and spring. Statistically there was a significant difference in the number of cones found on mounds and in the intervening areas. The greater number of fresh cones on the mounds may be associated with the location of seed bearing trees and area of cone drop. Assuming that the rate of cone drop is highest when cones are the heaviest, cones would have a tendency to drop in the area beneath the crown. No quantitative measurements were made of old cones but observations infer a greater number at the base of mounds than at the apex. Environmental agents would promote the acceleration of cones to lower regions.

Sensitivity to moisture causes an opening and closing of cone

Fig. 28. Water holding capacity of humus from mounds and intervening areas.

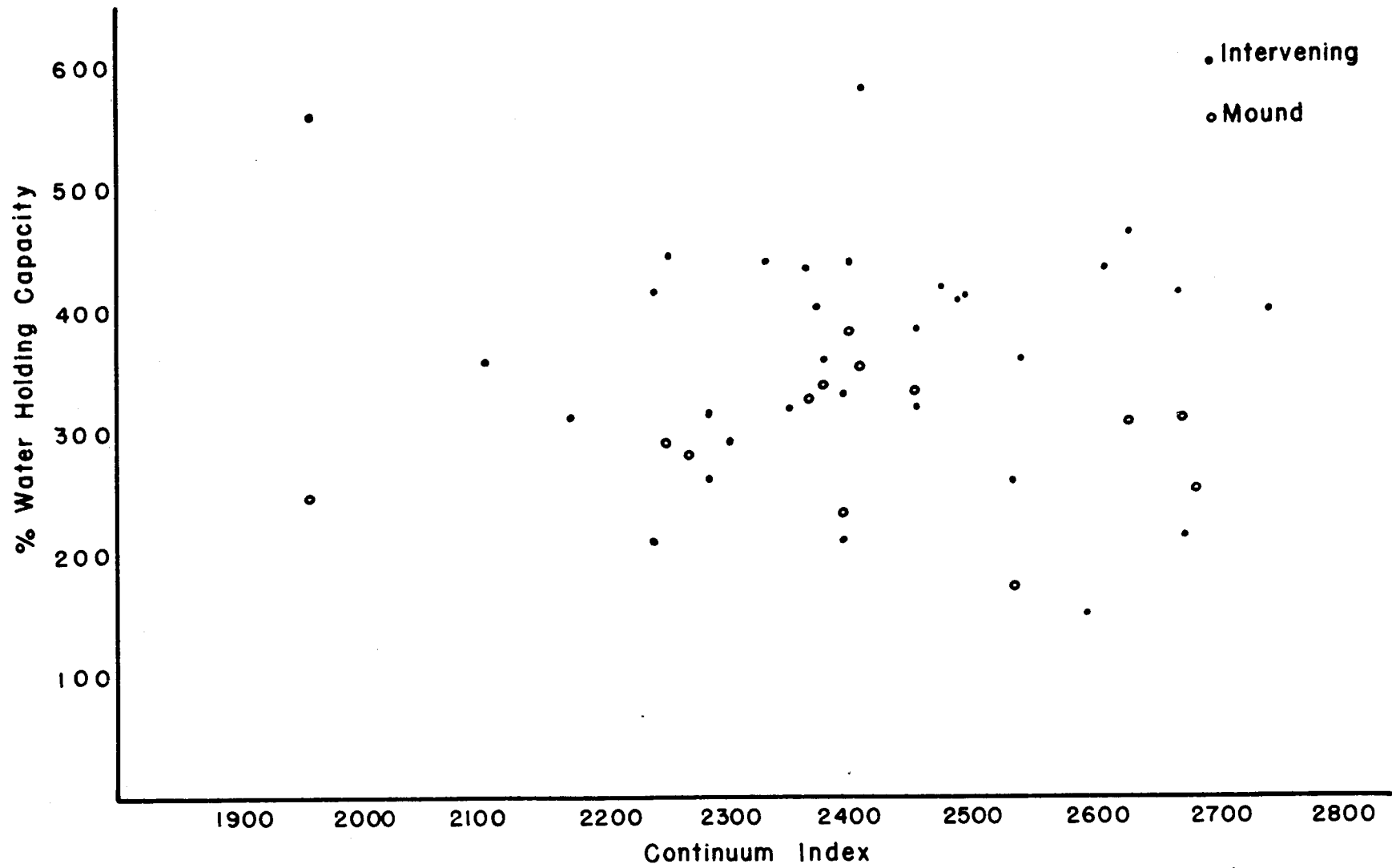
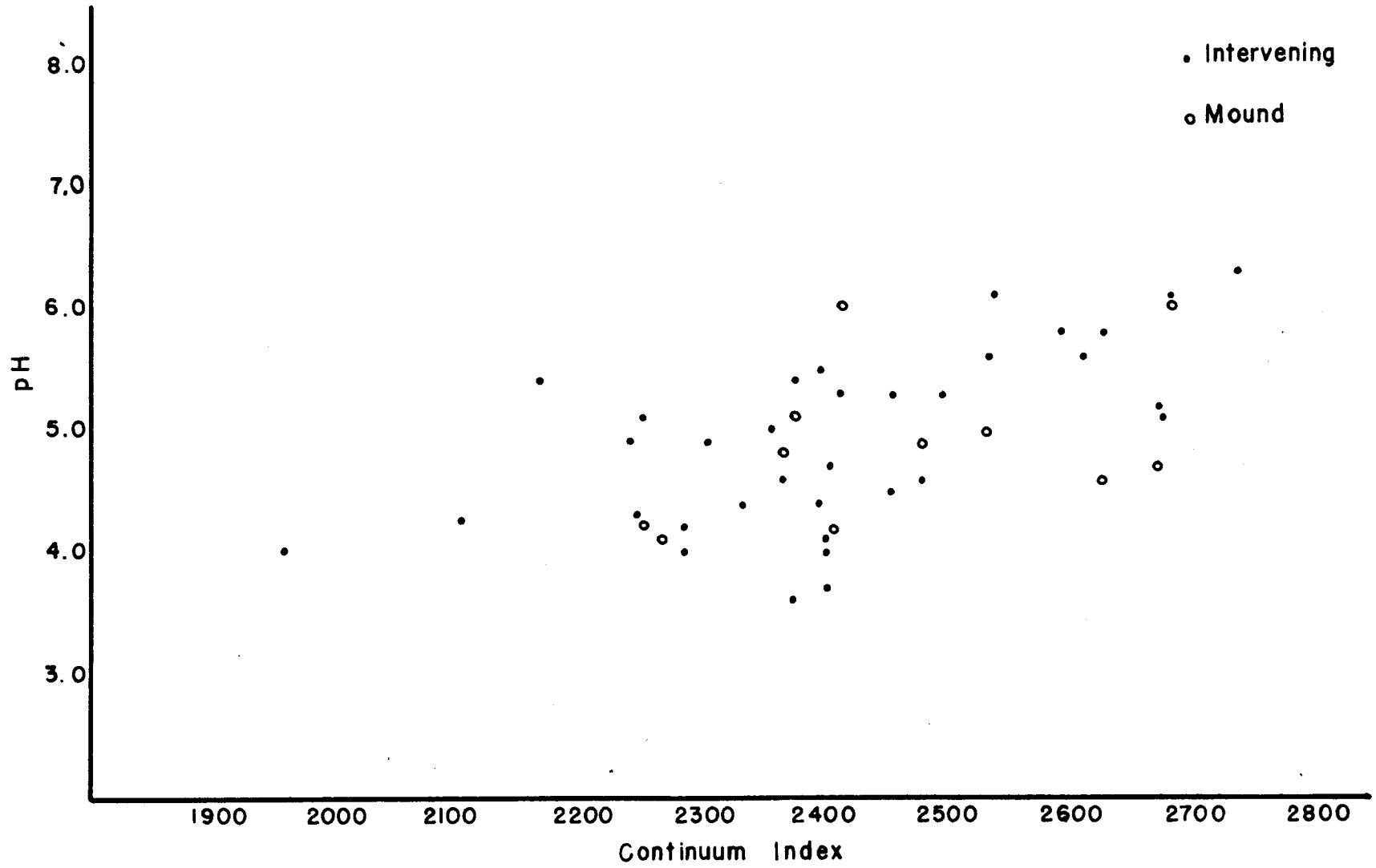


Fig. 29. pH of humus from mounds and intervening areas.



scales; the intermittent action allows successive sowings of seeds. Viable *Tsuga* seeds will germinate if moisture and light is available regardless of the environment. Seed germination, accordingly, occurs on all available substrata in a stand. Other investigators have pointed out that disturbed soil is favorable for establishment of tree reproduction, concluding that disturbed areas caused by windthrown trees are most satisfactory. Lutz (1940) completed a detailed analysis of undisturbed and disturbed forest soils. He concluded that a mixing of the upper and lower horizons by windthrow created favorable conditions for decomposition of organic matter and for establishment of seedlings. Successful establishment was further ascribed, in the disturbed soils, to greater air capacity, greater pore volume, and return to the upper surfaces of minerals which had been leached.

The high per cent of germinated seedlings on mounds cannot be correlated with the greater number of cones on mounds because the majority of seeds had been shed before the cones fell to the ground. Observations in late April, 1955 revealed seed germination on mounds but no indication of germination in other areas. Pit regions adjacent to drier mounds were extremely wet.

Etiolated *Tsuga* seedlings were observed between layers of matted deciduous litter composed mostly of *A. saccharum* leaves. It appears that *Tsuga* seedlings do not have enough energy to penetrate deciduous leaf matter. Friesner (1932) reported the inability of seedlings to penetrate *Quercus* sp. and *Carya* sp. leaves.

The deeper organic layer in pits is meshed with mycelium

of saprophytic fungi. Apparently these fungi limit the life of a seed lying in the duff. The depth and type of organic matter and extreme wetness are factors limiting *Tsuga* germination and successful survival in areas adjacent to mounds.

The presence of seed-bearing trees occurs from 83 to 100 per cent on mounds. According to Friesner (1932) the highest rate of mortality occurs during the first two growing years. Affecting this is the initial root habit of *Tsuga canadensis*. *T. canadensis*, according to Toumey (1926), develops a lateral root system and a short juvenile tap root. During critical months of low moisture, seedlings with poorly developed roots would have the highest mortality. *T. canadensis* is sensitive to high surface temperatures (Toumey, 1924). This susceptibility would account for the greater presence of trees on sides of mounds rather than the apex where extreme temperatures occur (Lutz, 1940).

## SUMMARY

The western termination of the range of Tsuga canadensis in the United States lies in north central Wisconsin. The boundary in the state extends west from Manitowoc County to Chippewa County thence north to Bayfield County. During the summers of 1953 and 1954, 34 Tsuga stands were studied at the termination of the border. The stands were distributed in 14 counties. To ascertain the composition of pre-settlement vegetation along the border, data of 465 townships were transcribed from original land survey books dating from 1836 to 1858.

Data taken from surveyor's records for an east-west and north-south transect extending through the entire range of Tsuga in Wisconsin were analyzed. Shorter transects along the western and southern borders were also studied. Importance Values were computed for all arboreal species occurring in each township. The dominant species were T. canadensis, A. saccharum, Populus spp., P. strobus, P. resinosa, and R. banksiana. Trends along the transects indicate that fire was a primary factor controlling the location of the boundary. Populus and Pinus species were used as indicators of the occurrence of fire. River systems provided a formidable barrier to the progress of fires. The diffuse boundary along the upper Chippewa River reveals that fires burned west and east of the river. Fires occurring east of the river were rare or of short duration. Similarly, the location of the southern border was attributed to fires.

Climatic factors were also considered as a limitation of the range of Tsuga. The range lies within gradients of higher rainfall,

greater snowfall, less evaporation, and cooler temperatures. It was concluded that *Tsuga* is not restricted along the border to favored locations of cool temperatures and greater moisture. In southern Wisconsin outliers of *T. canadensis* only occur on north facing slopes. Since there are no isopleths which correlate with the entire boundary, the correlation of climatic isolines with segments of the border may be a coincidence.

Surveyor's records of arboreal species were also used for a comparison with present day stands. The species composition of stands is similar but numerical numbers have changed. *Tsuga* Importance Values have increased along the border since the time of the surveys. The increase has been attributed to a recovery from decimation by lumbering and tanning industries at the turn of the century. It was concluded that *Tsuga* has reproduced along the border during the last 120 years. There have been minor fluctuations in the border during this period, but its geographical location in 1954 is similar to that of 1845.

A survey of present day stands was completed by the "Wandering Quadrant" method. High Importance Values indicate that *Tsuga* is the dominant species. *Tsuga* was dominant in 27 stands and *A. saccharum* in 7 stands. Reproduction of *Tsuga* was recorded in 32 stands. Replacement of dominant species occurs only after a catastrophe. Pioneer species have low reproduction frequencies in the stands studied.

*Tsuga* cones collected in the field had a mean length of 1.8 centimeters and a mean weight of 22.4 grams per 100 cones. Seeds

extracted from the cones were germinated in the greenhouse after being given various combinations of treatments. Germination capacities ranged from 0.1 to 19.8 per cent, varying according to the type of treatment and weight of the seeds. The earliest germination occurred 20 days after the seeds were planted.

Reproduction capacities and habitats were investigated in the field. Five Decay Classes were constructed for indicating the degree of decomposition of fallen logs and stumps. Optimum germination occurred on logs in Class 4 and on stumps in Class 5. As the moss cover of logs and stumps increases, the percentage germination of *Tsuga* increases. The greatest number of moss species were collected from logs of Decay Class 4. Herbaceous species also occur on logs in Class 4.

More germination occurs on mounds, logs, and stumps than in intervening areas or pits. From field observations, it was concluded that *Tsuga* seedlings do not have enough energy to emerge through deciduous leaf matter which accumulates in pits. Successful survival occurs principally on mounds which have three sources of origin: fallen tree trunk covered with organic matter, or decaying stumps, or a mound of disturbed soil.

Within a small area, a windthrow catastrophe is important for the perpetuation of *Tsuga* by opening the canopy and providing suitable germination habitats. *Tsuga* may remain suppressed for a number of years, but once released, grows rapidly.

Unless a drastic environmental change occurs, it appears that *Tsuga* will perpetuate itself along the present border. Reproduction

capacities indicate that it will remain a component of the northern hardwood forests with slight fluctuations in the geographic location of the border.

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Plate 1. Islet of immature Tsuga canadensis released  
from suppression by opening of canopy.

Plate 2. Mound of slumped soil and decayed roots.



Plate 3. Straight-line germination of Tsuga canadensis  
upon fallen log.

Plate 4. Mound area and pit Region.

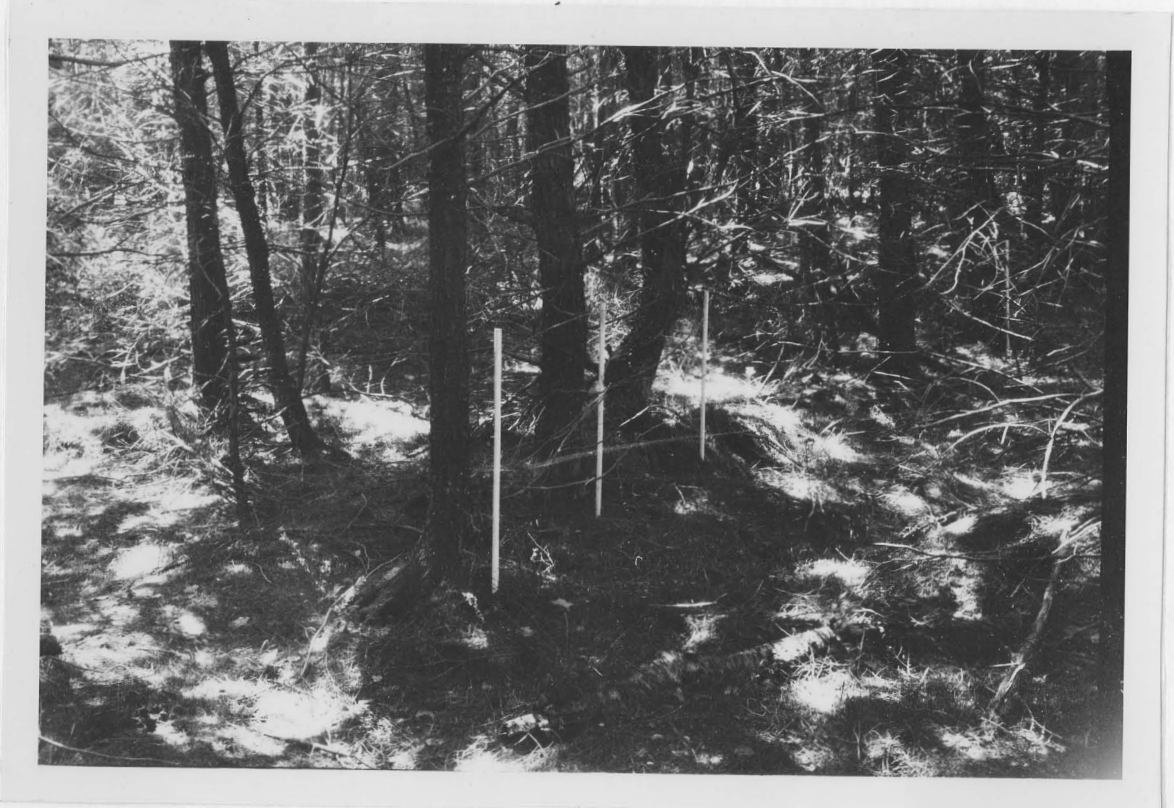


Plate 5. Uneven age grouping of trees on mound.  
Depression surrounding mound extremely  
wet.

Plate 6. Successful survival of Tsuga canadensis  
(in foreground) on side of mound.



TITLE OF THESIS A Phytosociological Study of Tsuga canadensis at the Termination of Its Range in Wisconsin

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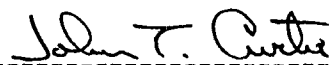
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